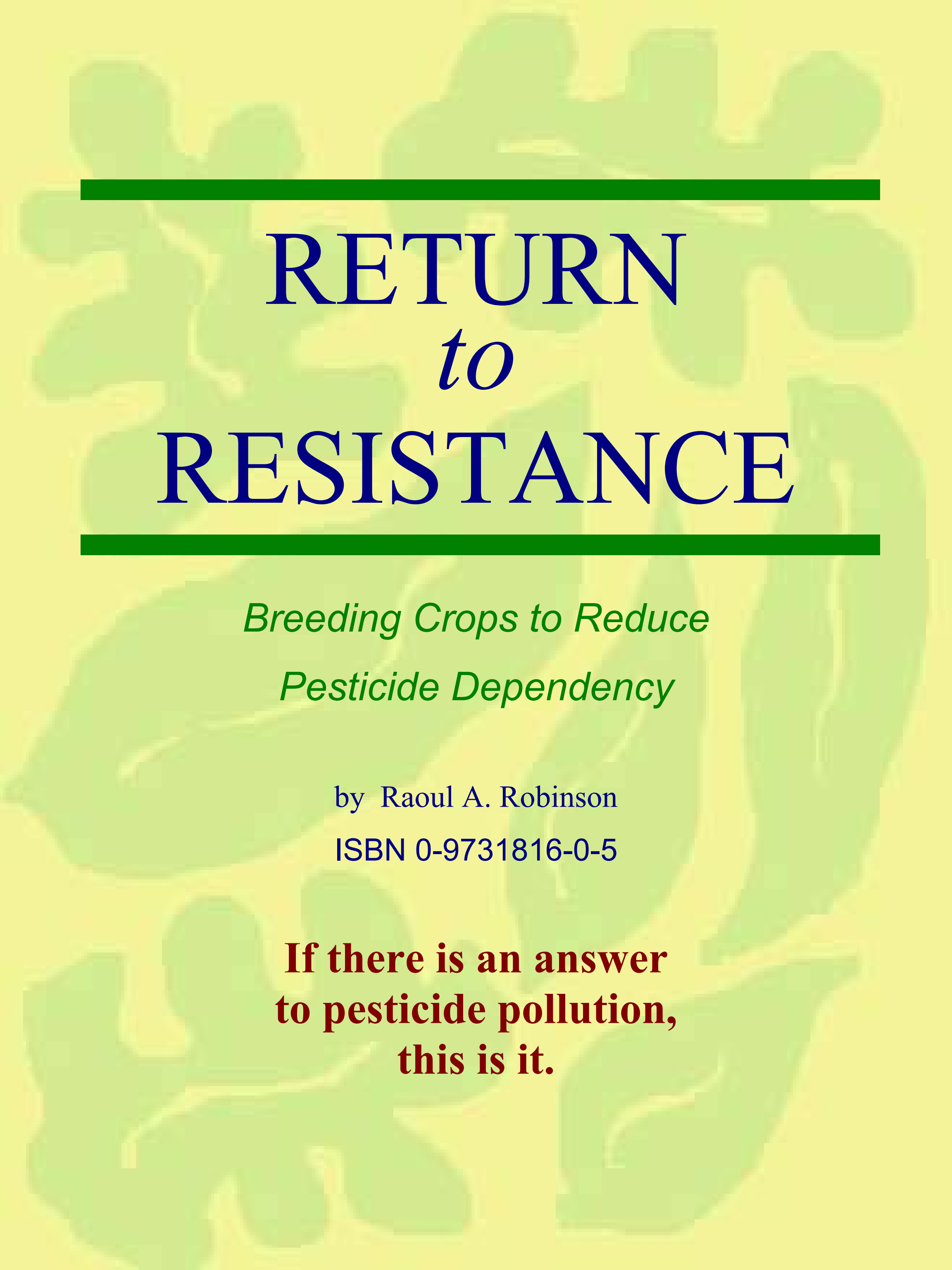

RETURN
to
RESISTANCE

Breeding Crops to Reduce Pesticide Dependency

by Raoul A. Robinson

ISBN 0-9731816-0-5

If there is an answer
to pesticide pollution,
this is it.

Copyright Notice

Part One: Explanations

Preface

To anyone who is concerned about the environment, it is obvious that all is not well with modern crop husbandry. One problem is that pests and diseases are destroying about one fifth of all crop production. A second problem is that these losses occur in spite of an extravagant use of chemical insecticides and fungicides that cost billions of dollars each year, worldwide. Indeed, in the industrial countries, the use of some kinds of crop protection chemicals has increased nearly tenfold since World War II. Crop production has increased also, very considerably, but so have the crop losses due to parasites, in spite of this increased use of crop protection chemicals. And these chemicals are also hazardous.

This kind of parasite damage obviously does not occur in wild ecosystems. After all, we do not spray wild plants, and the world is still green. So why should such appalling pest and disease losses occur in agro-ecosystems, in spite of all this spraying with crop protection chemicals?

This book is addressed mainly to readers who are concerned about the world food supply, and the pollution of our food and our environment with chemical pesticides, but who lack detailed scientific knowledge about these matters. It is also addressed to people who are not scientists, but who are prepared to make an effort to study a new subject that is outside their own fields of expertise. It presents a somewhat complicated and technical topic, but it is written in plain English which, I believe, will be readily comprehensible to anyone who is reasonably willing to persevere. I also believe that readers who do persevere will be excited by their new knowledge, and will feel amply rewarded for their trouble. The book is also addressed to activists who want to put things right, and it explains a possible way of doing this.

The Carrying Capacity of the Environment

A biologist has a rather special way of looking at human history, based on environment, and the carrying capacity of that environment. For any wild species, the carrying capacity of the environment is strictly limited. One square mile of land in a given area can carry only so many members of a species, and no more. It is also a fundamental law of nature that every species tends to reproduce *beyond* the carrying capacity of its environment. In any species, there is always a surplus of individuals which the environment cannot support, and it is always the weak that must go to the wall. This is the very basis of evolution, and it is the mechanism of natural selection, and the survival of the fittest. Indeed, it is probably more accurate to describe natural selection as the elimination of the least fit, rather than the survival of the most fit.

In the whole history of evolution, only one species has been able to increase the carrying capacity of its environment to any significant extent. That species is us. We did this with a series of cultural developments that are far ahead of anything achieved by the proto-cultures of wild primates. First we developed stone tools that turned puny man into a skilled, indeed a devastating, hunter of wild animals. Humankind then became a hunter-gatherer in an environment which, until then, had required up to twenty five square miles of territory to support one human adult.

Because humans continued to reproduce beyond the carrying capacity of their environment, there was always a surplus of people.

This surplus often survived by migrating to a new, uninhabited area. Humans could do this more readily than other species because they had the cultural developments of tools, animal skin clothing, fire, and artificial shelters. Eventually, our ancestors colonised all the habitable land surfaces of the planet. No one knows for sure what the size of the total human population was at that time, but it is estimated at only a few million.

When there was no spare land left to colonise, pressures of population began to be felt, and it was at this point that humankind began the process of domestication. Animals were domesticated first. People began to live with herds of wild herbivores, much as modern Lapps live with herds of reindeer. The people protected the herd from wild carnivores, but they also culled the herd of unwanted animals to provide meat, as well as leather, horn, and bone, for the manufacture of tents, clothing, and tools. These people were herders, and their population density was higher than that of the more backward hunter-gatherers. Herders occupied much of Africa and Asia for many millennia before the discovery of agriculture, and modern cattle, sheep, and goats are descended from their herds.

The next major development was the domestication of plants. People discovered that they could increase the density of edible plants in their environment by sowing the seeds of these plants. They also discovered that they could choose *which* seeds to sow. By sowing only the seeds taken from the best plants, with the highest yield, and highest quality of food, they tended to improve both the yield and the quality of their crops. In the course of time, this process changed some species of cultivated plants so much that their wild progenitors are now difficult to recognise. This domestication of plants was the basis of agriculture, because crops provide food for both people and domestic animals.

This series of technical breakthroughs during the past ten thousand years has increased the human carrying capacity of Planet Earth by several hundred-fold. But, unfortunately, the human species *still* continues to reproduce beyond the carrying capacity of its environment. Very recently, during the twentieth century, a series of medical breakthroughs has complicated this situation even further. Medical science has produced some dramatic reductions in the human death rate, particularly the infant mortality rate. As a result, some three billion people are now alive who would otherwise have died. This must surely rank as one of the greatest achievements ever accomplished by humankind.

Unfortunately, there has not been a corresponding reduction in the human birth rate. Medical science has produced the techniques necessary for reducing the human birth rate to levels commensurate with the reduced death rate, but much of humankind either cannot, or will not, use them. As a consequence, our population has been increasing even more rapidly. This means that agriculturists have had to increase the carrying capacity of our total environment at a comparable rate. So far, they have succeeded, but what of the next doubling of our population? And the doubling after that? This is quite a predicament. It is known as the world food problem.

The crisis of population growth and food supply is frightening and, if our population growth is not stabilised soon, we may yet see a wave of malnutrition, and death from starvation, that would make the contemporary epidemic of AIDS seem trivial in comparison. The problem is increased by the fact that even our current levels of agricultural production are possible only with an extravagant use of chemical pesticides. It appears that, if we are to reduce pesticide pollution, by reducing pesticide use, we can do so only at the expense of the world food supply, because reduced pesticide use will lead to increased crop losses from pests. And, conversely, if we are to increase the world food supply, to feed an increasing world population, we shall have to use additional pesticides, or more powerful pesticides. Environmentalists who abhor the use of crop protection chemicals must realise that there is a very real dilemma. We may be compelled to choose between food and pollution, on the one hand, or purity and famine, on the other.

In fact, there may be a solution to this dilemma, and that is what this book is about. There is a very real possibility that we can have both adequate food *and* freedom from crop protection chemicals, but few people seem to be aware of this. The purpose of this book, therefore, is to make public some rather specialised information that has remained obscure, indeed secret, because of its technical nature. I do not suggest that anyone has been secretive, or that any attempt at a cover-up has been made. There is no conspiracy. But the topic is both scientific and complicated, and it has remained hidden from the general public for this reason only. In writing this book, my task has been to explain this situation in terms intelligible to the scientific layperson. If I have been successful in this explanation, readers should have little difficulty in comprehending it, scientific and complicated though it may appear at first sight.

Readers are accordingly offered a brief description of crop science and crop parasites. They are then asked to study ten pairs of biological contrasts, and some general conclusions and specific examples.

Anyone requiring greater scientific detail is referred to appendices at the end of this book. Readers who require technical descriptions and scientific references are referred to a technical book of mine, as well as some of the writings of J.E. Vanderplank (see References). These technically informed readers will appreciate that the present account involves some deliberate over-simplification. This is essential because there is a limit to the scientific complexity that non-scientists can be expected to absorb. At the opposite extreme, readers who are willing to accept the scientific aspects of this account unread, may safely skip to Part II, making use of the glossary as necessary. The same comment applies to any reader who attempts Part I, but finds it too complex.

First, however, a disclaimer is necessary. This book may give the impression of being highly critical of modern plant breeding, but such an impression is not strictly true. Plant breeding has four broad objectives. These are to improve the yield, the quality of crop product, the agronomic suitability, and the resistance to pests and diseases, of the crop in question. Plant breeding has been impressively successful in the first three of these objectives. This is demonstrated by very large increases in agricultural production, and the fact that the world is still able to feed itself in spite of massive increases in the size of the human population. However, the breeding of crops for resistance to their parasites has been much less successful, and this is why we use chemical pesticides on our crops in such huge quantities. This book is accordingly critical only of the last of these broad breeding objectives, the resistance to pests and diseases.

Crop Science and Crop Parasites

The scientific study of agriculture is divided into a number of sub-disciplines, based on animals, plants, climate, and soils. The various disciplines that deal with crops are collectively known as crop science. They include plant breeding, plant physiology, plant pathology (i.e., plant diseases), crop entomology (i.e., insect pests of plants), weed science, crop husbandry, and horticulture.

Plant pathologists study plant diseases, which are mostly caused by pathogens, such as microscopic fungi, bacteria, and viruses. Crop entomologists study the insect pests that eat our crops. All the pests and diseases of crops are collectively known as crop parasites. Weeds are competitors, not parasites, and the use of the term ‘parasite’ specifically excludes weeds from the discussion. The chemicals that are used to control crop parasites are generally known as pesticides, and they include fungicides and insecticides.

This book is not concerned with the control of weeds, even though weeds are often included in the term ‘pest’. Nor is this book concerned with the group of chemicals known as weed-killers, or herbicides, even though these are often included in the term ‘pesticide’.

Parasites are organisms which feed on other organisms, known as their hosts, while these hosts are still alive, but usually without killing them. Throughout our discussion, the crop plant is the host, and the pest or pathogen is the parasite. The terms host and parasite may be applied to an individual or to a population. (However, parasites often have their own parasites, known as hyper-parasites, which keep their numbers down in a process known as biological control; see Chapter 14).

No one is quite sure how much damage parasites are doing to our crops because this happens to be an exceptionally difficult measurement to make. Most crop scientists accept the general estimate that crop parasites are destroying about thirty percent of all crop produce, worldwide. This loss includes both pre-harvest and post-harvest damage. That is, it includes the losses in both the field and the store. This book is about pre-harvest losses only, and these losses are thought to be about two thirds of the total. So, very approximately, pre-harvest parasites are destroying about twenty percent of our total crop production. In terms of food crops alone, pre-harvest crop parasites may be destroying enough food to feed about one billion people. What makes this sad story even more sad is that we are losing this crop produce in spite of an extravagant use of chemical pesticides on our crops. It is difficult to escape the impression that all is not well with modern crop science.

Chapter 1

Genetics: Biometricians and Mendelians

This story begins in 1900, which is a convenient date, being both easy to remember, and the start of the twentieth century. In that year, three European scientists simultaneously made an important discovery. These scientists were Hugo de Vries in The Netherlands, Carl Correns in Germany, and Erich Tschermak von Seysenegg in Austria. They discovered the now famous genetic work of Gregor Mendel. Within a year, Mendel's neglected paper had been re-published in German, French, and English, and biology would never be the same again. In particular, there were now two schools of thought in the study of genetics.

Members of the older school called themselves biometricians. They studied the inheritance of characters that are *quantitatively* variable. These are characters that differ in degree, with every grade of difference between a minimum and a maximum. For example, the colour pink can show every degree of difference, and every shade of pink, between the maximum, which is pure red, and the minimum, which is pure white. This was the kind of genetics studied by most of the great biological thinkers of the nineteenth century, such as Charles Darwin, Thomas Huxley, and Francis Galton. Their ‘bio-metrics’ (i.e., life-measurements) assessed quantitative data of many different variables, with continuous scales of measurement.

These variable data are usually analysed by a branch of mathematics called statistics, and their basis is the Gaussian, or bell-shaped, curve. The term ‘statistics’ has a pejorative use also, illustrated by the phrase “Lies, damn lies, and statistics”, which is discussed further in Chapter 14. However, in a mathematical context, the term is entirely respectable.

Typically, if two different parent plants, such as a red-flowered and a white-flowered, were crossed (i.e., cross-pollinated, or mated), the progeny would show all degrees of pink, but most of them would be a mid-pink, about halfway between the two parents. The proportion of each degree of pink in the progeny would be represented by a bell-shaped curve, and it would be called a normal distribution.

In 1900, the biometricians did not understand the mechanism of their genetics. They thought that inherited characters would blend, or merge, with each other, in much the same way as hot milk and chocolate would blend in a cup of cocoa. They could not see any possibility of the discrete units of inheritance, which we now call genes. This was where Mendel came into the picture.

The new school of genetics called themselves Mendelians. They studied the inheritance of characters that are *qualitatively* variable. These are characters that differ in kind, being either present or absent, with no intermediates. Thus, the character of blackness is either showing or not showing. A bean seed, for example, would be either black or white, and there would be no grey or spotted seeds at all. The importance of Mendel's laws of inheritance is that they postulate discrete units of inheritance, and they successfully predict the proportion of the progeny which will either show, or not show, a qualitative character.

Each discrete unit of inheritance is called a gene. Each gene is a unit of DNA code on a microscopic chromosome, and each chromosome occurs twice in an individual. One chromosome comes from the male parent, and the other from the female parent, because each of the reproductive cells, the pollen and the ovules, has only one set of chromosomes. Each chromosome has a copy of the gene, and each of these copies is called an allele.

A gene might control seed colour, which is either white or black. Conventionally, such a gene would be represented by a capital letter, such as *W*. The capital letter represents a *dominant* allele that eclipses the effects of a *recessive* allele which is represented by the lowercase letter, *w*. A plant that is *WW* has two dominant alleles for blackness, with one coming from each parent. A plant that is *Ww* has one dominant and one recessive allele. And a plant that is *ww* has two recessive alleles. A plant that is *WW* is black-seeded. So is a plant that is *Ww*, because the dominant allele eclipses the recessive allele. Only a plant that is *ww* is white-seeded.

Two other technical terms, and one further point, should be mentioned. A plant that is either *WW* or *ww* has two alleles that are the same. They are either both dominant, or both recessive. Such a plant is described as *homozygous*. However, a plant that is *Ww* has two different alleles, one dominant and one recessive, and it is described as *heterozygous*. These terms are derived from the Greek root *zygo*, meaning a yoke, as in the yoke that links two oxen pulling a cart, while *homo* = same, and *hetero* = different. A zygote is produced by the fusion of two sex cells.

Homozygous thus means that the two alleles, coming from the male and female sex cells, were the same genetically, while heterozygous means that they were different. The terms are normally used in this way, and are applied to a single pair of alleles. However, in plants, they can be applied to the entire genetic make-up of an individual. It is usual for all living things to be heterozygous in much of their genetic make-up, because this is the basis of variation, natural selection, survival of the fittest, and evolution. But it is possible for plants to be homozygous in their entire genetic make-up. This is an artificial situation resulting from deliberate agricultural practices, and its importance will become apparent shortly.

If a homozygous white-seeded plant (*ww*), is crossed with a homozygous black-seeded plant (*WW*) the progeny will all be heterozygous (*Ww*), and they will all be black-seeded, because black is dominant. If two of these heterozygous *Ww* plants are then crossed, their progeny will segregate as:

$$Ww \text{ x } Ww \rightarrow 1WW + 2Ww + 1ww$$

and the ratio of black to white seeds will be 3:1. This is the famous Mendelian ratio. It is also a clear indication that inheritance is controlled by discrete, independent factors, without any mixing, merging, or blending, as was thought by the biometricians.

Mendel published his results in 1865, in a paper called *Experiments With Plant Hybrids* but he won no recognition whatever. We shall probably never discover whether the great biological thinkers of that time, including Darwin, Huxley, and Galton, either saw the paper and decided that it was not important, or never saw it at all. The former alternative is the more probable, for several reasons. First, the so-called 'Mendel's Laws of Inheritance' were not explicitly stated by Mendel himself. They were formulated by later workers who generously attributed them to Mendel. Consequently, the importance of Mendel's original paper was far from obvious.

Second, these nineteenth century biologists were steeped in the biometrical tradition, and the geological concept of *gradualism*. This concept had first been proposed by James Hutton in the late eighteenth century, and it was later developed by Charles Lyell, who was one of the most influential of geologists. Darwin was profoundly inspired by the concept of gradualism, and it became the foundation of his theory of evolution. This concept postulated that all geological and evolutionary changes were slow, gradual, and quantitative. Mendel's laws of qualitative inheritance would have appeared irrelevant in this context, even if they had been explicitly stated.

Third, a fundamentally important discovery in science is often disturbing and disruptive and, for this reason, there will be a very natural human tendency to reject and deny it. If an important discovery forces a scientist to re-think all his ideas and, even worse, threatens much of his published work with obsolescence, that scientist can be forgiven if he has difficulty in accepting it.

Fourth, many people fall innocently into the error of judging new information on the basis of its *source*, rather than judging the information itself, on its own merits. If new information comes from a famous scientist, working in a famous university, and published in a famous journal, it is likely to be accepted uncritically, even though it might occasionally be downright wrong. And if the new scientific information comes from an utterly obscure *monk*, working in a scientifically unknown Augustinian abbey in Central Europe, and published in an unimportant local journal of natural history, it is likely to be ignored, even though it may be of seminal significance. Gregor Mendel was this monk.

Finally, it is likely that Mendel sent reprints of his paper to many famous scientists. This, after all, was the custom of his time.

So Gregor Mendel, who had made a scientific discovery of fundamental importance, and knew it, and who longed for recognition, died a disappointed man, unrecognised, in 1884, at the age of sixty two. This was nineteen years after the publication of his work, and a further sixteen years were to elapse before it was recognised. In fact, a Russian scientist, I.F. Schmalhausen had recognised the importance of Mendel's work soon after it was published, but he was ignored also. Mendel and Schmalhausen were more than thirty years ahead of their time. Which brings us back to the start of our story, in the year 1900.

With the recognition of Mendel's laws of inheritance, the two schools of genetics not only came into existence; they came into conflict. In those days, it seemed obvious to everyone that, if one school was right, the other must be wrong. The Mendelians believed, quite correctly, that Mendel's laws were fundamental, and that they would eventually explain the whole of genetics. The biometricians argued that virtually every inherited character of human, agricultural, or evolutionary importance was inherited quantitatively. They contended, with considerable justice, that qualitative, Mendelian characters were of little practical, economic, or evolutionary significance.

The chief protagonists of the Mendelian school were William Bateson and the same Hugo de Vries who had helped to re-discover Mendel's laws. They went so far as to claim that Mendelian genetics had proved that Darwin's theory of evolution, based on gradualism, was wrong. They postulated that all evolutionary change resulted from major mutations and that, as a consequence, evolution progressed erratically, in leaps and bounds that were separated by long periods of stagnation.

Karl Pearson was the chief protagonist of the biometricians, and of gradualism, and he used Darwin's favourite dictum *"Natura no facit saltum"* (Nature makes no jumps). As with so many famous scientific conflicts, the argument was conducted in print. It grew increasingly heated, and the writing became positively offensive, as the authors stooped to personal insult.

It is difficult to exaggerate the importance of this conflict because it is the foundation of the current, apparent dilemma between either food and pesticide pollution, on the one hand, or no pesticide pollution but famine, on the other hand. However, the resolution of this dilemma will be discussed in a moment and, at this point, we must consider the resolving of the conflict between the Mendelians and the biometricians.

The Mendelians were studying characters whose inheritance was controlled by single genes. As we have seen, a gene that conferred redness in flowers might be either present or absent. Accordingly, the flowers would be either pure red or pure white, and there were no intermediates, no pink flowers. This qualitative redness is now known as a single-gene (or *monogenic*) character.

It was then discovered that two-gene characters are possible. There could then be red and white flowers and, in addition, there could be pink flowers, halfway between red and white. If there were three, or possibly four or five genes controlling redness, there would be various different shades of pink. And if redness was controlled by many genes, each making a small contribution to either redness or whiteness, there would be every shade of pink between the two extremes of pure red and pure white. If the frequency of these many grades of redness is plotted on a graph, it produces the familiar bell-shaped curve, the normal distribution of the biometricians. In contrast to the single-gene character, this quantitative variable is known as a many-gene (or *polygenic*) character. So, the Mendelians were dealing with single-gene characters, while the biometricians were dealing with many-gene characters.

It seemed, therefore, that the battle was over. Both sides were right, and both sides had won. But, in fact, the conflict had left a scar, a distortion, that can be felt to this day. This brings us to the next pair of contrasts.

Chapter 2

Plant Breeding: Pedigree Breeding and Population Breeding

It was inevitable that the two schools of genetics would produce two entirely different methods of plant breeding. The Mendelians, it will be remembered, were dealing with single-gene characters that were either present or absent. They developed methods of plant breeding that are now known as pedigree breeding, and which involve *gene-transfer* techniques. The biometricians, on the other hand, were dealing with many-gene characters that were continuously variable. They were looking at all the degrees of difference between the extremes of a normal distribution. They developed methods of plant breeding that are now known as population breeding, and which involve *changes in polygene frequency*.

The problem that usually faced the Mendelians was that a single-gene character, which they wanted to utilise in a cultivated plant, would occur in a useless wild plant. The difficulty was in getting it transferred out of the wild plant, and into the cultivated plant. A gene, after all, is only a small piece of a DNA molecule. It is far too small to be seen, even with the most powerful electron microscope. Consequently, there is no question of being able to pluck it out of one plant, with a micro-dissector, and put it into another plant. Nevertheless, the Mendelians solved this problem in a way that is both ingenious and elegant.

Let us suppose that the single-gene character was resistance to a fungus disease called ‘blight’. (Plant diseases usually have the most colourful names, such as blight, mildew, blast, rust, smut, smudge, wart, streak, blister, and scorch). The wild plant carries this gene, and it is apparently immune to blight. Unfortunately, the yield of this wild plant is so low that it is not worth cultivating, and the quality of its product is so poor that no one would buy it anyway. The cultivated plant has a huge yield of an excellent product but, unfortunately, it is highly susceptible to blight, and it can be cultivated only if it is routinely sprayed with a fungicide. The crop yield and the crop quality are both many-gene characters, while the resistance to blight is a single-gene character.

The first thing the Mendelians would do was to hybridise the wild plant with the cultivated plant. The progeny were mostly about halfway between the two parents in their many-gene, quantitatively variable characters. The yield and quality were thus medium; not too bad, but not very good either. Some of the progeny carried the single gene for resistance while others did not, and the progeny accordingly segregated into individuals that were either resistant or susceptible. This segregation, obviously, would follow Mendel's laws of inheritance.

This is the beauty of Mendelian genetics. It is possible to tell at a glance which plants are carrying the gene for resistance, because they are not diseased with blight. This is a qualitative variable which is either present or absent. The Mendelian breeder would throw out all the blighted plants and keep all the blight-free plants. As these resistant plants approached maturity, the breeder would select the best one, in terms of its yield, and the quality of its product. The breeder would then cross this best plant with the original cultivated parent. This is a process known as *back-crossing*.

The progeny of this back-cross would have approximately three quarters of the yield and quality of the original cultivated parent, and only one quarter of the poor yield and quality of the wild parent. This progeny would also be segregating into resistant and susceptible individuals. The breeder would again throw out the susceptible individuals, and keep the best resistant individual for a second generation of back-crossing. This process of back-crossing can be continued for as many generations as are necessary to restore the yield and quality of the hybrids. Finally, the best of them will have a yield and quality as good as, or possibly even better than, the original cultivated parent. And it will also be carrying the gene for resistance. This gene-transfer technique is so beautiful, and so clever, that it captured the imagination of plant breeders all over the world.

The biometricians' technique of population breeding is entirely different. In principle, it is merely a refinement of the methods that farmers have been using since the dawn of agriculture. As the term implies, biometricians work with populations of plants, and these populations are usually large. They screen the entire population for a small minority of the best plants. These are randomly cross-pollinated among themselves, and they become the parents of the next generation. Each generation is a little better than its predecessor, and this process of small, quantitative improvements by recurrent mass selection can continue until no further progress is possible.

A classic example of population breeding occurred with fodder beet, which are cultivated to feed farm animals. These ‘roots’ contain about 4% of sugar. During the Napoleonic wars, the British blockade deprived most of continental Europe of sugar which, at that time, was produced exclusively from sugarcane, mainly in the West Indies. This shortage prompted the use of fodder beet for sugar extraction. The sugar content of fodder beet is a quantitative variable, controlled by polygenes. By population breeding methods, the sugar content of fodder beet was eventually increased to nearly 20%, and the total yield of roots was also increased very considerably. The result was an entirely new crop called sugar beet.

Let us now consider the method of pollination, which is one of the more important practical differences between pedigree breeding and population breeding. All flowering plants can be classified into one of two categories according to their natural method of pollination. The so-called *out-breeders* are cross-pollinating plants in which the seed-producing, female parent is normally fertilised with pollen that comes from a different plant. The so-called *in-breeders* are self-pollinating plants in which the female part of the flower can be successfully fertilised with pollen from the same plant, usually the same flower. Cross-pollination can and does occur among the in-breeders but, normally, it occurs at quite a low frequency.

Pedigree breeders, as their name implies, work with carefully controlled crosses in which the parents of each cross are known and recorded. These crosses are made by hand, by artificial pollination, and this can be labour-intensive, depending on the species of plant being pollinated. With chickpeas (*Cicer arietinum*), for example, one successful hand pollination will produce only one seed, and only sixty percent of hand-pollinations are successful. With potatoes, one hand-pollination will produce two or three hundred seeds. And with tobacco, it will produce about two hundred thousand seeds. One of the advantages of pedigree breeding is that relatively few crosses are necessary and, consequently, hand-pollination is feasible.

Population breeding, as we have just seen, uses large numbers of pollinations. This difference in technique had an important influence on the development of plant breeding, following the re-discovery of Mendel's laws.

The Mendelians, working with relatively few, carefully controlled, hand-pollinations, were unaffected by this difference in pollination. With in-breeding plants, they would have to prevent self-pollination by removing the immature male parts of each flower to be pollinated. However, this was not difficult.

The biometricians, on the other hand, depended on large numbers of natural cross-pollinations. With in-breeding species, the frequency of cross-pollination was usually so low that this method of plant breeding was slow, difficult, and often impractical. The biometricians consequently found it difficult to work with in-breeding species, and this gave a clear advantage to the Mendelians. It so happens that most of the important food crops of the world, such as wheat, rice, peas, and beans, are in-breeders. During the conflict between the two schools, the Mendelian plant breeders were not slow to exploit this advantage.

Nowadays, this difficulty is no longer a problem because there are various techniques for overcoming it. One of them employs a substance called a male gametocide, which will make an in-breeding species, such as wheat, male-sterile. The flowers of treated plants are then unable to pollinate themselves, and they must accept pollen from an outside source. Population breeders can now achieve millions of crosses in a crop such as wheat by treating part of their screening population with a male gametocide (Chapter 25). The treated part then becomes the male-sterile, seed-producing component, while the unsprayed part becomes the male-fertile, pollen-producing component. However, in the days of the genetic conflict, these alternative techniques were not available. In terms of practical plant breeding, the Mendelians appeared to be winning.

Then, in 1905, a Danish botanist, W.L. Johannsen, discovered the *pure line*, which is discussed later in the seventh pair of contrasts (Chapter 7: Populations: Genetically Uniform and Genetically Diverse). All we need note at the moment is that this was a technique for making seed-propagated crops breed ‘true to type’. Normally, seed-propagation leads to genetic variation, and this is a nuisance because agriculturally valuable characteristics, such as high yield and high quality of crop product, tend to be lost. Johannsen’s pure lines meant that these valuable characteristics could be preserved indefinitely, in spite of propagation by seed. This eventually increased the yield of many crops very considerably. It turned out to be a big boost for the Mendelians, and a further advantage in their conflict with the biometricians.

1905 was an even more important year for the Mendelians in yet another way. In this year, a British scientist, R.H. Biffin, made a discovery that was the most momentous help that the Mendelians could possibly have wished for. He published his discovery in a famous paper called *Mendel's Laws of Inheritance and Wheat Breeding*. Like Johannsen's pure lines, this discovery was truly seminal in the sense that it changed the course of history.

Biffin was working with a disease of wheat called rust. He showed that resistance to this disease was inherited in a Mendelian fashion, and nothing could have pleased the Mendelians more. Suddenly, they had a single-gene character of economic significance, and it quickly transpired that the inheritance of resistance to many other plant diseases was controlled by single genes. The Mendelians pursued this advantage with great vigour. It must be remembered that, at that time, they had no other single-gene characters of any economic significance whatever.

At this point, it is perhaps instructive to compare plant breeding with animal breeding. Although single-gene characters do occur in farm animals, none of them are economically important. As a consequence, animal breeding has remained quantitative, and in the hands of the biometricians, for the whole of the twentieth century. But for these single-gene resistances to crop parasites, plant breeding would undoubtedly have remained quantitative also.

As a result of Biffin's work in England, and similar work by W.A. Orton in the U.S.A., as well as energetic promotion from the members of the Mendelian school of genetics, it was not long before most crop scientists began to assume that *all* resistances to *all* crop parasites were controlled by single genes. Crop scientists also concluded that, if you wanted to breed plants for resistance to a parasite, you must first find a gene for resistance, in order to use the back-crossing technique of gene-transfer. They spoke of "first finding a genetic *source* of resistance". It will become apparent later that this belief became a shibboleth, a myth, that has both dominated and plagued the whole of twentieth century crop science.

Chapter 3

Resistance: Vertical and Horizontal

With hindsight, we can now appreciate that it was inevitable that the two kinds of plant breeding would reveal two entirely different kinds of resistance to the parasites of plants. However, few scientists recognised this until J.E. Vanderplank, who died in 1997, and was the most original of all plant pathologists, published a classic book in 1963. This book is called *Plant Diseases; Epidemics and Control* and, in it, Vanderplank distinguished between single-gene (monogenic) and many-gene (polygenic) resistances. He used the term *vertical resistance* to describe the single-gene resistance, and the term *horizontal resistance* to describe the many-gene resistance. However, this description is a deliberate simplification which will be elaborated in a moment.

Vertical resistance is the resistance of the Mendelians. It is normally qualitative resistance in the sense that it is either present or absent, and there are no intermediates. However, there are a few exceptions to this rule (see Glossary: quantitative vertical resistance). Horizontal resistance is the resistance of the biometricians. It is quantitative resistance in the sense that it can occur at every level between a minimum and a maximum. These terms are very important and three comments about them are necessary.

First, these are abstract terms that were intended to label a concept so new that words to describe it did not exist. The terms were not intended to be interpreted literally, and they have nothing to do with standing up or lying down. Vanderplank could equally have chosen other neutral words, such as hard and soft resistance, or *alpha* and *beta* resistance. As the original author of the concept, he had the privilege of choosing its terms, and we should respect his precedence.

Second is the question of why abstract terms were needed at all. Could not Vanderplank have used descriptive terms such as monogenic and polygenic resistance? Unfortunately, these descriptive terms are not accurate because there is rather more to the definition of the two kinds of resistance than just the number of genes controlling their inheritance. This will be explained more fully in a moment.

Third, the terms vertical and horizontal are derived from two classic diagrams. Differences in vertical resistance are parallel to the vertical axis of the diagram, while differences in horizontal resistance are parallel to the horizontal axis of the diagram. So the terms do have a minor descriptive connotation, and this makes their meanings a little easier to remember.

With vertical resistance, there are single genes for resistance in the host plant, and there are also single genes for parasitic ability in the parasite. This is a very important phenomenon known as the *gene-for-gene relationship*, and it is the definitive character of vertical resistance. The gene-for-gene relationship was discovered in 1940 by the American scientist H.H. Flor, who was working with a disease of flax (*Linum usitatissimum*) called rust (*Melampsora lini*). This discovery was later elucidated mathematically by my old, and very dear friend, the late Clayton Person, in Canada.

Flor showed that, for every resistance gene in the host, there was a corresponding, or matching, gene in the parasite. This relationship is an approximate botanical equivalent of the human system of antibodies and antigens . It is common knowledge that any person who catches a cold develops an antibody to that strain of the cold virus. The antibody provides protection against future infections with that strain of the virus, because the virus has an antigen which activates the antibody. Unfortunately, there are many strains of the cold virus, and we are often infected by a strain for which we have no antibody. This is why we keep catching new colds, although we tend to get fewer colds as we grow older, and as we accumulate more and more antibodies. Roughly speaking, each resistance gene in the plant host corresponds to an antibody, and each parasitism gene in the parasite corresponds to an antigen.

It is now realised that the gene-for-gene relationship evolved in plants to operate as a system of locking. Each resistance gene in the host corresponds to a tumbler in a lock. And each parasitism gene in the parasite corresponds to a notch in a key. An individual plant host may have several of these resistance genes, these tumblers, which collectively constitute a biochemical lock. And an individual parasite may have several of these parasitism genes, these notches, which collectively constitute a biochemical key.

When a parasite individual is infecting a host individual, its biochemical key either does, or does not, fit the biochemical lock. If the key fits, the infection is described as a matching infection, and it is a successful infection, because the ‘door’ of resistance has been unlocked and ‘opened’. When this happens, the vertical resistance is described as having broken down. If the parasite key does not fit the host lock, the infection is described as a non-matching infection. It fails because the ‘door’ of resistance remains ‘locked and barred’, and the parasite is denied entry. This system of locking is the definitive characteristic of the gene-for-gene relationship, as well as the Mendelian, single-gene, vertical resistances to crop parasites.

Horizontal resistance is the resistance of the biometricians. Its definitive characteristic is that it does *not* involve a gene-for-gene relationship. However, its most prominent characteristic is that it is usually, but not invariably, inherited polygenically. It can occasionally be inherited in a Mendelian fashion, but these Mendelian genes are not part of a gene-for-gene relationship. This means that horizontal resistance is normally quantitative in both its inheritance and its effects, and it exhibits every degree of difference between a minimum and a maximum.

Perhaps the best way of understanding horizontal resistance is to think of it as the resistance which invariably remains after a vertical resistance has been matched. When a parasite succeeds in unlocking a vertical resistance, it then comes up against a second line of defence which is the horizontal resistance. To use a military analogy, vertical resistance corresponds to the coastal defence that prevents a beach-head from being established. The invading forces are either destroyed or thrown back into the sea. Horizontal resistance corresponds to the defence that operates *after* a beach-head has been established. The invading forces must be prevented from breaking out of their beach-head.

What is so economically important about horizontal resistance is that it operates equally against all strains of the parasite, regardless of what biological keys they may have. In fact, horizontal resistance operates against *matching* strains of the parasite. Consequently, it does not fail, like vertical resistance, on the appearance of a matching parasite. Horizontal resistance begins to function at the moment a matching infection occurs, and at the moment the vertical resistance breaks down. This means that horizontal resistance cannot be matched, in the way that vertical resistance is matched, and it cannot break down, in the way that vertical resistance breaks down.

This is the main practical difference between the two kinds of resistance. Vertical resistance operates only against *non-matching* strains of the parasite. Because some matching always occurs, vertical resistance is certain to break down sooner or later. It is temporary resistance. Horizontal resistance operates against matching strains of the parasite, and it never breaks down. It is durable resistance.

Horizontal resistance completely escaped the attention of the Mendelians. They were not interested in quantitative variation. They were working with qualitative resistances, inherited by single genes. A gene for vertical resistance is either present or absent. For the Mendelians, a plant was either resistant or susceptible and, normally, there were no intermediates. As we have seen, this is one of the attractions of the Mendelian pedigree breeding method. It is possible to decide at a glance whether the resistance is present or absent. Obviously, the resistant plants in a screening population were parasite-free, and they were kept, and studied. The susceptible plants were parasitised, and they were discarded.

The Mendelian breeders never did notice that there were very considerable differences in the levels of parasitism among the discarded plants. These differences represented quantitative variation in the level of horizontal resistance. But the Mendelian breeders were not interested in such differences. In their view, a plant was either diseased or disease-free, and they treated the diseased plants as rejects. Why waste time studying rejects?

When Vanderplank published his new ideas in 1963, an immediate dispute arose concerning the relative merits of vertical resistance and horizontal resistance. But the conflict was very one-sided. There was vociferous and almost universal opposition to the very idea of horizontal resistance. I myself have witnessed respectable scientists so angry at the mere mention of horizontal resistance that they showed all the symptoms of incipient apoplexy. The Mendelian techniques of pedigree breeding, back-crossing, pure lines, and vertical resistance dominated the whole of crop science. To question this ‘received wisdom‘ was asking for trouble.

The dominance of the Mendelian school is vividly illustrated by the point that, until Vanderplank published his book, very few crop scientists had even realised that there were, in fact, two kinds of resistance to the parasites of crops. Indeed, many crop scientists vigorously denied the very existence of horizontal resistance. A few of them still deny it, and most of them are still quite unwilling to employ it, or even to investigate it.

It is now clear that the conflict over vertical and horizontal resistance was actually a revival of the original genetic conflict between the Mendelians and the biometricians. What is depressing about this story is that the original genetic conflict started in 1900. It was resolved scientifically about thirty years later. The two kinds of resistance were recognised by Vanderplank about thirty years later still. And, thirty years after that, in the early 1990s, the whole of crop science was still dominated by the Mendelian school of genetics, the Mendelian methods of plant breeding, and the Mendelian resistances to crop parasites. And the very new development of genetic engineering and transgenic plants also involves single-gene characters. However, as the second edition of this book goes to print, the merits of horizontal resistance are slowly being recognised.

We must now enquire why the two kinds of resistance to plant parasites should have evolved in plants in the first place.

Chapter 4

Infection: Allo-infection and Auto-infection

The word infection has many shades of meaning in the English language. In medicine, it is sometimes taken to mean the disease itself, and we speak of a patient having a ‘nasty infection’. In its adjectival form of ‘infectious’, it usually means a contagious disease that is caused by a biological agent, such as a virus or bacterium. However, we frequently speak of a laugh, or a yawn, being infectious.

Throughout this book, the term infection is defined quite strictly. It means the contact made by one parasite individual, with one host individual, for the purposes of parasitism. And there are two kinds of infection, just as there are two kinds of pollination.

It will be remembered that cross-pollination means that a plant is pollinated by pollen from another plant, while self-pollination means that a plant is pollinated by its own pollen. The technical term for cross-pollination is *allogamy*, while self-pollination is *autogamy*. These terms are derived from ancient

Greek. *Allo* means other, or different; *auto* means self; and *gamy* means marriage or reproduction.

The two kinds of infection are called *allo-infection* and *auto-infection*. Allo-infection is equivalent to cross-pollination, and it means that a host plant is infected by a parasite individual that has arrived from another, different host, or from an independent, dormant state. The parasite had to *travel* to its new host. Conversely, auto-infection is equivalent to self-pollination, and it means that a host is infected by a parasite individual that was born on, or in, that same host. The parasite had no need to travel.

There is a close analogy with travelling people. Think of the individual host plant as an island, surrounded by sea. Allo-infection is then equivalent to an immigrant arriving on that island, by boat or plane, from somewhere else. Auto-infection is equivalent to the colonisation of the island by the descendants of that immigrant.

This people analogy can also embrace the two kinds of resistance. Think of Ellis Island, in New York, in the bad old days. The parasite genes of a gene-for-gene relationship correspond to the immigration papers of an immigrant, and the host genes correspond to the immigration laws of the land. These papers and laws either match, or they do not match. The immigrant is accordingly allowed in, or is denied entry, as the case may be.

Horizontal resistance, on the other hand, is represented by the living conditions in the immigrant's new land, which make it either easy or difficult for that immigrant to prosper.

Three further points are worth making. If the island is deserted, the first person to inhabit it *must* come from outside. The first infection of any plant host *must* be an allo-infection. Second, colonisation can proceed only after a successful immigration. Auto-infection of a plant host can occur only *after* there has been a matching allo-infection. Third, when auto-infection, or colonisation, has continued for some considerable time, possibly for many generations of colonisers, the island becomes crowded. Some individuals may then leave the island in search for another, less crowded island, somewhere else. These explorers will be migrants, and they will allo-infect their new host, their new island.

Two real-life examples will further illustrate this difference between the two kinds of infection, which is critically important. Most people are familiar with the small insects known as aphids, green flies, or green bugs. Anyone who has grown roses will know what a pest they can be. Aphids have several, morphologically different forms, and each form has a special function. Among others, there is both is winged form, and a wingless form. The function of the winged individuals is clearly that of allo-infection, which is possible only by flying. The function of the wingless individuals is obviously that of auto-infection, which is possible by walking.

If a rose bush is completely free of aphids, it is the equivalent of a deserted island. The only possible infection is allo-infection, and this requires a winged aphid. Once it arrives, this allo-infecting aphid, which is invariably a female, will feed on its host and begin to reproduce. Unlike most other insects, it will reproduce without sex, and with live births rather than the laying of eggs. The sexless reproduction is the equivalent of vegetative propagation in plants, and all the progeny are genetically identical to their mother. They constitute a *clone*. The loss of the egg stage saves time, because the young are born alive. They are also born without wings, because flying is not necessary for auto-infection. The young are all female, and they grow very rapidly as a result of sucking the rich juices of their host. Soon, they too start their own sexless and eggless reproduction. There is then a population explosion of aphids, all auto-infecting the same host plant. All rose growers know how quickly a rose bush can become crowded with aphids. Eventually, crowding stimulates the birth of winged individuals, which then fly away to allo-infect a rose bush somewhere else.

Ecologists have a special term for this kind of reproduction. They call it *r*-strategy. An *r*-strategist species is one that reproduces very rapidly and very cheaply, with large numbers of very small offspring. It is a *quantity* breeder. It can exploit an ephemeral food supply very effectively by producing a population explosion. The population explosion is followed by a population extinction when the food supply disappears, usually with the onset of an adverse season. Only a very few individuals survive the winter, or the tropical dry season, but there are enough of them to produce another population explosion in the following favourable season. Most of the serious pests and diseases of our crops are *r*-strategists, and it is their population explosions that can be so alarming, so damaging, and so very difficult to control.

The second real-life example concerns a disease of coffee trees called rust (*Hemileia vastatrix*). This fungus parasite, like its coffee host, is a native of Africa. In 1970, coffee leaf rust appeared for the first time in Brazil, which is the world’s largest coffee producer, and a chill of fear spread among everyone in the coffee trade. Fortunately, the disease was not nearly as serious in Brazil as people had feared, and all of us can still have our morning cup of coffee.

Coffee rust is caused by a microscopic fungus which reproduces by means of spores so small that they are invisible. These spores are similar in size and shape to the pollen cells of flowering plants. When pollen cells are seen *en masse*, they are yellow, and when rust spores are seen *en masse*, they are the colour of rusty iron. Just as iron rust will leave an orange smudge on your finger or clothing, so will coffee rust. Hence its name.

Scientists in East Africa discovered that the spores of coffee rust are sticky, and that they are highly resistant to becoming airborne, and to being dispersed by wind. But they are freely dispersed in water, and every coffee tree gets wet when it rains. Shortly after this discovery was made, it became obvious that the newly introduced disease in Brazil was spreading at a rate of hundreds of miles each year. Brazilian scientists showed that the rust spores were wind-borne. One of those silly scientific disputes arose, with everyone assuming that, if one side were right, the other must be wrong. The spores had to be either water-borne, or wind-borne, and that was that. In fact, both sides were right.

It is now clear that coffee rust spores have two physically different states, and that they can apparently switch freely from one to the other. In one state, they are sticky, and resistant to wind dispersal, but freely dispersed in water. In the other state, they are not sticky, and they are freely dispersed by wind. No one has yet discovered what makes them change from one state to the other, but the most likely factor is atmospheric humidity.

What is important is that the function of the non-sticky state is obviously allo-infection, by wind, from one coffee tree to another. These two coffee trees, the infector and the infected, may be hundreds of miles apart. The function of the sticky state is obviously auto-infection, by rain splash, from one leaf to another leaf, within one coffee tree.

The analogy between the two kinds of pollination and the two kinds of infection is a close one. However, there is one important difference, and it is a historical one. The distinction between autogamy and allogamy has dominated crop science for the whole of the twentieth century. Self-pollinating (autogamous) plants were tailor-made for Johannsen‘s pure lines, Mendelian breeding methods, and vertical resistance. Other scientists modified these techniques to suit cross-pollinating (allogamous) plants, and produced the so-called hybrid varieties, of which the hybrid maize in the corn belt of the United States (Chapter 20) is the most famous example. As a result, the Mendelian school dominated the breeding of allogamous plants also. And the scientists working with vegetatively propagated crops, such as potatoes, pineapples, and sugarcane, also adopted the breeding techniques of the Mendelian school, perhaps unwisely. What matters here is that the distinction between cross-pollination and self-pollination was well recognised.

The distinction between allo-infection and auto-infection should also have dominated crop science for most of the twentieth century, because it is just as important. In fact, the distinction between the two kinds of infection was made only recently, and its importance is far from obvious. We must now examine that importance.

Chapter 5

Host-Parasite Interaction: Matching and Non-Matching

It was mentioned briefly, in the comparison of the two kinds of resistance, that there are two kinds of host-parasite interaction, defined in terms of the gene-for-gene relationship. It will be remembered that each host has a biochemical lock, and that each parasite has a biochemical key. When a single parasite individual is infecting a single host individual, its biochemical key either does, or does not, fit the biochemical lock of the host. If the key fits, both the infection, and the host-parasite interaction, are described as matching. If the key does not fit, they are described as non-matching. With a matching infection, the lock of resistance is opened, the infection is successful, and the parasitism proceeds. With a non-matching infection, the lock remains secure, the infection fails, and the parasitism is prevented.

It is now necessary to consider a *system* of locking. For the purposes of discussion, we may suppose that there are ten different locks, which occur randomly, and with an equal frequency, in a host population consisting of many thousands of individuals. We may also suppose that there are ten different keys, which occur randomly, and with an equal frequency, in a parasite population consisting of many thousands of individuals. If one parasite individual is allo-infecting one host individual, the probability that its key will fit the lock of that host is then only one in ten.

Now suppose there are one hundred different locks and keys, occurring randomly, and with equal frequency in the two populations. The probability of a key fitting a lock is now only one in a hundred. And, if there are one thousand different locks and keys, the probability of a key fitting a lock is only one in a thousand. Clearly, the greater the diversity of locks and keys, the more effective the system of locking becomes.

So long as we think in terms of a *system* of locking, operating in *populations* of the host and the parasite, the gene-for-gene relationship makes a lot of sense. If only one allo-infection in a thousand is successful, the entire epidemic will be slowed down, and stabilised, very considerably. Mathematically, this turns out to be the perfect method of controlling the population explosion of an *r*-strategist parasite.

The system of locking is also a very economical one. Simple mathematical models (Appendix C) reveal that a gene-for-gene relationship with only twelve pairs of genes will produce 924 different locks and keys, provided that each lock and key has exactly half of the available genes (i.e., six genes in this example). The probability of one matching infection in a thousand could almost be achieved with only twelve pairs of Mendelian genes. On the same basis, sixteen pairs of genes would provide 12,870 locks and keys, and twenty pairs of genes would provide 184,756 locks and keys. Both the diversity of locks and keys, and the effectiveness of the system, increase geometrically with only small increases in the numbers of pairs of genes.

One plant host, or one parasite, has thousands of genes, although bacteria and viruses have fewer. Nevertheless, for such an incredible effect to be produced with a mere dozen pairs of genes is truly remarkable. When compared with the complexity of a living cell, or a single chromosome, the simplicity, the beauty, and the elegance of this system of locking are profoundly suggestive of scientific truth. We must remember also that evolution has a knack of finding the best solution within the existing possibilities.

So far, the discussion has concerned allo-infection. It will be remembered that allo-infection involves travel from a distance by an airborne parasite. (Occasionally, the parasite does not travel, but remains dormant and immobile in the soil; the host and parasite come together when a growing root finds the parasite. But this is still allo-infection).

We must now consider auto-infection which involves a flightless parasite, such as a wingless aphid, or a water-borne coffee rust spore. Let us consider a model epidemic in which there are one thousand biochemical locks and keys. If each host is allo-infected once, one host individual in every thousand will have been matched, and successfully allo-infected. Parasitism can begin in these matched individuals. The parasite draws nutrients from its host and it begins to reproduce. Both the aphid and the rust reproduce without sex. This sexless, *r*-strategist reproduction is very rapid. Biologically, it is also very economical, and it produces very large numbers of progeny very cheaply. It has a further advantage for the parasite in that all the progeny are genetically identical to each other, and to their parent. They all belong to the same clone. This means that they all have the same biochemical key. And it is also the key that matches the lock of the host that they are auto-infecting. All parts of the one host individual are also genetically identical. The innumerable microscopic cells, in the many leaves, stems, roots, bracts, flowers, and fruit of one plant, all have the same lock. It follows that *all auto-infection is matching infection.* Vertical resistance cannot control auto-infection. It can control allo-infection only. And it can control non-matching allo-infections only. To put this another way, vertical resistance cannot control any of the consequences of a matching allo-infection. And one of these consequences is auto-infection.

Equally, it follows that auto-infection can be controlled *only* by horizontal resistance. It follows also that all the *consequences* of a matching allo-infection, including all auto-infection, and all the processes of parasitism, can be controlled *only* by horizontal resistance. To postulate that there is no such thing as horizontal resistance, as some Mendelians still do, is to postulate an absolute susceptibility, once a matching allo-infection has occurred. It need hardly be added that such an absolute susceptibility has never been observed.

It is clear, therefore, that the actual parasitism can be controlled only by horizontal resistance. This parasitism is the process by which the parasite steals nutrients from its host, and both grows and reproduces at its host's expense. It follows that horizontal resistance is universal, and that it occurs in every host against every parasite.

Vertical resistance cannot control this parasitism once it has started. It can only prevent the parasitism from starting, and it occasionally fails to do even this, because some matching always occurs. The sole function of vertical resistance is to control the *epidemic*, and to protect the host population as a whole, by slowing down the population explosion of an *r*-strategist parasite. It does this by reducing the proportion of allo-infections that are matching infections.

Now consider the subsequent development of the epidemic. When crowding produces winged aphids, or the rust spores become non-sticky and wind-borne, parasite individuals can leave their parent host and travel to another host. They are allo-infecting that new host and, because of the system of locking in our model, the chances are a thousand to one against their new host having the same lock as their parent host. The probability that their biochemical key will match the biochemical lock of the new host is still only one in a thousand. Vertical resistance continues to control allo-infection throughout the epidemic, during the many rounds of allo-infection that can occur during a single season.

Finally, we come to an odd biological fact. Not all species of plant have vertical resistances. Furthermore, species of host plant which do have vertical resistances have them against only *some* of their species of parasite. This has been the bane of Mendelian plant breeding. Before their breeding can start, Mendelian breeders must find a gene for resistance. If this genetic source of resistance cannot be found, for the simple reason that it does not exist, Mendelian plant breeders cannot breed for resistance. The breeding cannot even begin.

Conversely, every plant has horizontal resistance to every one of its parasites. This is one of the main advantages of this kind of resistance. The biometricians can breed for resistance to any species of plant parasite. We must now enquire why horizontal resistance is universal, but vertical resistance is not.

Chapter 6

Epidemics: Discontinuous and Continuous

An epidemic is just parasitism, or disease, at the systems level of the population. Some scientists consider that the term epidemic should be confined to people and medicine, on the grounds that its Greek derivation refers to people (*demos* = people). They argue that epidemics in populations of plants and animals should be called epiphytotics and epizootics respectively. However, this is a matter of taste. My own view is that 'epidemic' is an English word derived from the Greek, and that present usage is more important than ancient derivation. I also happen to think that the use of different terms for the same thing in people, animals, and plants is an entirely superfluous jargon.

Unlike people, and other mammals, plants have two quite different kinds of epidemic. They are called *discontinuous* and *continuous* and they are defined by the nature of the plants themselves.

Discontinuous epidemics occur typically with annual plants, and with the leaf parasites of deciduous trees and shrubs. With a discontinuous epidemic, the parasitism is intermittent. It stops completely during an adverse season, such as a tropical dry season, or a temperate winter, for the simple reason that there is no host tissue available to the parasite. Discontinuity thus involves *seasonal* host tissue. This discontinuity creates three difficult problems for the parasite.

First, the parasite must survive until host tissue again becomes available. Most species of plant parasite survive the adverse season by becoming dormant, but other mechanisms also exist. For example, the parasite might migrate to another region, with a different climate, where host tissue is available. Or it might find an alternative host species. Or it might change to a non-parasitic phase, and consume dead plant material.

The second problem is that the parasite must find a new host when the favourable season starts, and when host tissue again becomes available for parasitism. It will be recalled (Chapter 4) that the first infection of this new host tissue *must* be an allo-infection. Think of a host population consisting of millions of newly emerged seedlings of an annual species. If the epidemic is to develop fully, each one of those millions of plants must be allo-infected.

The third problem is that each parasite individual must match the biochemical lock of the host that is does manage to find. At the beginning of the epidemic, therefore, the parasite population must have many individuals that are going to be wasted, either because they could not find a host, or because they found a host that they did not match. It is obvious that allo-infection is much more important than auto-infection in discontinuous epidemics. It is equally obvious that the system of locking provided by the gene-for-gene relationship is a very valuable stabilising factor in discontinuous epidemics.

A continuous epidemic occurs with evergreen trees and many tropical herbs, in which there is no interruption in the supply of host tissue. The parasitism can then continue indefinitely, and life becomes much easier for the parasite. A Californian redwood, for example, is an evergreen tree that can live for more than two thousand years. An individual redwood need be allo-infected only once, and auto-infection can then continue without a break for many centuries. Obviously, auto-infection is more important than allo-infection in continuous epidemics.

It is a matter of observed fact that a gene-for-gene relationship has never been found in a plant host species that has continuous epidemics in its wild state. This is because allo-infection is relatively unimportant in continuous epidemics, and vertical resistance can control allo-infection only. The vertical resistance has too little survival value to evolve in a continuous epidemic.

It also transpires that discontinuity is essential to the proper functioning of the gene-for-gene relationship and the system of biochemical locking. A gene-for-gene relationship cannot function in a continuous epidemic. This is because a system of locking cannot operate on a basis of *un*locking only. If every door in the town could be unlocked, but not locked again, the system of locking would quickly become useless.

Plant hosts cannot re-lock their biochemical locks, but they solve this problem in another way. They regularly destroy all tissue that has a biochemical lock, and that has probably been matched by the end of a discontinuous epidemic. The only host tissue that has a lock is *seasonal* tissue, and it is discarded at the end of each season. All the locks that have been unlocked by the parasite are destroyed by leaf-fall in a deciduous tree, or the death of all tissues, except the seed, in an annual herb. Come the end of the season, the entire food base of the parasite disappears, and the parasite is out in the cold, and on its own.

The biochemical locks are not re-locked but, in the new season, they are replaced with new tissues that are both parasite-free, and have locks that are unmatched and functioning. This is the importance of discontinuity. In each new epidemic, there has to be a successful infection of each host individual, if the epidemic is to develop fully. That successful infection *must* be an allo-infection. And it *must* be a matching infection. At the beginning of each new season, the system of locking is fully functional again.

The loss of seasonal tissue represents the ‘recovery’ of vertical resistance, and this the converse of the ‘breakdown’. In the course of one complete seasonal cycle, the state of the vertical resistance can change from being unmatched and functioning, to being matched and broken down, to being unmatched and recovered. This corresponds to a system of both unlocking and re-locking. And the *system* of locking can endure indefinitely. For example, the system of locking continues to function as young deciduous trees replace old deciduous trees in a forest that might endure for millions of years. The only criterion is that the diversity of locks and keys must be maintained, and there are various genetic mechanisms that can ensure this. The system of locking will also endure indefinitely in an ecosystem of annual plants, as new unmatched plants replace the dead, matched plants of the previous season.

It seems that discontinuous epidemics are always caused by *r*-strategist parasites. They have to be *r*-strategists, if they are to exploit a food supply that appears very suddenly at the beginning of a favourable season, and then disappears, equally suddenly, a few weeks later, at the end of that season. Small organisms, such as microscopic parasites, and tiny insects, can take full advantage of such an abundant, but short-lived, food supply only if they have a population explosion.

However, there is a serious problem with population explosions. Like chemical explosions, they are tricky things. They are thoroughly unreliable, and they can very easily get completely out of hand. They are difficult to stop, once they have started, and they equally difficult to curb and restrain. And they can do a great deal of damage if they are not restrained. In an abnormal season that favoured the parasite, there could be a population explosion so vast that the very survival of the host population was seriously threatened. And, if the survival of the host is threatened, the survival of the parasite is threatened with it.

This, then, suggests the function of the system of locking conferred by vertical resistance. It is to slow down the population explosion of an *r*-strategist parasite. It is to stabilise an otherwise unstable, unreliable, unpredictable, and thoroughly dangerous situation. The host population simply cannot afford to be periodically devastated by a parasite population explosion. And the parasite simply cannot afford to devastate its host because, to do so, would threaten its own survival. So, the two species have evolved an incredibly elegant system of locks and keys that prevents damaging population explosions and, at the same time, ensures the survival of the parasite without excessive damage to the host.

Support for this conclusion comes from the vertical resistance to Hessian fly (*Mayetiola destructor*) which is a stem borer of wheat. This resistance is exceptional in that it is *quantitative* vertical resistance. Although its inheritance is qualitative (i.e., Mendelian), its effects are quantitative. That is, it confers incomplete resistance to non-matching strains of the insect, and no protection whatever against matching strains. This means that a non-matching strain of the fly can allo-infect a wheat stem, and survive within it.

With quantitative vertical resistance, a non-matching infection does not kill the parasite. It merely slows the growth of the parasite, and prevents it from reaching maturity. At first sight, this is ludicrous because this kind of resistance does not control the parasitism. Quantitative vertical resistance appears to have no evolutionary survival value. And, if it has no evolutionary survival value, why should it evolve at all?

The answer appears to be that quantitative vertical resistance did not evolve to prevent allo-infection, or even to prevent parasitism. It evolved to prevent damaging population explosions, and it can also do this by controlling the reproduction of the parasite. And this is probably the ultimate function of all vertical resistances. A few infections, and a little damage to the host population, are quite unimportant compared with the disaster of an uncontrolled population explosion in the parasite.

We have seen that vertical resistances appear to reduce parasitism by reducing the frequency of matching allo-infection.

And, at first sight, this reduction of parasitism appears to be the obvious function of vertical resistance. In fact, the ultimate function of vertical resistance is probably the control of population explosions in the parasite. Most vertical resistances achieve this by the simple expedient of controlling allo-infection. A few do it by allowing allo-infection, allowing some parasitism, and some growth of the parasite, but by either preventing, or greatly reducing, parasite reproduction.

But this is a digression. Let us return to the two kinds of epidemic. In practice, this difference between continuous and discontinuous epidemics is crucial to the functioning of vertical resistance. Consider the epidemics of a leaf parasite of a hypothetical tree. If the tree is deciduous, the epidemic is discontinuous, and the vertical resistance will function at the start of every new epidemic. If the tree lives for, say, five hundred summers, its vertical resistance will protect it through five hundred epidemics. By chance, in a few of these epidemics, the tree will be matched quite early in the season, and it will suffer accordingly. However, every tree can tolerate an occasional bad epidemic. Equally, in a few of these epidemics, the tree will be matched so late in the season that it suffers no parasitism at all. On average, it will be matched sufficiently late for the parasite to do only very minor damage in each season.

Now consider an evergreen tree which has a continuous epidemic. Its first infection must be an allo-infection but, after that, it can remain parasitised by auto-infection for the rest of its life, and all auto-infection is matching infection. Vertical resistance would protect this evergreen tree only until the first matching allo-infection occurred, probably when the tree was still a very young seedling. The vertical resistance would then be useless for nearly five hundred subsequent summers. A gene-for-gene relationship cannot function in a continuous epidemic and, consequently, its evolutionary survival advantage is negligible. For this reason, a gene-for-gene relationship never evolves in host-parasite systems that have continuous epidemics.

Most people think that deciduous trees shed their leaves in order to avoid a winter, or a tropical dry season. And so they do. But this is not the only reason. They also shed their leaves to achieve a break in their parasitism, and to resuscitate their biochemical locks. This additional function of leaf-shedding explains several conundrums that baffled botanists for years. For example, it explains why a temporary resistance should evolve in a tree that lives for centuries. It also explains why a tree such as rubber (*Hevea brasiliensis*) should be deciduous, and have vertical resistance to a disease called South American Leaf Blight (*Microcyclus ulei*), even though it occurs wild in the Amazon valley, which is continuously warm and wet. And it explains why the Mendelians could not find any single-gene resistances in various important crops derived from wild plants that have continuous epidemics, such as sugarcane, citrus, and olives.

This, then, was the bane of Mendelian breeding for resistance. If a crop is derived from a wild plant that is an evergreen perennial, it will have horizontal resistance but no vertical resistance. Conversely, if the wild progenitor of a crop is an annual herb, or a deciduous tree or shrub, that crop will have both horizontal and vertical resistances. The evolutionary survival value of a gene-for-gene relationship in a discontinuous epidemic is remarkable and, for this reason, it will often, but not necessarily, evolve in annual herbs, and against the leaf parasites of deciduous trees and shrubs.

A Mendelian breeder, looking for a genetic source of qualitative, vertical resistance, will not find it in evergreen perennials. He may find it in crops with discontinuous epidemics, but he will not necessarily do so. A biometrician, on the other hand, looking for quantitative, horizontal resistance, will invariably find it, in any crop, and against any parasite of that crop.

It will be remembered that a Mendelian breeder needs a genetic source of resistance. If he cannot find it, the resistance breeding cannot even begin. A biometrician, on the other hand, does not need a genetic source of resistance. He needs merely to increase an existing level of quantitative resistance by changing gene frequencies in a mixed population. He can thus breed any crop for resistance to any parasite, and he can do so without first finding a source of resistance.

We should note also that most of the crop species in temperate countries have discontinuous epidemics, and vertical resistances, because they evolved in a region that has winters. And most of the research in crop science has been done in temperate regions, and on temperate crops, grown in the wealthy, industrial nations. Conversely, many tropical crops have continuous epidemics, and they lack vertical resistance. But relatively little research has been done on these tropical crops, grown in impoverished, non-industrial countries.

These differences of climate and research have done much to exaggerate the importance of vertical resistance, and to disguise the importance of horizontal resistance.

Chapter 7

Populations: Genetically Uniform and Genetically Diverse

A plant population may be genetically uniform or genetically diverse. Agricultural crops are plant populations that are typically uniform, because uniformity is essential in modern crop husbandry. It is a great advantage, for example, if all the plants in a wheat crop are the same height, mature at the same time, and have the same milling and baking characteristics. There is a further advantage when all the wheat crops on one farm, and in one region, are identical, because the harvested wheat can then be stored and transported in bulk. In the old days, wheat would be stored and transported in sacks, and each sack would have to be man-handled many times, as well as labelled to show which variety of wheat it contained.

A second, very good reason for crop uniformity in agriculture has already been mentioned. This concerns the problem of preserving the agriculturally valuable traits of a cultivar (i.e., a *culti*vated *var*iety), such as its yield, its quality of crop product, its agronomic suitability, and its resistance to parasites. The natural method of reproduction by sexually produced seeds results in genetic diversity and variability. With variability, these valuable traits, which have been carefully accumulated by artificial selection, tend to be lost. This problem is normally solved in one of three ways, depending on the somewhat artificial method of propagation of the crop in question. As it happens, each of these solutions positively requires crop uniformity.

The first method of propagation is by true seeds in species that are inbreeders, and this includes important cereals, such as wheat and rice, and most of the protein producing crops, such as the many different species of peas and beans. These two categories of crop provide most of the world's food. As we saw earlier (Chapter 2), the Danish botanist Johannsen solved this problem by inventing the pure line, which breeds true to type. The best individual plant in a mixed population is selected as the parent of a new pure line. It is allowed to self-pollinate but, because it is heterozygous, its progeny are variable. The best individual in this second generation progeny is then selected, and allowed to self-pollinate. Its progeny are also variable, but less so. This process of reducing variability by self-pollination and selection is continued until no more variation is detectable. In theory, this process is complete after twelve generations of self-pollination but, in practice, 4-6 generations of selfing and selection are usually adequate. A modern cultivar of an in-breeding crop is thus homozygous, or very nearly so, in all of its genetic make-up. It is a genetically uniform pure line, it breeds true to type, and its valuable traits are preserved indefinitely. Even if some cross-pollination does occur within the cultivar, the two parents are genetically so similar that no significant variation results.

The second method of propagation is by true seeds in species that are outbreeders, such as maize, millets, sorghum, and various cultivated species of the onion and cucumber botanical families (*Liliacea* and *Cucurbitaceae*). A cross-pollinating crop is heterozygous. It often does not breed true to type, and its valuable traits can be lost with seed propagation. Nor can it be self-pollinated without a totally unacceptable loss of vigour. This problem is solved by using hybrid varieties, a method which is described in Chapter 20. The details do not matter here, other than to comment that hybrid varieties also lead to genetic uniformity during cultivation.

Finally, many species of crop are so heterozygous that propagation by true seed is impossible, because the loss of valuable traits is almost total. The classic wine grapes, as well as apples, potatoes, sugarcane, figs, olives, dates, and pineapples are typical examples. In yet other species, the process of domestication has led to an almost complete loss of true seed, and seed propagation is then doubly impossible. These seedless species include crops such as bananas, garlic, ginger, horseradish, sisal, turmeric, and yams. In all these crops, valuable traits can be preserved only by vegetative propagation. Each cultivar is then a clone, characterised by the fact that all the individuals in it are genetically identical.

So, let us make no mistake about it. Population uniformity is essential in modern, commercial crop husbandry. There are very few exceptions to this rule, and they involve only a few out-breeding pasture species, such as alfalfa, otherwise known as lucerne (*Medicago sativa*), that are cultivated as so-called ‘synthetic varieties‘, which are genetically improved, mixed populations.

It should be added, however, that most subsistence crops in the tropics are grown as mixtures. First, there is usually a mixture of different species, such as maize, beans, and sweet potatoes in one field. Second, each of these species is genetically diverse, and is either a landrace or a mixture of several different clones. This is one of the reasons why the need for crop protection chemicals is usually less in subsistence crops, because epidemics develop more slowly in a mixture. However, this kind of genetic diversity is not practical in commercial farming, mainly because it is so labour-intensive, and because of problems of weed control with chemical herbicides.

In complete contrast to commercial agriculture, wild plant populations are always genetically diverse. Although all the individuals in a wild plant population may belong to the same species, they vary among themselves to such an extent that no two individuals are alike. In this respect, they are like human populations, in which no two individuals are genetically identical, apart from monozygotic (i.e., identical) twins. It is a matter of common observation that humans vary considerably in every inherited trait, and the same is true of wild plant populations. A few wild species of plant have a natural vegetative reproduction, and they can produce clones in which all the individuals are genetically identical. However, there is always a limit to this vegetative reproduction, and the total tissue of a natural clone rarely exceeds the size of a large tree. The overall population of clones then has a genetic diversity similar to that of a mature forest.

This contrast between uniformity and diversity of population brings us to the crux of the whole discussion. We saw earlier that the Mendelian method of breeding discriminates in favour of single-gene, vertical resistances that are part of a gene-for-gene relationship. We saw also that the gene-for-gene relationship operates as a system of locking with, possibly, only one allo-infection in a thousand being a matching infection. The essential feature of a system of locking is that it can work only if there is diversity. A system of locking is ruined by uniformity. Consider what happens when every door in the town has the same lock, and every house owner has the same key, which fits every lock.

This, then, is how the Mendelians went wrong. They would transfer a single lock from a genetically diverse wild population to a cultivated plant. They would then multiply that cultivated plant into a genetically uniform pure line, hybrid variety, or clone, which would become a new cultivar. That cultivar might be grown on a huge area of land in a uniform plant population that totalled millions, probably billions, possibly even trillions, of individual plants, all with the same lock.

These uniform populations would remain resistant only because the parasite was often strangely slow to respond to this bizarre situation. Several years might elapse before a parasite with a matching key appeared but, when it did appear, it would respond with the population growth of an *r*-strategist. This growth would be a population explosion and, because the system of locking had been destroyed by uniformity, it would be a completely uncontrolled population explosion. Because of the genetic uniformity, every allo-infection, from one host individual to another, within that cultivar, would be a matching infection. There was nothing to stop the population explosion, except some residual horizontal resistance. But, as we shall see in a moment, the Mendelian breeding method actually reduces the level of horizontal resistance, and a modern cultivar with a matched vertical resistance is usually very susceptible.

The failure which follows the appearance of a matching strain of the parasite is known as the ‘breakdown’ of vertical resistance. Within a single season, an apparently immune cultivar can suddenly become extremely susceptible. This cultivar must then be abandoned, and replaced with a new one which has a different vertical resistance that has not yet been matched. And the process is repeated, again and again. This has been called the ‘boom and bust‘ cycle of plant breeding. It need hardly be added that nothing can be more disheartening for a plant breeder than to see a wonderful cultivar, the result of years of patient and painstaking work, ruined, because its resistance has suddenly ceased to function.

During all this time, almost no one was thinking in terms of horizontal resistance. No one bothered to measure the susceptibility of a failed cultivar, or to study its remnant horizontal resistance. For much of this time, the very existence of horizontal resistance was not even recognised. And, even if the possibility of horizontal resistance was acknowledged, it was not believed to have any practical value. Furthermore, there was such an urgent need to produce replacement cultivars that no one had time to study such apparently unimportant and secondary issues. Besides, these scientists were all Mendelians. They were not interested in quantitative variation.

Some of the very few scientists who were exceptions to this rule, and who both studied and utilised horizontal resistance, are mentioned in the chapters on wheat (19), maize (20), potatoes (18), coffee (21), sugarcane (22), lupins (25), and tropical roots (27). One quite exceptional scientist, in this regard, is Luigi Chiarappa, of the Food & Agriculture Organisation of the United Nations. He had the foresight, and the intellectual courage, to initiate the International Program for Horizontal Resistance (FAO/IPHR) in 1975, at a time when hostility to the very concept of horizontal resistance was at its height. Another exceptional scientist was D.H. Lapwood, at Rothamsted, in England, who was studying the mechanisms of horizontal resistance to potato blight, even before Vanderplank published his classic book in 1963. Another was Helen Hart, who was working with horizontal resistance to wheat rust in St Paul, Minnesota, more than sixty years ago. Her originality was neither recognised nor rewarded. It should also be added that Vanderplank himself did many years of successful work in South Africa, breeding potatoes for horizontal resistance, but he published little concerning this innovative and creative research.

A few scientists have attempted to improve the efficiency of vertical resistance by cultivating crops with a diversity of vertical resistances. In Britain, they have been growing mixtures of several different barley cultivars with some success. And, in the United States, they have used so-called ‘multilines’ in oats. A multiline is a population which contains several different pure lines, that are morphologically very similar, but which have different vertical resistances. However, the use of genetic diversity in commercial agriculture involves considerable technical difficulties and, in agriculture as a whole, it is not very practicable.

This, then, is the real dilemma of crop science, and of the world food problem. We must have genetic uniformity in our crops. But, if we are to employ vertical resistance effectively, as the system of locking for which it evolved to function, we must have genetic diversity in our crops. The conclusion is obvious. Genetic uniformity is essential in our crops and, consequently, we cannot expect to protect them successfully with vertical resistance. We have to consider the use of horizontal resistance, if we wish to avoid the use of chemical pesticides. The use of transgenic resistances, produced by genetic engineering, is not a valid option because these single-gene resistances are likely to fail just like vertical resistances.

So it turns out that the early Mendelians never did have any economically important, single-gene characters after all. They thought they did, but they were wrong. They had single-gene resistances all right, but their value was entirely spurious. And the fact that the Mendelians so dominated plant breeding for most of the twentieth century stems from an unnecessary and, indeed, deplorable, scientific dispute. It was a dispute that made the Mendelians unnecessarily assertive, and needlessly competitive. It was also a dispute that was resolved, scientifically, more than sixty years ago.

During the past half century, crop scientists have been gradually abandoning vertical resistance breeding because its value was so obviously limited. But, these scientists usually concluded either that vertical resistance was the only kind of resistance that occurs, or that horizontal resistance cannot be useful. They then came to the false conclusion that the only alternative to vertical resistance is to use crop protection chemicals. This is the main reason why we now use these chemicals in such depressingly large quantities.

Chapter 8

Response to Selection Pressure: Genetic Flexibility and Inflexibility

There is another aspect of population diversity and uniformity which is of special relevance to plant breeding. This is the question of genetic flexibility. Genetically speaking, a plant population can be either flexible or inflexible. In this context, geneticists speak of selection pressures, using the word ‘pressure’ in the sense of bringing pressure to bear, persuasion, influence, or coercion.

A genetically flexible population will respond to selection pressures, and its genetic composition then changes. For example, if a host population has too little horizontal resistance to a parasite, there will be selection pressure for more resistance. The flexible population then responds to this selection pressure and, in a few generations, it becomes more resistant.

The mechanism of this response is that resistant individuals in the population produce more progeny than susceptible individuals, simply because they are less parasitised. The resistant individuals have a reproductive advantage and, consequently, in the next generation, there are more of them. The susceptible individuals have a reproductive disadvantage and, consequently, in the next generation, there are fewer of them. A similar response can occur to selection pressures for all other variables, including tolerance to environmental factors such as frost, drought, high winds, long days, or acid soils.

This genetic flexibility is totally dependent on genetic diversity. If there is population uniformity, no individual can have a reproductive advantage over any other individual, because they are all identical. Such a population cannot respond to selection pressures. It is genetically inflexible.

Obviously, modern crop populations are genetically uniform and genetically inflexible. They cannot respond to selection pressures. We positively want them that way in order to preserve their valuable agricultural characteristics that have been so carefully accumulated by artificial selection.

Wild plant populations, on the other hand, are genetically diverse and genetically flexible. They can and do respond to selection pressures. If a wild plant population has too little horizontal resistance, it will accumulate an adequate level of resistance in the course of a few generations. And this is true of any inherited character that is quantitatively variable.

Ecologists are familiar with this concept of diversity and flexibility, and they recognise it with the term ‘ecotype’. An ecotype is a sub-population of a species, and it possesses special characteristics suited to its own particular locality within the ecosystem. The selection pressures vary from one part of an ecosystem to another, and different selection pressures produce different ecotypes. Ecotypes are genetically diverse and genetically flexible. One ecotype can be changed into another simply by exposing it to the appropriate selection pressures, for a sufficient number of generations.

The rate of change of ecotypes depends on two factors. First is the frequency of generations. Annual plants have at least one, and sometimes several, generations each year. Their ecotypes can accordingly change quite quickly, within a matter of two or three few years. The ecotypes of long-lived trees will obviously change much more slowly.

The second factor is the strength of the selection pressures. When an ecotype is well suited to its environment, there are no selection pressures, and the ecotype can then remain unaltered for many generations. But when the selection pressures are strong, the rate of change is rapid. This is exactly what happened with the maize crops in tropical Africa, when they were exposed to a re-encounter disease, discussed in Chapter 20.

This question of genetic flexibility brings us right back to the beginning of the discussion, and the comparison between the Mendelians and the biometricians. The ability of a character to vary quantitatively, in response to selection pressures, is very valuable in a natural ecosystem. On the other hand, a single-gene character is not quantitatively variable, and it will not change in response to selection pressures. Its frequency in the population can change, but the character itself is fixed and, in an individual, it is either present or absent, with no intermediates. Single-gene characters can be extremely valuable in special circumstances, such as providing a system of biochemical locks and keys in a plant pathosystem. But these circumstances occur rather infrequently. This explains why polygenic inheritance is so much more common than monogenic inheritance. Single-gene characters are rather rare in plants, and the Mendelians consequently had great difficulty in finding single-gene characters of economic importance.

Crop scientists do not normally think in terms of genetically flexible ecotypes. They tend to think in terms of cultivars, which are genetically uniform, and genetically inflexible. Because they do not normally work with wild ecosystems, crop scientists are less familiar than ecologists with this concept of genetic flexibility, and they often do not appreciate the extent to which plant populations can respond quantitatively to selection pressures. In particular, they rarely appreciate just how much a genetically diverse plant population can respond to selection pressure for horizontal resistance. This type of response is the basis of the biometricians' method of plant breeding.

There can be little doubt that, for the cultivation process, crop scientists should think agriculturally, in terms of genetic uniformity, and genetic inflexibility. But, for the breeding process, crop scientists should perhaps think ecologically, in terms of populations, quantitative genetics, genetic diversity, genetic flexibility, and horizontal resistance.

Chapter 9

Damage: Frequency and Injury

At this point, it might be useful to make a distinction between the frequency of parasitism, which is the proportion of host individuals that are parasitised, and the injury from parasitism, which is the damage suffered by those parasitised host individuals. Injury is usually expressed as the average for the population as a whole.

An example will illustrate the point. A pride of lions may be said to parasitise a herd of zebras. The lions may kill one zebra, which they then consume entirely. This represents the minimum frequency of parasitism, but the maximum injury from parasitism. In ecological terms, the parasitism has a ‘patchy distribution’, and this extreme is often called the predator-prey relationship.

At the other extreme, every zebra is parasitised with ticks, but the injury caused by these ticks is negligible. This opposite extreme represents a maximum frequency of parasitism, but a minimum injury from parasitism. In ecological terms, the parasitism now has a ‘uniform distribution’, and this extreme is often called the host-parasite relationship.

The combination of frequency and injury represents the total parasite damage to the host population. In wild plants, this total damage never exceeds a rather low level. This low level is governed by the fact that the parasite must not impair the ability of its host to compete, either ecologically or evolutionarily. This is axiomatic, because any parasite that impaired its host’s ability to survive would also threaten its own survival. For this reason, the frequency of parasitism, and the injury from parasitism, are inversely correlated in wild plants. A high frequency always results in a low injury, while a high injury always occurs with a low frequency.

In wild plants, frequency and injury are directly related to vertical resistance and horizontal resistance respectively. Vertical resistance provides a system of locking, which obviously reduces the frequency of parasitism. Horizontal resistance provides a second line of defence which, equally obviously, reduces the injury from parasitism. In a continuous epidemic, which has horizontal resistance only, there will be a high frequency of parasitism, but a low rate of injury. In a discontinuous epidemic which has vertical resistance as well as horizontal resistance, the frequency of parasitism will be low, particularly in the early part of the epidemic. But the individual injury from parasitism will be correspondingly higher in those individuals that were matched early in the epidemic.

In modern crops, on the other hand, we often have both a high frequency of parasitism, and a high injury from parasitism. The total damage is then high. This is because the vertical subsystem no longer operates as a system of locking, and the level of horizontal resistance is low.

Because we cannot employ a system of locking in our crops, it follows that we should aim at artificially high levels of horizontal resistance. We should domesticate horizontal resistance in the same way that our ancestors domesticated other continuous variables such as the yield and quality of wheat, rice, and maize. This would result in high frequencies of parasitism which, however, would not matter because the level of injury would be negligible.

Chapter 10

Pathosystems: Wild Pathosystems and Crop Pathosystems

The concept of the pathosystem is based on the general systems theory. There are many different kinds of system, such as solar systems, political systems, ecological systems (ecosystems), mechanical systems, legal systems, electrical systems, and so on. The general systems theory concerns the properties that systems have in common. It is often helpful to study a system in terms of this theory, and in terms of other systems. (Recently, the general systems theory has developed remarkably in the direction of complexity theory, which concerns dynamic systems that are both complex and adaptive. The Belgian scientist, Ilya Prigogine, discovered that such systems have the crucially important property of self-organisation, and they include economic systems, social systems, ecosystems, evolution, and life itself. But this is another story).

One of the more useful concepts to emerge from the general systems theory is the notion of systems levels. For example, a book is a simple static system which has subsystems called chapters. Each chapter has subsystems called paragraphs. Each paragraph has subsystems called sentences, and so on down through words, syllables, and letters. The book itself is a subsystem of a supersystem called a library. There is a hierarchy. Each of these subsystems is a systems level, higher than the one below it, and lower than the one above it.

In biology, systems levels can often be described with the word population. Thus, epidemiologically, a forest is a population of trees, a tree is a population of leaves, a leaf is a population of microscopic cells, and a cell is a population of interacting organelles.

An ecosystem is a biological system. It usually occupies a well-defined area, and it involves the interactions of all living organisms within that area, both with each other, and with their environment. A pathosystem is a special kind of subsystem of an ecosystem, and it is one which involves parasitism. A pathosystem usually involves the interaction of a population of one species of parasite, with a population of one species of host, but some pathosystems are more complicated than this. A plant pathosystem is one in which the host population is a plant, and the parasite is any species in which each individual spends a major part of its life cycle inhabiting, and obtaining nutrients from, one host individual. The concept of the pathosystem thus embraces both crop entomology and plant pathology, but the larger herbivores, which graze entire populations of plants, are normally considered to be outside the conceptual boundaries of the pathosystem, and to belong to the higher systems level of the ecosystem.

A pathosystem may exist physically, in the sense that you can walk into it and study its populations, and their interactions. Alternatively, a pathosystem may exist only conceptually, in the form of a computer model, a diagram, or a mental picture.

Plant pathosystems also have systems levels. Any pathosystem is part of a supersystem, the ecosystem. And many plant pathosystems have two subsystems called the vertical subsystem and the horizontal subsystem. As we have seen, the vertical subsystem involves a gene-for-gene relationship. Its function is to control the epidemic, and the frequency of parasitism, at the systems level of the population. It does this by controlling allo-infection with a system of locking, in a discontinuous, genetically diverse pathosystem.

The horizontal subsystem does not involve a gene-for-gene relationship. Its principle function is to control the parasitism, and the amount of injury, at the systems level of the individual host. It does this by controlling all the consequences of a matching allo-infection. The vertical subsystem is thus a first line of defence, while the horizontal subsystem is a second line of defence.

A special aspect of recognising systems levels is the concept of an emergent. This is a property that is possible at one systems level but which is impossible at any lower systems level. For example, the system of locking of the gene-for-gene relationship is an emergent. It has emerged at the pathosystem level of the system, and it cannot exist at lower systems levels, such as the individual plant host, or the individual parasite. It can function only if there is a mixture of many different locks and keys, and this diversity can occur only at the pathosystem level, which involves the two populations of host and parasite. At the subsystem level of the individual, there can be only one lock, or only one key. And, at the subsystem level of single gene in a gene-for-gene relationship (i.e., a single tumbler in the lock, or a single notch in the key), there can be only one tumbler, or only one notch.

People who work at a lower systems level, such as studying a single host plant, or a single resistance mechanism, may fail to see these emergents which occur at higher systems levels, and this omission results in a phenomenon called sub-optimisation. This word means the analysing or managing of a system in terms of only one, or a few, of its subsystems. This is the equivalent of “not seeing the forest for the trees” and of “arguing from the particular to the general”. To analyse or manage a system of locking, using only one pattern of lock, and one pattern of key, would be suboptimisation. And it is now clear that the Mendelians were suboptimising no less than three times. They attempted to control the crop pathosystem using only the vertical subsystem, employing only one biochemical lock at a time, on a basis of uniformity, and employing a lock that was made up of only one tumbler, one vertical resistance gene.

For our purposes, there are two entirely different kinds of plant pathosystem. These are the wild pathosystem and the crop pathosystem. The differences between these two kinds of pathosystem are the foundation of this entire discussion. It was mentioned at the beginning of this book that we do not treat wild plants with crop protection chemicals, yet the world is still green.

We do treat most of our crops with crop protection chemicals, at a cost of billions of dollars each year. In spite of this, we suffer crop losses that would feed about one billion people.

The wild plant pathosystem is a self-organising, complex, adaptive system in which people have not interfered. Natural selection has ensured that it is a balanced, dynamically stable system which has survived millions of years of evolutionary and ecological competition. The wild pathosystem is also a flexible system. It has genetic diversity and its populations respond to selection pressures. The overall effect is that the parasite does not impair its host's ability to compete, and to survive.

As we have already seen, any parasite which threatens its host's evolutionary survival also threatens its own survival. If the host becomes extinct, the parasite becomes extinct with it. So, wild parasites do not threaten the survival of their hosts. We can conclude with absolute certainty that every wild plant pathosystem, that has survived until the present, is a dynamically stable system in which neither the host's evolutionary survival, nor its ability to compete in a wild ecosystem, is impaired by its parasites. The crop pathosystem is very different, and all these differences are due to the activities of people. First, the host population has been changed in various ways. The species itself has been changed genetically by the process of artificial selection and domestication. Domesticated plants have been further changed by modern plant breeding and, as we have seen, these plants are now cultivated in large areas of genetically uniform populations, in the form of pure lines, hybrid varieties, and clones. These uniform populations also have population densities that are usually much higher than those of most wild pathosystems. Both genetic uniformity and a high host population density assist the parasite very considerably.

Second, the environment has been changed. Land that may once have been covered with mixed forest has been cleared, drained, ploughed, harrowed, seeded, weeded, manured, treated with pesticides, and, perhaps, irrigated.

Third, the parasite population has been subjected to some very strange selection pressures that would never occur in a wild pathosystem. Because of the use of pesticides, the parasite has also been liberated from the constraints of many of its own enemies (Chapter 14), and its population explosions are much greater as a result.

One of the effects of all this artificiality is that the genetic diversity, the genetic flexibility, and the discontinuity of the wild pathosystem have been replaced with uniformity, inflexibility and, because of modern monocultures, a large measure of epidemiological continuity. As a direct consequence, the crop pathosystem is now an unstable, unbalanced system. Without the use of chemical pesticides, some of our crops could not be grown at all, and many others would suffer intolerable reductions in the yield and quality of their crop product.

The positive side of this somewhat dismal picture is that our greatly expanded human population can still feed itself. Some environmentalists talk romantically of a ‘return to nature’, and they deplore the artificiality of modern agriculture. But we must be realistic. We must remember that modern agriculture supports a human population density that is some hundreds, perhaps a thousand times, greater than the population density of our primate ancestors, who inhabited the world before the emergence of human culture. If we abolished agriculture, so that only hunter-gatherers could survive, most of the people in the world today would die of starvation. Even a return to the pre-industrial agriculture of the nineteenth century, with its harvesting by hand, and its horse-drawn ploughs and wagons, would kill off more than three quarters of the world's present human population. So, however much we may deplore the artificiality of agriculture, we must appreciate that the only alternative (at present) is a really massive human mortality. (There is a third possibility which is several decades into the future, and which is discussed in the last chapter in this book). However, the main purpose of this digression is to emphasise that the crop pathosystem is very different from the wild plant pathosystem.

The conclusion seems inescapable. The vertical subsystem is the wrong subsystem for the crop pathosystem. Since 1905, crop scientists have had a choice between the two subsystems. Because of a concatenation of circumstances, which included a silly scientific dispute, and the vociferous clamour of the Mendelians, who had single-gene resistances, but nothing else of economic significance, the whole of crop science was led up a blind alley. And it is still stuck in there, apparently unable to back out.

In fact, that option still exists. We can investigate the horizontal subsystem at any time. And, if these investigations are satisfactory, we can employ horizontal resistance at any time also.

This is the best hope we have and, apparently, the *only* hope we have, of reducing, or even eliminating, both the crop losses caused by parasites, and the use of crop protection chemicals in our crops.

Chapter 11

The Disadvantages of Vertical Resistance

At this point, it may be useful to summarise the disadvantages of vertical resistance, while recognising that it does have three very considerable advantages.

Three advantages of vertical resistance

It was mentioned earlier that the beauty and elegance of the Mendelian gene-transfer techniques captured the imagination of plant breeders all over the world. This is the main attraction of vertical resistance. It is so scientifically elegant, and so easy to see, and to manipulate in a breeding program. Vertical resistance also has the very considerable practical advantage that it normally confers a complete protection against the parasite in question. It confers an apparent immunity. Lastly, vertical resistance has a wide climatic adaptability, and this is important for plant breeding institutes which are often required to provide cultivars for a large geographical area. Opposing these three advantages, however, vertical resistance has several, very serious disadvantages.

Temporary resistance

First, as is now abundantly obvious, vertical resistance is temporary resistance when it is employed on a basis of host population uniformity. It fails to operate on the appearance of a matching strain of the parasite. And this disadvantage has tormented most of twentieth century crop science, either directly or indirectly.

Genetic Source of Resistance Essential

The second disadvantage of vertical resistance has already been mentioned. This is the need, indeed the necessity, of first finding a genetic source of resistance. If a source of resistance cannot be found, the breeding cannot begin. There are some famous crop parasites, such as Colorado beetle (*Leptinotarsa decemlineata*) of potato, and Take-All disease (*Gäumannomyces graminis*) of wheat, for which a source of vertical resistance has never been found, and Mendelian resistance breeding has never been attempted. If it is concluded that breeding for resistance is not possible, alternative methods of control must be used. Usually, the only alternative control involves chemical pesticides, and this is another reason we now use these substances in such horrifying quantities.

A side-effect of this need for a genetic source of resistance comes from a natural difference between pests and diseases. As it happens, gene-for-gene relationships occur much more frequently with plant diseases than with the insect parasites of our crops. There are good biological reasons for this difference, which is related to asexual reproduction in an *r*-strategist parasite. Sexless reproduction leads to much more rapid population explosions. It is also much more common among crop pathogens than it is among the insect pests of crops. As we have seen (Chapter 6), the importance of a gene-for-gene relationship is the control of parasite population explosions.

What matters here is that the Mendelians could not often find a source of resistance to insect pests. As a direct consequence, there was much less breeding of crops for insect resistance than there has been for disease resistance. This is yet another indication of how the Mendelian school has dominated, and distorted, plant breeding during the present century.

There is another, rather disturbing, side-effect of the need for a genetic source of resistance. As we have seen (Chapter 6), a gene-for-gene relationship, and vertical resistance, cannot evolve in a continuous pathosystem. Because of winters, most temperate crops are derived from discontinuous wild pathosystems, and they have many vertical resistances. Many tropical crops, on the other hand, are derived from continuous wild pathosystems, and they have no vertical resistances. Consequently, it was mainly in the poorest, non-industrial, tropical countries that resistance breeding programs were never even started, because genetic sources of resistance could not be found.

The ‘Red Queen’ Situation

The third disadvantage of vertical resistance may be called the ‘Red Queen’ situation, named after Lewis Carrol‘s *Alice Through The Looking Glass*. It will be remembered that the Red Queen said to Alice “Now here, you see, it takes all the running you can do to keep in the same place”. If a plant breeder is under continuous pressure to produce new cultivars, in order to replace those whose vertical resistances have failed, it is difficult to make progress in other directions. It will be remembered that resistance to crop parasites is only one of the four primary objectives in plant breeding. The others are the yield, the quality of the crop product, and agronomic suitability.

A breeder may be forgiven if he concludes that these other objectives are collectively more important than parasite resistance. He may also conclude that the control of crop pests and diseases is really the responsibility of the entomologists and plant pathologists. It is *their* duty to ensure that these pesky parasites do not damage the magnificent yield, superb quality, and agronomic excellence of his new cultivars. So, the breeder abandons resistance breeding, and dumps this problem in the lap of his colleagues. Sadly, almost the only weapons available to the entomologists and pathologists are crop protection chemicals. This ‘Red Queen’ situation, and the consequent abandoning of the resistance objective in plant breeding, is perhaps the chief reason why we now use these chemicals in such large quantities. (One review of the first edition of this book had a delightful typing error that the computer spell-check could not find, and it quoted the Red Queen as saying: “Nowhere, you see…”).

The Vertifolia Effect

There is a fourth disadvantage to breeding for vertical resistance that is insidious, and largely unappreciated, but dangerous for this very reason. This is the decline in the level of horizontal resistance that slowly but inexorably occurs. This effect was first observed by Vanderplank, who called it the ‘vertifolia effect‘ after a potato variety of this name which had vertical resistance to blight (*Phytophthora infestans*). It was only after this vertical resistance had broken down that it was discovered that the *Vertifolia* potato was quite unusually susceptible to blight, because it had a remarkably low level of horizontal resistance.

Horizontal resistance can be observed and measured only in terms of the level of parasitism. If there is no parasitism, because of a functioning vertical resistance, or because the breeder is protecting his screening population with insecticides and fungicides, the level of parasitism, and the level of horizontal resistance, cannot be observed. Individuals with high levels of horizontal resistance are relatively rare in a breeder’s genetically mixed population. This means that individuals with only low or moderate levels of horizontal resistance are more likely to be selected, on the basis of their other attributes. In the course of many breeding generations, the level of horizontal resistance in the breeding population as a whole declines until it reaches dangerously low levels. This explains why the breakdown of vertical resistance is so very damaging in most modern cultivars. The second line of defence, the horizontal resistance, is largely lacking.

This cryptic loss of horizontal resistance also explains why many modern cultivars need such large quantities of chemical pesticides if they are to be cultivated at all. Not a few breeders, who abandoned resistance breeding years ago, have been protecting their screening populations with crop protection chemicals. This makes the breeding work incomparably easier (Chapter 18). Sadly, it also leads to this hidden decline in the level of horizontal resistance. It leads to a progression of cultivars that are increasingly susceptible to a widening range of parasites, and requiring an escalating need for pesticide protection. We have actually been losing horizontal resistance to crop parasites for most of the twentieth century, and most modern cultivars have considerably less horizontal resistance than the cultivars of 1900.

(To avoid possible confusion, it should be mentioned that pedigree breeding can increase the level of quantitative variables, such as yield, although it is not necessarily the best method for doing this. This is why modern plant breeding has generally been successful in the objectives of improved yield, quality of crop product, and agronomic suitability. These characters were visible, and could be selected, even though they were quantitatively variable. The vertical resistance was used because it was so suitable for the back-crossing process, even though it later proved to be ephemeral. The horizontal resistance was valuable, but it was not selected because its effects were invisible, being concealed by either vertical resistance or crop protection chemicals. And, on the occasions when its effects were visible, they were completely ruined by parasite interference, Chapter 14).

Problems with Comprehensive Resistance

There is another disadvantage in breeding for vertical resistance. Most species of crop have many pests, and many diseases. Unfortunately, it is not really feasible to breed for vertical resistance to more than one species of parasite at a time. The basic idea of pedigree breeding is to produce one cultivar with vertical resistance to one species of parasite, a second cultivar with vertical resistance to a second species of parasite, and so on. This results in a series of cultivars, each with one vertical resistance to a different species of parasite. Using gene-transfer methods, these vertical resistances are then all combined in a single cultivar, a ‘super-cultivar’ with resistance to everything. At least, that is the idea. And it is a neat idea. Unfortunately, it is almost impossible to achieve in practice. The sheer volume of breeding work is so exorbitant that one or more vertical resistances are likely to be matched before the breeding is completed. Furthermore, such a super-cultivar is like a chain, in that it is only as strong as its weakest link. And, like the chain, the super-cultivar would be ruined with the failure of only one weak link, one short-lived vertical resistance.

Loss of Genetic Diversity

Vertical resistance usually confers complete protection against a parasite, and this protection functions over a very wide climatic range. This means that a vertical resistance is relatively insensitive to climate, and a single cultivar can then be cultivated over a huge area. This was an essential aspect of the early cultivars of the green revolution. This degree of crop uniformity has certain economic advantages but it also has two drawbacks. First, a huge area of a single cultivar is very vulnerable to a new, matching strain of the parasite. And, second, the widespread use of a single cultivar leads to a loss of genetic diversity. In its turn, this threatens to destroy unexplored sources of resistance. Our preoccupation with vertical resistance is the main reason for the current concern over genetic conservation (Chapters 19 & 20).

Man-Made Problems

It is difficult to avoid the conclusion that most of our crop parasite problems are man-made. And that most of these problems stem either directly or indirectly from our misuse of vertical resistance, and our neglect of horizontal resistance.

The happy corollary of this sad situation is that all these man-made problems can be corrected. And the discerning reader may already have observed that Part Three of this book is labelled ‘Solutions’.

Chapter 12

Horizontal Resistance Compared

Horizontal resistance does not have these disadvantages. It undoubtedly has some disadvantages, which I shall describe in a moment, but, in general, its advantages are striking.

Permanent Resistance

The first, and most obvious, advantage of horizontal resistance is that it is durable resistance. It cannot be matched, because it always *is* matched. It operates against strains of the parasite that have already matched the vertical resistance of the host, and that have already commenced the process of parasitism. Consequently, horizontal resistance cannot break down, like vertical resistance. Horizontal resistance occurs in all plants, independently of any vertical resistance genes that they may be carrying, and it operates against all strains of the parasite, independently of any vertical parasitism genes that they be carrying. For all practical purposes, it is permanent resistance.

Complete Resistance

Second, horizontal resistance is a quantitative variable, with all degrees of difference between a minimum and a maximum. This means that the level of horizontal resistance can be changed. An inadequate level of horizontal resistance can be increased by further breeding. In theory, at least, the level of horizontal resistance can be increased until the parasite in question is controlled completely. In practice, this may require a level of horizontal resistance that approaches, or even exceeds, the maximum and, unfortunately, no one knows what the maximum levels of horizontal resistance actually are. It is a measure of the neglect of horizontal resistance, during the twentieth century, that the maximum level has not yet been determined against any species of parasite, in any species of crop. The opponents of horizontal resistance are apt to claim that the maximum levels will be inadequate, but they are just guessing, because no one knows for sure.

However, some evidence is available. The difference between the near-minimum and the near-maximum levels of horizontal resistance can be enormous. This has been clearly demonstrated, for example, in potato blight (Chapter 18), tropical rust of maize (Chapter 20), coffee rust (Chapter 21), coffee berry disease (Chapter 21), *Phylloxera* of grapes (Chapter 23), and various diseases of sugarcane, such as smut, rust, and mosaic virus (Chapter 22). With all these parasites, in the absence of crop protection chemicals, very low levels of horizontal resistance can lead to a complete loss of the crop, while very high levels provide a control of the parasite that is effectively complete.

This range of differences is to be expected because, in the wild, the epidemiological competence of parasites can vary to a similar extent. In a suitable part of an ecosystem, the parasite will have an epidemiological competence that is maximal, and wild host ecotypes in that area will accordingly accumulate the maximum levels of horizontal resistance. Conversely, in an unsuitable part of an ecosystem, in which the parasite can only just survive, or in the physical absence of the parasite, the need for horizontal resistance will be minimal. In these circumstances, host ecotypes will lose most of their horizontal resistance, and they will then be highly susceptible. This susceptibility will be revealed if such an ecotype is taken to an area where the parasite has a high epidemiological competence.

It appears, therefore, that plant breeders have a very wide range of levels of horizontal resistance available to them. Artificial selection for high levels of horizontal resistance should accordingly provide a total control of many parasites, of many crops, in many areas. Consequently, it is probable that horizontal resistance can provide protection that is *complete*, as well as permanent.

Genetic Source of Resistance not Necessary

A further advantage of being quantitatively variable is that no genetic source of resistance is necessary when breeding for horizontal resistance. With horizontal resistance, we can breed for resistance to those many species of crop parasites, particularly the insect pests, for which no resistance breeding was ever attempted by the Mendelians, simply because no source of single-gene resistance could be found. This emancipation from the practical constraint of first finding a source of resistance is critically important, and the reason for it should be explained.

Let us suppose a hypothetical plant population in which every individual has only ten percent of the alleles contributing to horizontal resistance. Every individual in that population is thus highly susceptible. And this means that the population as a whole is highly susceptible. But let us suppose also that this population is genetically diverse. Each of the individuals in it has a *different* ten percent of resistance alleles. This means that all the alleles for horizontal resistance are present in the population, but they are spread so thinly that every individual is susceptible.

As we saw earlier, breeding for horizontal resistance by recurrent mass selection involves changing gene frequencies. In the course of each generation of plants exposed to suitable selection pressures, the percentage of those resistance alleles increases by transgressive segregation (Chapter 20). This is a process of concentration that can continue until it approaches one hundred percent, which is a very high level of resistance. This concentration of resistance alleles can be compared, somewhat loosely, with the concentration of alcohol that occurs when wine is distilled into brandy.

It follows that breeding for horizontal resistance requires a reasonably broad genetic base (i.e., a reasonably diverse parent population) to ensure that all the alleles are present. But, apart from that, all the plants in that parent population can be susceptible. If it later transpires that the genetic base was too narrow, and that it could not provide the level of horizontal resistance required, the breeding base can be broadened by adding new genetic material to it.

Comprehensive Resistance

There is yet another advantage to horizontal resistance. A little-known aspect of recurrent mass selection is that it permits screening for many different variables *at the same time*. This means that the breeder can exert simultaneous selection pressures for all the breeding objectives. In effect, the breeder need screen his plants for only four things: high yield, high quality of crop product, good agronomic suitability, and good health in the presence of all locally important parasites. In systems terminology, this means working at the highest systems level. It is called the *holistic* approach.

In each screening generation, the criterion of good health means simply the least parasitised host individuals, taking all locally important species of parasite into account. In practice, this is usually very easy to measure. The greenest individuals, or those with the highest individual yields, are the least parasitised. Severely parasitised plants cannot be the most green, or have the highest yields. In each screening generation, the best plants are selected as parents for the next generation, regardless of how poor they may be. In each generation, the best plants are better than those of the previous generation, and a steady improvement in all the desired variables is achieved.

This means that, in addition to being permanent resistance, and complete resistance, horizontal resistance can also be *comprehensive* resistance, in the sense that it operates against all the locally occurring species of parasite. It need hardly be added that, if a cultivar has resistance that is permanent, complete, and comprehensive, it will not need any chemical pesticides to protect it from its parasites. And if this were true of all cultivars of all crops, the use of chemical pesticides on our crops would cease. (However, it must be remembered that the herbicides, or weed-killing chemicals, are not included in this discussion).

A full appreciation of the potential of horizontal resistance requires a comparison with the ‘Red Queen‘ situation of vertical resistance breeding. It will be remembered that this takes all the running you can do to stay in the same place, and it leads eventually to the abandonment of resistance breeding. In complete contrast, breeding for horizontal resistance is progressive and cumulative. A good cultivar need never be replaced, except with a better cultivar. Ideally, the better cultivar should be superior in all respects, including its yield, its quality of crop product, its agronomic suitability, and its horizontal resistance to all locally occurring parasites. This progress can continue, no doubt with diminishing returns, until a plateau is reached beyond which no further progress is possible.

This plateau represents the ultimate practical productivity of a pesticide-free agriculture. It is a level of productivity that is *at least* twenty percent higher, on average, than our current levels, because that is the present rate of loss to crop parasites. It may be a level of productivity that is considerably higher still, because of the many constraints that the Mendelian breeding methods have imposed on crop improvement as a whole. No one seriously suggests that the Mendelians have taken crop husbandry to the limits of production, even with the use of crop protection chemicals. But, if we use horizontal resistance, that plateau is in full, clear view.

So, how realistic is the possibility of attaining this ultimate level of production? The fact is that no one knows for sure, and scientific opinions differ widely. At the very least, it is reasonable to suggest that the matter merits investigation. After all, if true, these prospects would solve many problems. If only partly true, they would be worth pursuing. And, even if they were proved completely false, their investigation would still have been justified. For the present, readers of this book can form their own judgment from the examples of horizontal resistance that are given in Part Two. But, first, we must consider some of the disadvantages of horizontal resistance.

Disadvantages of Horizontal Resistance

Quantitative variables, such as horizontal resistance, require the entirely different breeding methods of the biometricians. Many crop scientists are loyal to the Mendelian outlook, and they are reluctant to switch to these alternative techniques. Furthermore, there are many pedigree breeding programs which represent decades of patient and painstaking work. These programs cannot be changed to breeding for horizontal resistance, and no one wants to abandon them. Not yet, anyway. There would have to be some very convincing demonstrations of the feasibility and value of horizontal resistance before anyone would seriously consider abandoning such old and well established programs. And these demonstrations take time. Horizontal resistance breeding programs will thus require entirely new research projects.

Another difficulty with horizontal resistance is that gene-transfers are impossible. It is just not possible to transfer a good level of horizontal resistance from a resistant to a susceptible cultivar. This type of hybridisation would normally lead to a halving of that good level of horizontal resistance. On average, there would be a further halving of whatever resistance remained with every generation of back-crossing to the susceptible cultivar. Horizontal resistance is not amenable to gene-transfer methods. As we have seen, when breeding plants for horizontal resistance, it is necessary to select for all desirable variables simultaneously. This is the main reason why the existing vertical resistance breeding programs could not be converted to breeding for horizontal resistance.

Another of the problems with quantitative variables is that they have a maximum. There is a genuine fear that the maximum attainable levels of horizontal resistance may not be enough to provide a complete control of all the parasites of a crop. This point can only be resolved by practical experiments. And these experiments have still to be done. Indeed, it is high time they were started. In the meanwhile, all we can say with complete confidence is that even small increases in the current levels of horizontal resistance would be an improvement, and would lead to a reduced use of chemical pesticides.

Even small increases in the level of horizontal resistance would make all other aspects of crop pest management more effective, easier, cheaper, and safer. This would happen because crop protection chemicals would need to be applied less frequently, in lower concentrations, of less hazardous chemicals. But, for all other conclusions, we have to wait and see. In the meanwhile, any opponent of horizontal resistance, who claims that these experiments are not worth doing, can only be guessing. We should also remember that, in science, a blanket hostility towards something new must always be suspect.

A further disadvantage of horizontal resistance is that the weather is variable, and an occasional freak season may so favour the parasite that a normally adequate level of resistance becomes inadequate. However, we can now handle meteorological data well enough for farmers to be given sufficient warning of a freak epidemic, and they can then use crop protection chemicals. Given an appropriate level of horizontal resistance, this should not happen more than once or twice each century. If it happened more often than this, the level of horizontal resistance could probably be increased by further breeding.

A minor disadvantage has already been mentioned. The primary function of horizontal resistance in a wild plant pathosystem is to reduce the *injury* from parasitism, rather than the *frequency* of parasitism. This means that cultivars with high levels of horizontal resistance are likely to have negligible injury from their parasites, but they are likely to show a very high frequency of parasitism. In other words, every plant will be parasitised, but only to a trifling extent. Most consumers have got used to fruit and vegetables that are entirely free of pest and disease blemishes. This is part of the pesticide mentality. Perhaps we should encourage the public at large to regard a few quite minor blemishes as evidence for freedom from crop protection chemicals. We should also remember that a few parasites are necessary in order to maintain the agents of biological control. This topic is discussed in Chapter 14.

A further drawback of horizontal resistance is that it is ‘site-sensitive’. Let us consider two different sites, two different agro-ecosystems. A cultivar might be in perfect balance with the first of these sites. That is, it has exactly the right amount of horizontal resistance to control every species of parasite at that site in, perhaps, ninety seven seasons out of every hundred. The second site, however, is climatically different, and the epidemiological competence of parasites varies with climate. A difference of temperature, or rainfall, can increase or decrease the population explosion of a parasite. Consequently, a cultivar which is perfect in one site may be unsuitable in another site, because it has too much resistance to some parasites, and too little to others.

In practice, this means that there must be a separate breeding program for each site. This is called *on-site selection*. However, this need for a multiplicity of breeding programs is no great hardship because most epidemiological sites are usually quite large. Much of a country the size of England, for example, would normally be a single site or, at most, two or three sites, for most species of crop.

Some environmentalists might even consider this site sensitivity to be an advantage, because it helps to maintain genetic diversity in our crops. The use of vertical resistances, which operate over a much wider climatic range, can lead to a dangerous loss of genetic diversity and, as we have seen (Chapter 7), this is one of the main causes of the current concern about genetic conservation.

Another disadvantage of quantitative variables is that they can be lost just as easily as they can be accumulated, and horizontal resistance is no exception. A loss of horizontal resistance is called the *erosion* of horizontal resistance, and is discussed more fully in a moment. Fortunately, the various techniques, already described, for preserving agricultural traits in seed-propagated in-breeding crops, seed-propagated out-breeding crops, and vegetatively propagated crops, will normally prevent the erosion of horizontal resistance.

Finally, many of the opponents of horizontal resistance claim that there is a fundamental conflict between this kind of resistance and the components of yield, quality, and agronomic suitability. They agree that the levels of horizontal resistance can indeed be increased, but they argue that this can be done only at the expense of these other valuable traits. This conclusion is based on the general observation that wild plants have high resistances but low yield and quality, while cultivated plants have high yields and quality, but low resistances. However, such a conclusion is not necessarily sound, because this situation in our crops could also have arisen, and probably did arise, from the use of Mendelian breeding methods.

The converse argument is that one of the biggest constraints on yield and quality today is the damage caused by crop parasites, in spite of the use of chemical pesticides. If we could reduce, or even eliminate, that damage by using horizontal resistance, then this resistance would improve the yield and quality, rather than lessen them. To say nothing of reducing, or even eliminating, those crop protection chemicals. So who do we believe? For ease of discussion, only yield need be considered, while bearing in mind that the same arguments can be applied to other quantitative variables, such as the quality of crop product, and agronomic suitability.

Both horizontal resistance and yield are quantitative variables. Each has a minimum and a maximum. We want the maximum of both of them but, before the maximum of either can be reached, there is probably a point at which they come into conflict. The horizontal resistance can then be increased only at the expense of the yield, and the yield can be increased only at the expense of the horizontal resistance. The obvious questions are: Where does this point of conflict appear? And is it of practical significance?

This problem can be illustrated by the example of wheat. The world average yield of wheat is 1.4 tonnes/hectare. The average for the North American prairies is 2.2 t/ha. The average in Western Europe is 5.0 t/ha, while the best individual farm yields in that region produce 10.0 t/ha. The experimental maximum (but commercially uneconomic) yield is 15.0 t/ha, which is more than ten times the world average. No one knows the ultimate potential yield of wheat. It might be 20.0 t/ha. Somewhere between the minimum and the maximum yields, there is almost certainly a point at which horizontal resistance and yield come into conflict. But where?

Obviously, this point can be determined only by experiment and, unfortunately, these experiments have yet to be done. In the meanwhile, we can only guess. My own guess is that the point of serious conflict between yield and resistance is close to the maximum commercial yields now being obtained on the highest yielding farms in Western Europe. That is, at about 10 t/ha, which is approximately halfway between the theoretical minimum and the theoretical maximum. But let us be conservative, for the sake of equable discussion, and put it at half this level, at 5 t/ha.

At first sight, this would mean that the successful and universal use of horizontal resistance would increase the world average yield of wheat from 1.4 t/ha to 5 t/ha. This would more than treble the world's wheat production without any increase in the area of cultivation. But the calculation is not that simple, and not that rosy. The constraints on the world average yield are not all due to parasites. Other constraints include low rainfall, bad soils, inadequate fertilisers, storms, weeds, poor farming, and so on. So let us suppose that half of the total constraints are due to parasites. The universal use of comprehensive and complete horizontal resistance, combined with the maximum yield that can be combined with that resistance, might then increase the world average yield of wheat from 1.4 t/ha to 3.2 t/ha, which is an increase of rather more than 125%.

Which is not bad, even if it is a mere estimate, based on guesswork. Nevertheless, this level of improvement, in all our crops, could to do a lot to alleviate the world food problem, possibly right up to the time when human population growth is finally stabilised. It could also do a lot to alleviate the pesticide pollution problem. The real point, of course, is that we need to know for sure. This matter merits scientific investigation. We simply cannot afford to neglect it any longer.

Chapter 13

The Erosion of Horizontal Resistance

It must be clearly recognised that horizontal resistance can be *eroded* in a number of ways. But this quantitative loss of horizontal resistance is very different from the qualitative breakdown of vertical resistance, and it is important not to get the two of them confused. At first sight, the very thought of an erosion of horizontal resistance is upsetting, even alarming. Horizontal resistance is supposed to be durable, and to persist indefinitely, or at least during the foreseeable, agricultural future.

For people who understand horizontal resistance, and who are working with it, erosion is important only occasionally, and these occasions can usually be avoided, or they are easily controlled. However, for people who do not understand horizontal resistance, such as Mendelian breeders working exclusively with vertical resistance, the mere possibility of an erosion of horizontal resistance often provides an adequate excuse to deride it, and to neglect it experimentally.

Host Erosion

The erosion of horizontal resistance that occurs most commonly is a result of genetic changes in the host population. This kind of erosion is called the *host erosion* of horizontal resistance, and it is the converse of the accumulation of horizontal resistance that occurs when there is positive selection pressure for it.

A host erosion can occur either during breeding, or during cultivation. Horizontal resistance can be lost during breeding because of the absence of a parasite. As we shall see in later chapters, such an absence can occur naturally (Chapter 20), or because of a functioning vertical resistance (Chapter 18), or because of protection with pesticides (Chapter 18), or during breeding of a crop with parasites that accumulate only slowly, such as the potato viruses (Chapter 18). In other words, horizontal resistance is eroded if there is no selection pressure for it during the breeding process. Most of the current susceptibilities in modern crops are the result of a host erosion during breeding.

A host erosion of horizontal resistance during *cultivation* can occur only if the crop is genetically flexible, as happened with the open-pollinated, subsistence maize crops in tropical Africa (Chapter

20). This kind of erosion occurs either when the parasite is absent from the agro-ecosystem in question, as with tropical rust of maize, or when the parasite has a very limited, patchy distribution, as with maize streak virus (Chapter 20). In practice, these days, very few commercial crops are genetically flexible during cultivation, although many subsistence crops are flexible. In those commercial crops that are flexible, such as alfalfa (*Medicago sativa*), the selection pressures for resistance must be continuously maintained in populations that are being used for seed production.

A host erosion of horizontal resistance can also occur in special circumstances. For example, there is a north American insect parasite of the roots of grapes, called *Phylloxera*. In the 1860s, *Phylloxera* was found in France and it caused so much damage that the European wine industry was faced with total ruin. The problem was solved by grafting the very susceptible, classic wine grapes on to rootstocks of wild American grapes which have very high levels of horizontal resistance to *Phylloxera*. That resistance has now endured for more than a century in Europe.

In California, however, there is a different situation. Because the resistant rootstocks depress the yield of grapes somewhat, Californian vines are often grafted on to hybrid rootstocks. These hybrids are half wild American, and half European, and their use increases the yield of grapes. Unfortunately, they were inadequately tested before being issued to farmers. They are moderately susceptible to *Phylloxera*, and this pest has recently become a serious nuisance in some Californian vineyards that have these hybrid rootstocks. It is important not to misinterpret a situation such as this, and to attribute it to a breakdown of vertical resistance, or to a parasite erosion of horizontal resistance (see below).

Parasite Erosion

An erosion of horizontal resistance can occasionally occur as a result of population changes in the parasite. This is called the *parasite erosion* of horizontal resistance. It is an *apparent* erosion which, in fact, is not due to any change in the resistance itself. There is an increase in the level of parasitism, resulting from an increased parasitic ability in the parasite.

Most species of parasite have a strict limit to their parasitic ability and they cannot increase it beyond that limit, at least during the foreseeable agricultural future. (This argument follows logically from the fact that any parasite which endangers its host's ability to survive, also endangers its own survival). In practice, a parasite erosion of horizontal resistance is normally important only with a special category of parasite called a *facultative* parasite. This is a parasite that can change between the ability to extract nutrients from a living host, and the ability to extract nutrients from dead plant material. These two abilities are inversely proportional. That is, the greater the one, the less the other.

For example, there is a soil-inhabiting fungus called *Fusarium oxysporum* f.sp. *lycopersici* that causes a wilt disease of tomatoes. If tomatoes have not been grown in that soil for many years, the non-parasitic form of the fungus predominates. Under these circumstances, tomatoes can be grown with very little loss from wilt disease. However, if tomatoes continue to be grown in that soil, season after season, the parasitic ability of the fungus increases. This causes an increase in the frequency of wilt disease, and an apparent loss of resistance in the tomatoes.

A parasite that can obtain nutrients only from a living host is called an obligate parasite. It appears that there is not a single known example of a significant parasite erosion occurring with an obligate parasite.

Environment Erosion

In addition to host and parasite erosion, an *environment erosion* of horizontal resistance is possible. This again is an apparent erosion of resistance, and it occurs when someone takes a cultivar from an area where the parasite has a low epidemiological competence, to an area where its epidemiological competence is considerably higher. Typically, this happens when a cultivar that is suited to a dry climate is taken to an area with a humid climate. This happened when the coffees of arid Harrar were taken to the much wetter areas of south-west Ethiopia (Chapter 21). Environment erosion also accounts for many susceptibilities in ancient clones being grown in new areas (Chapter 23), and it is also the main reason for practicing on-site selection (Chapter 12).

A good example of an environmental erosion of horizontal resistance occurred with beans (*Phaseolus vulgaris*) in Kenya. The cultivar Canadian Wonder of these beans were introduced in about 1900 and, although a self-pollinating crop, some 3-5% of cross-pollination occurs. By mid-century, these beans had accumulated high levels of resistance to all locally important pathogens. At this point, a scientific colleague of mine decided to re-introduce Canadian Wonder from North America, in order to compare it with the acclimatised beans. The introduced beans had levels of resistance adequate for North America, but quite inadequate for the Kenya agro-ecosystem, and they were highly susceptible to both rust and anthracnose.

False Erosion

Finally, there can be a *false erosion* of horizontal resistance. This can result from sloppy experimental work, inaccurate measurements, mixing of labels, and so on. It can then transpire that a genetic line has rather less resistance than was first thought. This happened typically with some new sugarcane cultivars that had not been adequately tested for resistance to mosaic virus (Chapter 22). These cultivars were mistakenly believed to be resistant. When they later became severely diseased with mosaic, in farmers' fields, some scientists concluded, quite incorrectly, that there had been a breakdown of vertical resistance.

A false erosion of resistance can also result from psychological errors. For example, there may be a cultivar that is the standard of resistance, against which all other lines are compared. As resistance accumulates in the entire breeding population, during a number of years of breeding, the resistance of that standard cultivar *appears* to decrease, relative to the population as a whole. This is obviously an illusion, but it can be an alarming one, if its cause is not understood.

Chapter 14

Three Sources of Error

There are three phenomena, called parasite interference, population immunity, and biological control, which all suggest that considerably *less* horizontal resistance than we may think will achieve a satisfactory control of many crop parasites.

Parasite Interference

It was mentioned earlier (Chapter 1), that there are lies, damn lies, and statistics. Although statistics is a perfectly respectable branch of mathematics, it can be misused and abused. In the study of crop parasites, statistics has been misused and, as a consequence, it has caused a level of confusion and uncertainty that boggles the imagination. This is not the fault of the statistics. It is the fault of the scientists who misused these mathematical techniques.

When I was in my first job, in Africa, statistically controlled field trials were all the rage. Various ‘treatments’, such as the amounts and kinds of fertiliser, had to be laid out in carefully measured field plots which were both replicated and randomised. And there had to be ‘local control’, which involved untreated plots for purposes of comparison. The mathematics were quite complicated, and they were the bane of non-mathematical crop scientists. This was in the days before computers, when calculating machines were mechanical, would do only simple arithmetic, and had to be cranked by hand.

The mathematics had been worked out during the 1930s, mainly by the British mathematician, R.A. Fisher, and the standard text was a book by Fisher and Yates. This statistical methodology was excellent for investigating agronomic variables, such as the spacing between the plants, or the yields of different cultivars, but it was a source of major error when it came to crop pests and diseases. This was first recognised by J.E. Vanderplank who called it the ‘cryptic error‘ in field trials. The error occurred because crop parasites are mobile. They can move from one field plot to another, and this phenomenon is now called inter-plot interference, or parasite interference.

This parasite interference can easily increase the levels of parasitism in test plots by a hundred-fold, and sometimes by as much as a thousand-fold. This happens because the ‘control’ plots, included for purposes of comparison, contain plants that are highly susceptible, and highly parasitised. These parasites then move into neighbouring plots in huge numbers.

Perhaps the most dramatic example of parasite interference is seen in the small plots used by wheat breeders. These plots consist of only a few plants taken from the seeds of one head, and each plot consists of a single row of wheat. (This technique, called ‘family selection’, or ‘head to row’ selection, is genetically excellent but epidemiologically disastrous). One row of vertically resistant wheat might have several very susceptible plots on each side of it. Invading rust spores cannot match the resistant wheat. They can only produce minute, hypersensitive flecks that indicate non-matching allo-infections. But these flecks occur in their millions. There can be so many of them that the resistant wheat appears diseased, and the wheat breeders warn that this phenomenon must not be mistaken for true disease.

Parasite interference is responsible for three different kinds of error. The first error concerns vertical resistance. It will be observed that parasites moving from one field plot to another are allo-infecting the new plot. If the receiving plot has an unmatched, and functioning, vertical resistance, the interference will have no effect at all, other than the possible hypersensitive flecks mentioned above. The function of vertical resistance, after all, is to control allo-infection. Consequently, under the conditions of maximum interference, which occur typically in pedigree breeders' small screening plots, vertical resistance looks perfect, in the sense that there is no parasitism. But this perfection is an illusion, because the temporary nature of the vertical resistance, and a related low level of horizontal resistance, are not apparent. This illusion has been deceiving Mendelian plant breeders for the whole of the twentieth century.

The second error concerns horizontal resistance. This kind of resistance can be seen and measured only after vertical resistance has been matched. If the matched plot in question has the level of its parasitism increased by, perhaps, one hundred-fold, or even one thousand-fold, because of parasite interference, the horizontal resistance will look terrible. Under these circumstances, Mendelian breeders can hardly be blamed if they conclude that horizontal resistance is useless or, even, that it does not exist. Far more important is the fact that this level of horizontal resistance may be entirely adequate to control the parasite completely, when it is employed in farmers' fields that are free from interference.

No one can be blamed for not appreciating this, when gazing at those frightful looking pedigree breeders' plots, with their parasitism increased several hundred-fold because of parasite interference. But it is sad to think that countless numbers of good lines, with perfectly adequate levels of horizontal resistance, have been needlessly thrown out in the past, because of the entirely false appearance of susceptibility produced by parasite interference.

The third error concerns the use of crop protection chemicals. If test plots sprayed with a pesticide suffer parasite interference, they will need more pesticide than if there were no interference. Recommendations to farmers, concerning pesticide use, are often based on erroneous field trials. This error occurred so commonly during the 1950s and 1960s that no one can be quite sure how excessive our use of crop protection chemicals was during that period. Indeed, no one is quite sure how excessive our current use of crop protection chemicals may be, because of this error in field trials. It is an error that the people who sell crop protection chemicals are not keen to correct.

To sum up, parasite interference has misled crop scientists in three ways. Interplot interference has glamorised vertical resistance, far beyond its merits. Second, interplot interference has obscured the value of horizontal resistance to such an extent that, for years, most crop scientists never realised that this kind of resistance even existed. And, finally, it has repeatedly produced false results in pesticide spray trials and, as a result, we probably use more crop protection chemicals than are strictly necessary.

Population Immunity

Population immunity is a term coined by J.E. Vanderplank to describe the fact that a plant population may be effectively immune to a crop parasite, even though the individuals in that population are less than immune. At first sight, this appears to be arrant nonsense but, in fact, it really happens, and it is quite important. This effect also suggests that, when breeding plants for horizontal resistance, we probably need considerably less resistance than we may think.

Population immunity is a consequence of population growth. Unlike an individual's growth, a population's growth can be positive or negative. If there are more births than deaths, the population size is increasing, and its growth is described as positive. If the births and deaths cancel each other out exactly, the population size is unchanging, its growth is zero. And if there are more deaths than births, the population size is decreasing, and its growth is negative.

Consider the population growth of a crop parasite. If the parasite population growth is positive, this means that, on average, each parasite individual spawns more than one new individual. In the case of an *r*-strategist parasite, each individual may spawn very many new individuals, in a very short time, and the positive population growth is then so rapid that it becomes a population explosion.

Now suppose that the crop in question has a level of horizontal resistance that severely restricts the reproductive rate of the parasite. On average, each parasite individual spawns only one new individual before it dies. The parasite population growth is then zero. Finally, suppose a slightly higher level of horizontal resistance. On average, each parasite individual now spawns less than one new individual. In practice this means that most individuals spawn one new individual, but a few spawn none at all. The parasite population is now decreasing. Its population growth is negative.

An epidemic can develop only when the parasite population growth is positive. And a damaging epidemic can develop only when the population growth is strongly positive. If the parasite population growth is zero or negative, there is no epidemic, and the host population is effectively immune, even though the individuals in it are less than immune. This is population immunity.

One of the dangers of measuring horizontal resistance in the laboratory is that population immunity cannot easily be taken into account. A level of horizontal resistance that looks like susceptibility in the laboratory may prove to be population immunity in farmers' fields. For this reason, laboratory measurements of horizontal resistance should be *relative* measurements. That is, the level of resistance should be described as being either higher or lower than that of other cultivars of known field performance.

While discussing population immunity, it is perhaps worth making the point that both vertical resistance and crop protection chemicals increase the *death rate* of the parasite, while horizontal resistance reduces the *birth rate*. Reduction of the birth rate is a more effective control method than increasing the death rate, because unborn parasites never take nutrients from the host. Dead parasites may have stopped taking nutrients from the host, but they may have already taken a lot before they died.

Biological Control

“Little fleas have lesser fleas, upon their backs to bite ‘em”. Plant parasites are ‘little fleas’ and they have their own ‘lesser fleas’ which are hyper-parasites and predators which eat them, and keep their numbers down. Many parasites also have competitors, which are harmless on our crops, but which also help to keep the parasite numbers down. There may also be antagonistic micro-organisms which restrict the parasite population growth. The term ‘biological control‘ refers to the overall effect of these various biological control agents. It is sometimes possible to vanquish a crop parasite completely by the careful manipulation of its natural enemies, its parasites, predators, competitors, and antagonists.

However, in modern crop husbandry, the opposite effect is far more common, and far more important. This opposite effect is the loss of natural biological controls because of the excessive use of crop protection chemicals, which also kill hyper-parasites, predators, competitors, and antagonistic organisms. There is apparently no recognised word or term that describes this loss of biological control, and this is an indication of how little its importance has been appreciated. We might, perhaps, call it *biological anarchy*.

Biological anarchy occurs most commonly with the insect pests of crops, but the effect can probably be detected, to a greater or lesser extent, with all categories of plant parasite that have been treated with chemical pesticides. There is a clearly established case, for example, with coffee berry disease (Chapter 21). This microscopic fungus is parasitic only on coffee berries. Between berry-bearing seasons, it resides harmlessly in the bark of the coffee tree, constituting about 5% of the innocuous, microscopic, bark inhabitants. When coffee trees are sprayed with a fungicide to control coffee berry disease, most of these competing bark inhabitants are killed, and the coffee berry disease fungus population then increases to occupy most of the bark. In the next season, the severity of the disease is increased accordingly.

An example of aphid reproduction might also be useful. Suppose that every aphid has ten offspring, and that all the offspring survive to produce ten more offspring in each generation. After ten generations, there will be 10^{10} aphids (i.e., 10,000,000,000). Now suppose that ladybirds are eating half of the aphids, so that only five of each aphid's offspring survive to reproduce in each generation. After ten generations, there will be 5^{10} aphids (i.e., 9,765,625) which is approximately one thousandth of the earlier total. And, if only one aphid survives to reproduce in each generation, after ten generations there will be only one aphid. In practice, ladybirds really do eat a lot of aphids. But if all the ladybirds are killed by an insecticide, and all the aphids are resistant to that insecticide, there will be many more aphids than if the insecticide had never been used in the first place.

The loss of biological control is possibly at its most conspicuous in the cotton crop. Cotton is a ‘political’ crop, in the sense that it is excessively regulated by marketing boards, growers’ associations, banks, chemical corporations, and departments of agriculture. Very often, the farmer himself is given no choice in the use of crop protection chemicals. He is compelled to conform with general regulations which ensure that all the cotton crops of an entire region are treated in the same way. Because high yields and high quality are so important to the various regulating bodies, the tendency is always to use too much pesticide, rather than risk using too little. This tendency has been dubbed the ‘pesticide overload‘, or the ‘pesticide over-kill‘. The immediate effect of the overload is a control of the cotton pests, but the long-term effect may be an increase in pests, because of the biological anarchy. This, in its turn, often leads to a further increase in the pesticide over-load.

In fact, there are two biological factors to be taken into account. The first is biological anarchy, the loss of biological control, because of the destruction of natural predators, hyper-parasites, competitors, and antagonistic organisms. The second factor is that a crop parasite may develop a new strain that is less affected, or even completely unaffected, by that pesticide. This is an effect closely similar to the failure of vertical resistance. The farmers must then use a different pesticide, and there is then a ‘boom and bust‘ in pesticide effectiveness which is likely to be repeated, again and again. In the meanwhile, the population explosion of a new pesticide-resistant strain of a major pest is liable to become worse, because (i) it is unaffected by the old pesticide, (ii) a new pesticide is not immediately available, and (iii) all the parasite’s natural enemies have been destroyed by the pesticide overload, and there is biological anarchy.

Very minor parasites of cotton are liable to become major parasites, when there is biological anarchy, because their natural enemies have been destroyed. The classic example of this was in America, and was the tobacco bud worm, which normally never parasitises cotton. But, under the influence of the pesticide overload, it became a major pest of cotton, because it was unaffected by all the available crop protection chemicals, and its natural enemies had all been killed.

This biological anarchy is a general effect which must be assumed to occur in most crops that are treated with chemical pesticides. Consequently, in many crop pathosystems, the biological controls are no longer functioning, or they are functioning at a reduced efficiency. This is the basis of the concept of integrated pest management (IPM) which is a crop parasite control technique that depends heavily on the restoration of biological controls. Pesticide use is minimised, so as to interfere with biological controls as little as possible. IPM can be dramatically successful in crops that have been subjected to a serious pesticide overload. The very success of IPM is an indication of how important this loss of biological controls, this biological anarchy, can be.

The overall effect of biological anarchy is that many crop parasites become much more serious than they need be. This has two important consequences which must be emphasised. First, when a pesticide-resistant strain of the parasite appears, it is likely to behave with a ferocity that would be impossible if its natural enemies were keeping its numbers down. This means that a new pesticide-resistant strain of a parasite is likely to be far more damaging than if we had never used the crop protection chemicals in the first place. And, if we decide to abandon the use of crop protection chemicals in a particular crop, we shall have to endure serious, although rapidly diminishing, crop losses for several seasons until such time as the natural biological controls are fully restored.

Second, if we want to measure the level of horizontal resistance in potential new cultivars, we must do this under conditions in which there is no biological anarchy. If we measure horizontal resistance under field conditions, in which the parasite has considerably increased numbers, because of biological anarchy, that level of resistance will appear inadequate. But, once the biological controls are restored, that same level of resistance might be high enough to control the parasite completely. In practice, this means that field measurements must be made in quite a large area that is free of crop protection chemicals. It may not always be possible to find such an area. The only alternative would then be to use laboratory measurements which, once again, must be relative measurements. A closely similar problem is in trying to assess how much horizontal resistance we are likely to need in a breeding program. To do this, we must use a parasite whose biological controls are functioning to their full extent.

Once again, we may need much less horizontal resistance than we may think, in order to control crop parasites in a pesticide-free agriculture. In fact, this is a reciprocal effect. *The best way to restore lost biological controls is to use horizontal resistance. And the best way to maximise the effects of horizontal resistance is to restore lost biological controls*.

It was mentioned earlier (Chapter 9) that the use of horizontal resistance will lead to a very high frequency of parasitism, but a negligible injury from parasitism. It is doubtful if even artificially high levels of horizontal resistance will ever provide an absolute control of a crop parasite, in the sense that the parasite disappears completely. But this is a good thing. If we are to maintain a population of hyper-parasites and predators for the purposes of biological control, we must also maintain a small population of crop parasites for them to feed on. This small population will exist because even the maximum levels of horizontal resistance will always permit the parasite to cause minor blemishes that are economically unimportant, but ecologically crucial. These minor blemishes will maintain both the crop parasites, and the agents of their biological control.

These three factors of parasite interference, population immunity, and biological control, suggest that levels of horizontal resistance that appear to be quite inadequate at present, will achieve a control of many crop parasites that, for all practical purposes, is effectively complete.

Chapter 15

The Disadvantages of Crop Protection Chemicals

At this point, it might be appropriate to take a cool look at crop protection chemicals, quietly and objectively, and free from the rhetoric of some of the more passionately involved activists. There is one over-whelming advantage, and there are seven quite serious disadvantages, to the use of crop protection chemicals.

The overwhelming advantage is that we still produce enough food to feed everyone in the world. This achievement depends, beyond question, on using crop protection chemicals. If we were to stop using crop protection chemicals, completely, tomorrow, hundreds of millions of people would soon die of starvation. Much as we may hope to abandon the use of these chemicals, we cannot do it overnight. It will require at least a decade to produce a significant alleviation in pesticide use, and probably several decades to achieve the maximal replacement with horizontal resistance. This is fact. We have to recognise it and accept it.

We must recognise also that the efficiency and safety of crop protection chemicals has been improving steadily. Gone are the days when we treated our crops with compounds of lead, arsenic, mercury, and cyanide. After World War II, DDT became available and it had to be applied to crops at a rate of 2kg/ha. Later, the much less hazardous synthetic pyrethroids were developed, and these need be used at only one twentieth of the DDT rate, namely at 0.1kg/ha. A relatively new insecticide called aldicarb need be applied at a rate of only 0.05kg/ha. In other words, it is forty times more effective than DDT, and it has less hazardous side-effects. Much as we may dislike the use of crop protection chemicals, we must recognise this general trend of improvement, which is likely to continue.

Readers who would like to know more about pesticide use are advised to study *The Pesticide Question*, edited by Pimental and Lehman, 1993 (See References).

Let us now consider the seven disadvantages of crop protection chemicals, and compare them with the use of horizontal resistance.

Cost

Crop protection chemicals are expensive, both to buy, and to apply. But there is no question that they are economic, and that they pay for themselves, usually 4-5 times over, in increased yields, and an increased quality of crop product. When I was a child, for example, before the days of DDT, it was quite common to find a grub inside a half-eaten apple. This can be a revolting experience, particularly if half the grub appears to be missing.

The cost of these crop protection chemicals, and their application, is passed on to the consumer. In comparison, the use of resistant cultivars costs nothing and, if the same effect could be achieved with resistance, the costs of buying and applying the pesticide would be eliminated.

In practice, the use of a resistant cultivar is not necessarily cost-free. That resistant cultivar may have a lower yield, or a lower quality of crop product, even when parasite-free, than the susceptible cultivar does when it is treated with crop protection chemicals. Furthermore, in some crops (e.g., apples, and the grubs of the codling moth), it may prove impossible to achieve adequate levels of resistance. But, provided all other things are equal, crop protection chemicals are expensive, while the use of horizontal resistance costs nothing.

Repetition

Second, the effect of a pesticide application is usually lost quite quickly, and the pesticide must then be applied again. Most crop protection chemicals have to be re-applied every 10-20 days, but some have to be applied more frequently than that. This is partly because the pesticide tends to be washed off in rain, partly because it is non-persistent (i.e., it decomposes), and partly because the new parts of rapidly growing plants require additional protection. In comparison, vertical resistance usually lasts for several years, and horizontal resistance lasts for ever.

Breakdown

Third, many crop protection chemicals behave like vertical resistance, in the sense that the parasite is able to produce a new strain that is unaffected by that chemical. DDT-resistant houseflies are the classic example. The use of that pesticide must then be abandoned, and it must be replaced with a new one. This has happened so frequently with modern crop protection chemicals that many people now believe that there is no limit to the capacity for change of our crop parasites.

In practice, this accumulation of pesticide resistance in crop parasites is often quantitative. This means that the recommended rates of pesticide application become inadequate. These rates are then increased but, in their turn, these too become inadequate. This gradual increase in the use of a pesticide can continue until the rates of application are absurd. This quantitative loss in effectiveness is a prime cause of pesticide overload.

Some crop protection chemicals have remained effective for a century or more without any suggestion of resistant strains of the parasite appearing. This is true of Bordeaux mixture, for example, as well as natural insecticides such as rotenone and pyrethrins. Nevertheless, most synthetic crop protection chemicals eventually succumb to new strains of the parasite, either qualitatively or quantitatively. Vertical resistance also breaks down to new strains of the parasite, but horizontal resistance does not.

Expertise

Fourth, most crop protection chemicals require considerable expertise in their use. This expertise is required first of the person who decides which chemical should be used. All too often, this decision depends on a salesman, and pesticide use is then governed, at least in part, by irrelevant factors, such as advertising and sales skills. The same criticism applies to the rates of application, which are often too high, or too frequent, because of an over-zealous sales pitch. Expertise is also required by the farmer himself, and his employees, if the pesticide is to be fully effective, and the safety precautions are to be properly implemented. All too often, this expertise is either lacking or inadequate. It need scarcely be added that, at the farmer level, the control of parasites by the use of horizontally resistant cultivars requires no expertise whatever.

Hazards

Fifth, many crop protection chemicals are hazardous, either to people, or to the environment, or both. The hazards to the consumers of crop products are often slight or insignificant, but they concern very large numbers of people. The dangers are more keen for the much smaller numbers of people who actually work with these chemicals. These are mainly agricultural workers, and the dangers can become serious, even acute, when safety precautions and supervision are inadequate.

However, it is becoming apparent that the greatest danger may be to pregnant mothers and growing children. There have been a number of very disturbing developments in human health which coincide very closely with the expanded use of crop protection chemicals. Obviously, correlation is not proof, but crop protection chemicals remain high on the list of suspects. These health developments appear to result from damage to the unborn foetus, and to young children. It seems that a developing foetus has certain ‘windows of opportunity’ when a toxin in the mother’s bloodstream can do irreversible damage. However, this damage may not become apparent until years later and, for this reason, it is extremely difficult to establish a causal relationship. Similarly, young children eat 3-4 times as much food per kilogram of bodyweight as do adults, and they drink 4-5 times as much water. This means they are absorbing many more toxins, per kilogram of bodyweight, as do adults, and they are more susceptible than adults to these toxins because all their tissues and organs are actively growing.

These disturbing developments affect the brain, the immune system, and the reproductive system. The hyperactivity attention deficit syndrome in school children is becoming distressingly common, with a reported two million children affected in the United States alone. So too are asthma and allergies that are occasionally life-threatening. And sterility problems also appear to be increasing. There seems to be little doubt that expecting mothers and growing children should be fed exclusively with organic food.

The hazards caused by crop protection chemicals to the environment are many and various. The best known dangers are the killing of non-target animals, such as birds and pollinating insects. Occasionally, there is a risk of irreversible damage, when a rare species is threatened with extinction. Some animals are particularly sensitive to the presence of crop protection chemicals. For example, there is now a serious decline in the world population of frogs, and several rare species appear to have disappeared, probably for ever. Amphibians, such as frogs, have skin that is much more absorbent than that of other land animals, and they are more susceptible for this reason. Other species suffer from the side-effects of crop protection chemicals. For this reason there has been a dramatic decline in the numbers of insect-eating birds. Butterflies, which were so common, and so beautiful, when I was a child, are now rare. Usually, pesticide hazards are not discovered until considerable environmental damage has been done. There is then, quite rightly, a public outcry, and the difficult task of crop parasite control becomes even more difficult.

Sadly, many of these hazards are not due to the pesticide itself, so much as to its misuse. DDT, for example, was an excellent replacement for the old compounds of lead, arsenic, mercury, and cyanide. It was also incredibly cheap. Unfortunately, it was applied to agricultural crops with such abandon, and in such enormous quantities that there was serious environmental damage. It must be remembered, however, that not all crop protection chemicals are hazardous. To the best of our knowledge, a century of use of Bordeaux mixture has not harmed anyone or anything.

One again, a comparison with horizontal resistance is illuminating. Horizontal resistance is absolutely safe, both to people and to the environment.

Destruction of Biological Controls

Sixth, the routine use of many crop protection chemicals has led to the debilitation, or even the local elimination, of biological control agents. This has made many crop parasites more serious, and more difficult to control. This biological anarchy has already been discussed (Chapter 14) and it is difficult to assess its overall importance. The best indication comes from the fact that the many successes of integrated pest management (IPM) depended on a restoration of biological controls that were lost because of pesticide use. This damage to biological control may turn out to be a much more important side-effect of pesticide use than many crop scientists currently realise. It is needless to add that the use of horizontal resistance does not damage biological controls. Indeed, it is the best means of restoring them.

Incomplete Effectiveness

Lastly, the effectiveness of crop protection chemicals is far from complete. As we saw earlier, we are still losing about 20% of pre-harvest crop production because of parasites, in spite of the massive use of crop protection chemicals costing billions of dollars each year. In food crops alone, this pre-harvest loss is enough to feed about one billion people. So what is wrong? Is it possible that our farmers are using too few crop protection chemicals, at too low a concentration, too infrequently? Is it possible that our farmers are applying these chemicals in the wrong way, at the wrong time, or too inexpertly? Is it possible that the crop protection chemicals themselves are not much good? Or is possible that crop protection chemicals are not the answer anyway? If crop protection chemicals are not the answer, there is really only one alternative. Guess what it is.

Chapter 16

So How Did Things Get So Out of Hand?

When I was an undergraduate, in the late 1940s, we were actually taught that *all* resistance to crop parasites was temporary resistance, and that *all* parasite resistance in plants was bound to fail sooner or later. Our teachers seriously questioned the wisdom of breeding plants for resistance, and of constantly trying to keep "one jump ahead of the parasite". They told us about some recent and dramatic crop losses resulting from failures of resistance. They suggested that we would do better to study crop protection chemicals. They quoted some remarkable new chemicals that were being discovered. One of them was very new, and very exciting. It was di-chloro, di-phenyl, tri-chlor-ethylene, commonly called DDT. Its Swiss discoverer, Dr Paul Müller, had just been awarded the 1948 Nobel Prize for Physiology or Medicine, because DDT was so effective in killing mosquitoes for the control of both malaria and yellow fever, to say nothing of killing houseflies for the control of both typhoid and cholera, and fleas for the control of bubonic plague. These were just some of the human diseases. There were many insect-borne animal diseases as well, not to mention the innumerable crop pests, that could be controlled with this chemical. DDT was also safe, or relatively so, when it is remembered that commonly used insecticides in those bad old days included lead, arsenic, mercury, cyanide, and the fumes of burning sulphur. Furthermore, DDT was incredibly cheap. There was even talk, in those days, of combining it with paint, to produce insect-free houses.

Obviously, our teachers said, the future lay with chemicals, not with host resistance. There was nothing special about this teaching. It was typical of its time, and what is often called ‘state of the art’. It also represented the ‘cutting edge of research’, and the ‘received wisdom’. It is perhaps worth adding that modern scientists often debate which of two chemicals has saved more human lives. Is it DDT, through the control of malaria, yellow fever, typhoid, and cholera, or is it penicillin?

It should also be mentioned that, in spite of the received wisdom in the 1940s, there are a few examples (a mere half dozen) of vertical resistance which has proved durable over many decades.

Thus, wheat in Canada has durable vertical resistance to a disease called stem rust (*Puccinia graminis tritici*), and tomatoes in the United States have durable vertical resistance to a wilt disease (*Fusarium oxysporum* f.sp. *lycopersici*). The reasons for this durability are too complex to discuss here, but the durability itself merits two comments. First, if we can demonstrate that a vertical resistance is durable then, obviously, we should use it. However, we should note also that vertical resistance that is durable in one part of the world is usually temporary resistance in another.

Second, these few examples of durable vertical resistance have done much to mislead the Mendelians, and to make them hope that many other examples of single-gene resistance would also prove to be durable. It was perhaps this misplaced hope, as much as any other factor, that persuaded the Mendelians to persist so doggedly, and for so long, with the breeding of plants for temporary resistance.

Because of the ‘Red Queen‘ effect (Chapter 11), plant breeders have been abandoning *vertical* resistance breeding ever since World War II. What they should have done was to consider the use of horizontal resistance. But, at that time, horizontal resistance was so little understood, and its value was so doubted, that breeding for it appeared to be both a daunting task, and a futile task.

We must recognise also that the effects of Bordeaux mixture in the 1880s, and of DDT in the 1940s, were stunning. Crop scientists were completely dazzled. As more and more of them began to abandon vertical resistance breeding, they chose crop protection chemicals because they were so dazzled. In comparison, there was nothing very dazzling about horizontal resistance.

We should remember too that, during the whole of the twentieth century, crop scientists have been faced with the world food problem. During this one century, the world population of people increased from about 1.5 billion to six billion. With the human population increasing so fast, crop scientists were compelled to increase agricultural production equally fast. Much of that increase came from putting more land under the plough. Nevertheless, it was production, *per se*, that was given the first priority in crop science. The manner of that production was a secondary consideration.

The corollary of this situation must also be recognised. There has been some truly remarkable progress in improving the yield, quality, and agronomic suitability of crops during the twentieth century. The human population has increased dramatically, since the Mendelian school came into existence, yet we still produce enough food for everyone. The famines we have witnessed in recent years are due to local disasters, and to political incompetence, even malice, rather than to a world shortage of food. The success of crop science in feeding the world has been impressive. The complaint of this book is not about the amount of food we produce, so much as the fact that, in the field, we lose about one fifth of our production to crop parasites, in spite of an extravagant use of crop protection chemicals.

A complete lack of public interest, combined with a largely incomprehensible, technical jargon, has made crop science a closed shop, almost a secret society, for most of the past century. What crop science needs now is a healthy dose of public scrutiny. And that is one of my most carefully considered objectives in writing this book.

Chapter 17

Cultivar Cartels

There are some powerful vested interests that are determined to maintain the *status quo* concerning crop breeding and crop pesticides. These vested interests are both scientific and commercial.

Crop scientists have ignored horizontal resistance, so consistently, and for so long, that many of them are now reluctant to admit that it may constitute a superior alternative. So long as it was believed that there was only one kind of resistance to the parasites of plants, it was possible to blame nature for the failure of resistance breeding. If a new strain of the parasite appeared, and the resistance failed, that was clearly the fault of Mother Nature, not of the scientists. If a genetic source of resistance could not be found, and the breeding could not even be started, that too was the fault of Mother Nature.

In these circumstances, resistance breeding was clearly an unprofitable business. And, it seemed, the only alternative was to use crop protection chemicals, apart from a few subsidiary pest control methods such as crop rotation, and the burning of crop residues. (Modern entomologists also have some neat tricks to induce sterility, such as swamping the female part of a population of insects with sterile males, or luring all the males into traps with sex attractant chemicals. These artful dodges are occasionally very effective, but only occasionally.)

Against the apparent failure of resistance breeding, we must also recognise the success of crop protection chemicals. If you happen to believe that vertical resistance and crop protection chemicals are the only alternatives, then it is reasonable to choose success over failure, and crop protection chemicals over vertical resistance breeding. Nonetheless, crop scientists have known for decades that there was a third alternative, now called horizontal resistance. It was wrong of them to ignore it, and it is now difficult for them to admit this. Hence their vested interest in the *status quo*.

The large breeding institutes that produce vertically resistant cultivars that are 'big space, high profile, small time' also have vested interests in the *status quo*. This is particularly true of the dwarf rices and wheats produced by the International Research Centres.

Various seed producing industries have commercial vested interests. The most prominent of these is the certified potato seed industry, although some even more prominent ones are beginning to appear with the new GMOs (genetically modified organisms), described in a moment. Highly specialised farmers produce crops solely for seed purposes, and these crops are approved by government inspectors who certify them free of various parasites. The inspectors usually certify them in other ways also, such as trueness of variety, and purity of variety. Ordinary farmers then buy this certified seed for planting their crops. But this certified seed is expensive. With potatoes, for example, the cost of certified seed is usually the biggest single input in commercial potato cultivation. About a century of advertising by the seeds industry has convinced modern farmers to buy new seed for every crop. Given good horizontal resistance, much of this expense is unnecessary.

The producers of certified seed positively resent any suggestion of new resistant varieties that can be grown from the farmer's own harvests, without any need of seed certification. These producers of certified seed actually want susceptibility to seed-borne parasites. Without it, there would be little need for their expensive seed, certified free from parasites.

There can be no doubt that resistance which was complete, comprehensive, and durable, would largely destroy these specialised seed industries. Indeed, we are forced to conclude that these seed industries would never have been born, but for the susceptibilities which make seed certification necessary. This need for certified seed of cultivars that are susceptible, is also a clear indication of the overall failure of resistance breeding. (If the need for certification for freedom from diseases were to disappear, there would still be a need for seed certified for both identity of variety, and purity of variety. But the seed industries would be greatly diminished.)

A second source of commercial vested interests is even more important. This lies with the manufacturers of crop protection chemicals. These chemical corporations have no intention of promoting horizontal resistance, which threatens a major reduction of their market. Indeed, these chemical corporations are apparently doing the very opposite. They are buying up plant breeding institutes, presumably with a view to controlling plant breeding policy. And they are buying up seed production and marketing organisations, presumably with a view to controlling the crop varieties that are available to farmers. We may be forgiven for assuming an ulterior motive, and for suspecting that these varieties are likely to have very high yields, and a high quality of crop product, but that they are also likely to have very high susceptibilities to various parasites. They would then require large amounts of crop protection chemicals for their successful cultivation. What better way could there be of guaranteeing the market for crop protection chemicals?

Indeed this situation is occurring already. Farmers is western Europe now routinely spray their wheat crops with crop protection chemicals. This is a very recent, and very disturbing development. It arose because the European wheat breeders largely abandoned resistance breeding. They produced new wheat cultivars that have very high yields, but that are also susceptible to various wheat parasites. The spraying process requires a tractor to be sent through the wheat, and the tractor wheels flatten some of the wheat, producing characteristic ‘tramlines‘ that can be seen from the air. However, the loss of this wheat in the tramlines, and the costs of spraying, are more than made up by the increased yields resulting from the use of crop protection chemicals.

The pesticide manufacturers often refer to their take-overs of plant breeding and seed production organisations as “diversification”. But appearances are against them, and their apparent desire to control plant breeding, and the cultivars available to farmers, is highly suspect. There is not the slightest doubt that they positively need susceptible cultivars, which are essential if there is to be a large market for crop protection chemicals.

A third source of commercial vested interests lies in GMOs such as patented cultivars carrying the insecticidal *Bt* gene, or the glyphosate-resistance gene. In order to purchase seed of these cultivars, farmers are often required to forfeit their rights to the ‘farmer’s privilege’. The cost of this seed is so high that much of the profit from food production is taken from the farmer, and goes to the seed producer.

The pesticide industry is a powerful, self-interested group of multi-national manufacturers that has the financial resources necessary for intense political lobbying, widespread commercial advertising, and the establishment of powerful cartels in farmers’ seeds. There appears to be only one possibility of frustrating this monopolistic development. And that is what this book is all about.

Part Two: Examples

Reiteration

Readers who chose to skip most of Part One may care to have a brief reiteration. There are two kinds of resistance to crop parasites, called vertical resistance and horizontal resistance. Vertical resistance operates as a system of locks and keys and, like any system of locking, it requires a diversity of locks and keys. Its function is to control an epidemic in a population of plants, and it does this because relatively few parasites have a key that fits the lock of the host plant they are trying to infect. Horizontal resistance is a second line of defence. It operates after a vertical resistance lock has been unlocked by a parasite, and its function is to control the actual parasitism within an individual plant.

For most of the twentieth century, crop science has been dominated by the Mendelian school of genetics, and by the use of the locks of vertical resistance. Unfortunately, the Mendelians employed this resistance on a basis of uniformity, with every plant within a crop variety having the same lock. This uniformity is the equivalent of every door in the town having the same lock, and every house owner having the same key, that fits every lock. This crop uniformity explains why the resistance of that variety is liable to fail when a matching strain of the parasite appears. Under these circumstances, vertical resistance is temporary resistance. For many years, crop scientists believed that this was the only kind of resistance available to them.

Since World War II, the spectacular promise of chemical pesticides, combined with the repeated failures of vertical resistance, persuaded crop scientists to favour crop protection chemicals over resistance breeding. They chose this course under the extreme pressure of human population growth, which led to a comparable growth in the world food requirements.

During all of this time, horizontal resistance was neglected to the point of being almost totally ignored. It is still being neglected. Nevertheless, it promises to solve the problem of crop parasites which currently destroy about one fifth of all crop production in spite of an extravagant use of crop protection chemicals. Properly utilised, horizontal resistance could provide us with a largely pest-free agriculture, and a largely pesticide-free agriculture as well.

Part Two of this book attempts to substantiate this claim, by providing some examples of how horizontal resistance can do just this.

(Scientific readers who require a comprehensive scientific review of breeding work on horizontal resistance are advised to see Simmonds, 1991; *Biol. Rev*., **66**: 189-241).

Chapter 18

A Short History of Potato Parasites

Introduction

When the Spanish first introduced potatoes (*Solanum tuberosum*) to Europe, from the New World, in the sixteenth century, this crop was little more than a botanical curiosity. This was because potatoes were tropical plants that were acclimatised to the short days of equatorial regions. Consequently, they would not form tubers during the long days of a European summer, and the delayed crop would be ruined by frost before it was mature. Ireland was the first country in Europe to cultivate potatoes on a large scale because it has a very moist and mild climate, with little frost. For this reason, potatoes are often called the Irish potato, among English-speaking people, to distinguish them from the very different, tropical, sweet potato (*Ipomea batatas*).

About two centuries of largely unconscious selection by European horticulturists, assisted no doubt by some natural selection, eventually produced new, day-neutral varieties of potato that were insensitive to day-length, and were suitable for cultivation during the long summer days of Europe. The original potatoes were ‘short-day’ plants in which tuber-initiation would occur only during the twelve-hour days of late September. These tubers would usually be destroyed by winter frosts before they were ready for harvest. The newly modified potatoes also had improved agronomic characteristics, such as larger tubers on shorter stalks. These genetic changes were completed in the eighteenth century, and potatoes quite quickly became a major food crop.

There were two reasons for this rapid rise in popularity, apart from the fact that potatoes are an excellent food. The first was the industrial revolution, and the growth of urban populations living in manufacturing towns. These people needed cheap food and, in those days, potatoes were much cheaper than bread. Bread was expensive because of protective tariffs on wheat imports, imposed by European governments to encourage their own farmers. Wheat also had to be harvested by hand, because this was before the days of mechanical reapers. Because labour was always in great demand at harvest time, it was both scarce and expensive. This set an absolute limit to the amount of wheat that a country could produce.

The second reason for the popularity of potatoes was that much of Europe has soils that are unsuitable for growing wheat, and the people who lived in these areas traditionally grew rye, and lived on rye bread. Ireland cannot easily grow wheat because its climate is too wet, and this was another factor contributing to its adoption of potatoes.

Today, rye bread is something of a luxury but, in those days, it was a sign of poverty. This was because rye has a disease caused by the fungus *Claviceps purpurea*, which produces poisonous granules called ergots. The ergots would be milled with the rye, to produce poisonous flour, and poisonous bread. The poison causes a disease known as ergotism, or ‘Saint Anthony’s Fire‘, which results from a restriction in the circulation of the blood. Mild cases produced hallucinations and cramps, but more severe poisoning would lead to gangrene, loss of limbs, abortion in pregnant women, and death.

At that time, the cause of the poisoning, which varied greatly in severity from year to year, was not known, although its association with rye bread was recognized. When potatoes became available as an alternative food, they quickly became popular in the rye growing districts, and the widespread outbreaks of ergot poisoning became a thing of the past. To this day, the old rye districts of eastern Germany, Poland, and western Russia still have the highest rates of potato consumption in the world.

Potato Blight

In the 1840s, there was a major tragedy. There were some rotten potatoes in the galley of a ship travelling from Mexico to New York. These potatoes were carrying a fungal parasite of wild Mexican potatoes. This parasite has the ugly name of *Phytophthora* (pronounced fie-TOFF-thora) *infestans*. Shortly after this, the potatoes in the galley of a ship travelling from New York to Europe also went bad, and this potato parasite was introduced to the Old World. The potatoes of Europe had evolved in South America, far away from Mexico, and they had never encountered this fungal parasite before. Accordingly, it was a ‘new encounter’ disease.

The wild potatoes of Mexico occur North of the equator, at altitudes of about 8,000 ft., and they are separated from the highlands of South America by both sea, and a belt of lowland, tropical jungle. Botanically, the two areas are entirely isolated from each other. Consequently, the South American potatoes in Europe had little resistance to this new encounter Mexican parasite, and a really dreadful new plant disease appeared. This was the first time in history that anyone had seen an exceptionally bad plant disease. After a few days of cool, moist weather in high summer, the green potato fields of Europe would turn into a black stinking mush, with not a speck of green to be seen anywhere. When the tubers were dug up, it was discovered that they too were rotten.

The disease was first observed in northern France in 1842 and, by 1845, it was the cause of major concern. It was also the cause of a major controversy which, indeed, represented the birth of the science of plant pathology. The Rev. M. J. Berkeley, in England, proposed the astounding view that the microscopic fungus, which was always associated with the disease was, in fact, the *cause* of the disease, and not one of its effects. Berkeley was anticipating Louis Pasteur‘s germ theory of infectious diseases by nearly a quarter of a century. Inevitably, Berkeley was widely disbelieved and his opponents offered many alternative suggestions. The newly discovered and mysterious ‘electricity’ was widely blamed, as was the atmospheric pollution caused by that new abomination, the steam railway. Berkeley's view was not popular, but he was right.

In 1845, potato blight was found in Ireland, and all thinking people knew that great trouble was in store. At that time, the Catholic Irish were still being cruelly exploited by the Protestant English. Potatoes had been introduced to Ireland in the late sixteenth century, at about the time of the Desmond rebellion. Gerald Fitzgerald, 14th Earl of Desmond, was an Irish Catholic who led an army of Italians and Spanish, backed by the Pope, fighting for the defence of Catholicism, against the Protestant English. The English won this war, and they brutally suppressed the insurgents. English rule in Ireland became harsh. In 1649, Oliver Cromwell waged a ruthless campaign against the Irish, and gave much of their land to English Protestants, who became the new, land-owning aristocracy. By this time, potatoes were well established in Ireland and they became the staple food of the peasants.

Irish agricultural labourers had niggardly wages, and they paid back a considerable proportion of them as rent to their English landlords. With the appearance of potato blight, the landlords feared for their rents, and for the safety of their country mansions, should rioting begin. But the peasants feared for their lives, because they lived almost exclusively on potatoes, and they had no money to buy alternative foods.

In these days of universal social security, old age pensions, medical plans, and other expressions of government concern for the individual voter, we are apt to forget that the more ancient role of governments was to make laws and wars, and little else, other than collecting the taxes required to pay for these functions. If the poor and the starving needed help, this was the function of the church, the aristocracy, and various public charities supported largely by private benefaction. But, when a major disaster struck, such as the failure of the potato crop in Ireland, these non-governmental organizations were quite unable to cope. The very poor then starved, and died. The slightly less poor voted with their feet, and went somewhere else.

In the 1840s, Britain was already in the process of moving away from this primitive type of government towards a more concerned and caring administration. Britain had already abolished slavery, for example, decades before either Russia or the United States. Nevertheless, the prime minister, Robert Peel, made very cynical use of the Irish famine, in connection with one of the great political controversies of nineteenth century Britain. This was the issue of the corn laws. These laws imposed import duties on wheat, and they helped British farmers by maintaining the scarcity prices which had prevailed since the time of the Napoleonic wars at the turn of the century.

Peel had been elected on a mandate to maintain the corn laws, but he used the potato famine as an excuse to repeal them, and to initiate a great period of free trade. This brought down the price of bread dramatically. And it also had a considerable influence on Mid-West America because it opened up an important new market for wheat. This development came soon after Patrick Bell‘s invention of the mechanical reaper, in Scotland, in 1827, which he took to Canada in 1833. Four years later, Cyrus Hall McCormick started manufacturing his famous reapers in Chicago. The repeal of the corn laws also coincided with the building of the Erie canal, which opened up the North American prairies, via the Great lakes, to the East Coast of the United States, and the markets of Europe.

However, all this happened too late for the poor in Ireland, who lived in turf hovels, went bare foot, and dressed in rags. They owned nothing except their potato crops, and sometimes a pig, which was also fed on potatoes. When the potatoes died, their entire supply of food was lost.

Potatoes are a very productive and nutritious food crop and, consequently, the population of Ireland had increased considerably since the use of potatoes had become widespread. In 1800, the population was estimated at four million but, by 1845, it had increased to eight million. In Europe, the 1840's were known as the 'Hungry Forties' because of the shortage of potatoes. In Britain, however, this period was called 'The Great Irish Famine' because the Irish were so totally dependent on potatoes. No accurate figures are available, but it is estimated that about one million Irish people died of starvation. This was twelve percent of the population. Another million and a half people emigrated, mainly to America. This was another twenty percent of the population, making a total of one third of the whole population. The remaining two thirds suffered very serious hunger and malnutrition.

It has been related how an Irish priest, one Father Matthew, travelled from Cork to Dublin on July 27th, 1846, and observed that all the potato crops were luxuriant and healthy. He praised God for His Mercy and Goodness, because he believed that the potato crops would once again be productive. In those days little was known about infectious disease epidemics, and still less was known about plant diseases. Father Matthew believed that the rotting of the potatoes during the previous summer was a rare phenomenon, unlikely to be seen again. But, when he travelled back to Cork on August 3rd, he observed with sorrow a wide waste of black and putrefying vegetation.

In those days, the government would provide poor relief only on a basis of 'fair' exchange. The destitute were put into a workhouse, and were expected to do work for the government in exchange for board and lodging. Nothing would be given for nothing and, in practice, this meant that the destitute had to work at menial and often meaningless tasks, such as picking oakum out of old ropes. When the potato crops failed, there was no way that the government could provide workhouses for millions of starving Irish so, believing itself to be both benevolent and enlightened, the government provided work on the roads.

Starving labourers were expected to do back-breaking work building new roads, in exchange for little more than a bowl of porridge. Many of these roads went from nowhere to nowhere. The people were weak and under-nourished, and quite unfit for manual labour. Furthermore, they often had to walk long distances to their work. One road contractor commented that he was ashamed, as an engineer, to allot so little work to each daily task, but that, as a man, he was ashamed to exact so much.

Forty Years of Blight Damage

When potato blight first appeared in Europe, it was extremely damaging, and entire crops of potato were wiped out. Nevertheless, the blight epidemics declined in severity, and they were never again so damaging. At the time, this was attributed to a mysterious (and inexplicable) decline in the virulence of the blight fungus. We now know that it was due to a fundamental change in the overall population of the potatoes themselves.

Each potato variety is a clone. It is propagated without sex, by vegetative propagation, from ‘seed’ tubers and, consequently, all the plants within one clone are genetically identical. New potato clones are produced from true seeds, which develop in a fruit from sexually pollinated flowers, and which differ genetically among themselves because they are the result of genetic recombination.

There were many potato clones in Europe at that time and, among other things, they differed considerably in their susceptibility to blight.

In the first year of the blight epidemic, the most susceptible potato clones were totally destroyed. They became extinct. In the second year, the slightly less susceptible clones became extinct and, by the fourth year, only moderately resistant clones remained. The entire potato population of Europe had been fundamentally changed towards blight resistance, and the blight epidemics declined accordingly.

New varieties of potato were repeatedly being produced from true seed by breeders, seed merchants, farmers, and even amateurs. In those days, plant breeding was an art, rather than a science, and there was a powerful incentive to breed new potato varieties because, at that time, this was the only way to avoid the severe loss of vigour that was apparently caused by vegetative propagation with seed tubers.

With the benefits of modern science, we now know that this loss of vigour occurs because of an accumulation of virus diseases, which are transmitted by seed tubers, but which are not transmitted through true seed to new seedlings. Consequently, the potato breeders had to produce many new varieties from true seed, in order to solve the problem of this loss of vigour. Modern potato farmers do not need to do this because they use certified seed potatoes which have been officially inspected and shown to be free of viruses.

After the arrival of blight in Europe, resistance to this disease became the first selection priority when choosing which seedlings should become new clones. Indeed, any seedling that was not resistant to blight would be killed by the fungus, and only those which could survive the blight stood any chance at all of becoming a new clone. Like the changing of potatoes from short-day to long-day responses, this was another example of unconscious selection. Whether or not the breeders wanted blight resistance, or even knew about it, they had no choice in the matter, because it was only the resistant seedlings that could survive, let alone yield a good crop.

This process of selection for blight resistance continued for some forty years following the first appearance of blight. However, the genetic base of potatoes in Europe was a narrow one, and it was apparently derived almost entirely from the original material introduced by the Spanish. This meant that there was a limit to the level of blight resistance that could be achieved within this breeding stock. There is little doubt that the breeders of Europe achieved that limit of resistance, at least in some clones. No further progress was possible without a broadening of the genetic base by the introduction of new breeding stock from South America. Nonetheless, that limit was enough resistance to allow an economic cultivation of potatoes without any fungicidal spraying against blight. Potatoes were cultivated in spite of the blight, and they yielded enough to make them an important food crop throughout Europe. This was a very considerable increase in resistance when compared to those susceptible clones of the Hungry Forties, reduced to that black, stinking mush.

As we now know, this blight resistance in potatoes was the resistance of the biometricians. It was the continuously variable, polygenically inherited, horizontal resistance. It is safe to assume that the potatoes in Ireland, at the time of the great famine, had levels of horizontal resistance that approached the minimum. And, as we have seen, this level of resistance leads to the complete destruction of the crop, with not a speck of green to be seen anywhere. In a moment, we shall discuss new potato clones in

Mexico which have levels of horizontal resistance that approach the maximum. In many areas, these clones can be grown without any spraying, and without any losses from blight. The difference between the minimum and the maximum levels of horizontal resistance to blight can thus be enormous. It can be the difference between a *complete* loss of crop, and *no* loss of crop, in the absence of crop protection chemicals.

An even more important observation is that this European resistance to blight developed without any ‘source’ of resistance. It will be remembered that the members of the Mendelian school believe that resistance breeding cannot begin without first finding a source of resistance.

Bordeaux Mixture

In the 1870s the vineyards of France began to be ravaged by another foreign fungus, called *Plasmopora viticola* (pronounced Plaz-MOP-ora vitty-cola), which had also been introduced from the New World, and which is distantly related to the potato blight fungus. This second foreign fungus causes a disease of grapes called downy mildew. At the time of its introduction to Europe, it too was a new encounter disease, and it did nearly as much damage to the vines as the blight had first done to the potatoes. But there was one important difference. The clones of classic wine grapes are the result of many centuries, if not millennia, of selection, and they are among the most difficult of all crops to breed. There could be no question of replacing the susceptible vines with resistant ones, without a totally unacceptable loss of wine quality. There was consequently no possibility of the downy mildew epidemics declining as the potato blight epidemics had declined, because of genetic changes in the host population. The French wine industry was faced with absolute ruin.

Then, in the summer of 1882, a certain Professor Pierre Marie Alexis Millardet was examining mildewed vines in the famous Médoc area of Bordeaux, when he noticed that some of the vines at the Château Beaucaillon were green and healthy. This was so extraordinary that he made enquiries, and he discovered that it was a local custom to spatter the vines near the public road with a poisonous looking substance in order to discourage passers-by from eating the grapes. He also learned that this substance was a mixture of copper sulphate and lime, and that it was intended to resemble the verdigris of corroded copper vessels.

Millardet realised that he had found a substance that would solve the problem of downy mildew. He called it *Bouillie bordelaise* which, in English, meant *Bordeaux mixture*, and it was the first fungicidal spray for crops. An explosion of research followed. The best proportions of copper sulphate and freshly slaked quicklime were worked out. The best concentration of the mixture was determined, and spraying schedules were devised. Entirely new kinds of machine, called sprayers, were invented for applying the mixture to the vines. Endless other mixtures were tested but, almost without exception, they were found to be either useless, or positively toxic to the vines. Soon, all the vineyards of Europe were being sprayed with Bordeaux mixture. And all the potato crops too, because it was quickly discovered that Bordeaux mixture would also control potato blight.

It was not long before all the paraphernalia of wooden tubs, water carts, sprayers, copper sulphate, and lime, were seen in the potato fields, as well as in the vineyards. Spraying potatoes against blight became a routine part of potato cultivation throughout Europe and, later, the world. This was over one hundred years ago, and we may note in passing that we *still* spray our potato crops with fungicides to control blight, although Bordeaux mixture itself has been supplanted with more convenient proprietary products.

At this distance in time, it is difficult to appreciate the impact that Bordeaux mixture must have made on people's minds. To begin with, both potato blight and the downy mildew of vines had had powerful social consequences. Throughout Europe, few people had escaped being personally effected by one or the other of them, if not both. After all, people were starving because of potato blight. These two plant diseases had also had an enormous economic impact. It has been said the mildew of the vines cost France more than the Franco-Prussian war. And the efficiency of Bordeaux mixture was spectacular. It controlled these two diseases cheaply, efficiently, safely, and completely. Crop scientists can scarcely be blamed if they have been looking for comparable pesticide successes ever since.

There was another aspect of this story that also concerns us. When Bordeaux mixture was first introduced, there was some vociferous opposition to it. "Copper is poison" its opponents cried, quite incorrectly. And they claimed that the people of Europe would all die from eating poisoned potatoes, and drinking poisoned wine. As a matter of historical fact, not one person died in this way. Nor was human health endangered. Indeed, the very opposite was true. Had Bordeaux mixture been discovered forty years earlier, it could have saved at least a million lives in Ireland alone, during the great potato famine, and probably as many again in the potato eating districts of continental Europe. Not all crop protection chemicals are hazardous. Bordeaux mixture is not only the oldest crop fungicide. It is also the safest.

Forty Years of Bordeaux Mixture

The effect of Bordeaux mixture on potato *cultivation* was dramatic and wonderful. But the effect of Bordeaux mixture on potato *breeding* was disastrous. For the next forty years, potato breeders were able to protect their new seedlings with this fungicide. This meant that they could then ignore blight susceptibility, and concentrate on the other main breeding objectives which, as we have seen, are tuber yield, tuber quality, and agronomic suitability. The breeders concluded, no doubt, that blight resistance was no longer important, because the crops could be protected so easily, and so effectively, with Bordeaux mixture. Suddenly, all the pressure for finding blight resistant seedlings was gone. Breeders could screen their potato seedlings under the protection of this fungicide, and this made the breeding incomparably easier. They could then ignore the problem of blight killing off the majority of their precious seedlings, the problem that had so dominated their work for the previous forty years.

Between about 1885 and 1925, some of the most famous of all potato varieties were produced. Many of them are still being cultivated, such as *Russet Burbank* (1890) in the United States, *King Edward* (1902) and *Majestic* (1911) in Britain, *Bintje* (1910) in Holland, and the old Dutch variety *Alpha* (1925) in many other parts of the world, and they remain some of the most popular potatoes among consumers.

But there was one great drawback to this easy breeding. The accumulation of blight resistance not only stopped. It went into reverse. This happens with any inherited character which is quantitatively variable, and which is not contributing to survival. If it has no survival advantage, it tends to be lost from a population that is genetically flexible because of sexual reproduction.

As we have seen (Chapter 8), plant breeders talk of selection pressure, using the word pressure in the sense of ‘bringing pressure to bear’. They also talk of *positive* and *negative* selection pressures. When blight first appeared in Europe, there was very strong, positive selection pressure for resistance, because only resistant clones could survive, and the entire potato population was quickly changed genetically towards an increased resistance. But, when Bordeaux mixture was introduced, there was negative selection pressure for resistance. This happened because spraying with Bordeaux mixture made it impossible to distinguish between resistant and susceptible seedlings, and susceptible seedlings were in the majority. The chances of being selected were then greater for a susceptible seedling than for a resistant one. And the trend of the previous forty years was reversed. Resistance began to be lost. As we have seen also (Chapter 13), this loss is known as the erosion of horizontal resistance, and the erosion continued for another forty years, until the potato breeders were jolted out of their complacency by World War I.

As a consequence of Bordeaux mixture, the progression of new potato varieties gradually became more and more blight susceptible. *Bintje*, for example, is one of the most blight susceptible varieties known. It is widely cultivated because of its culinary popularity, but its cultivation is difficult because of its susceptibility, and its need for fungicidal protection. Equally, *Alpha* is the most popular potato in Mexico, but it is also the standard of blight susceptibility used in the measurement of blight in the remarkable potato breeding of that country, to be discussed in a moment.

This loss of resistance to blight first became apparent during World War I, when there were acute shortages of food in Europe. There were also acute shortages of other commodities, such as copper, which was needed by the armaments industry, for the manufacture of brass rifle cartridges, and brass shell cases for the field guns. Copper was also needed for spraying the potato crops, particularly as the potato varieties of that time were so susceptible to blight. Germany was critically short of copper, and could not spray many of her potato crops which were consequently ruined. Food shortages undoubtedly contributed to her defeat, and these shortages resulted mainly from savage blight damage to the unsprayed potato crops. Various countries (on both sides of the firing line) decided that potato blight had strategic significance, and that the time had come to breed potatoes for resistance to this disease, so that potato crops would not have to be sprayed. And they decided to use the very latest scientific knowledge and techniques. That is, they decided to use the newly discovered Mendelian breeding methods.

Forty Years of Scientific Potato Breeding

From about 1925, until about 1965, potato breeders were using resistance to blight that was genetically controlled by single genes. These genes had been discovered in wild potatoes growing in Mexico and, with some difficulty, they were transferred to cultivated potatoes. Each gene conferred an apparent immunity to blight. When a potato possessing such a gene was crossed with a susceptible potato, the seedlings would segregate according to Mendel's laws of inheritance, with a ratio of three resistant seedlings to each susceptible seedling.

This breeding strategy was initiated at the potato research institute at Grosse Lusewitz, in Germany, and it produced potato clones known as the 'W' varieties. Soon, potato breeders in the

United Kingdom, the Netherlands, the United States, and other countries were copying this approach. There was a lot of optimism, and a lot of talk of abolishing blight, and abolishing the need for Bordeaux mixture. Sadly, this optimism was premature. It was found that this blight resistance was ephemeral. It ‘broke down’ to new races of the blight fungus.

In 1953, a group of British and Dutch scientists published an important discovery. They showed that, for every Mendelian resistance gene in the potato host, there was a corresponding, or matching, gene in the blight parasite. They published this discovery unaware that H.H. Flor, working with rust of flax, in the United States, had made the same discovery in 1940. It was a measure of how compartmentalised crop science had become, that the scientists working on one crop were ignorant of such an important discovery made in another crop. As we have seen (Chapter 3), Flor called this genetic link between the host and the parasite the gene-for-gene relationship, and this is the definitive characteristic of vertical resistance.

The potato breeders discovered that the resistance they were using to control potato blight was likely to fail after only a few years of commercial cultivation. It was vertical resistance. As the breeding of a new, potato cultivar requires about eight years of work, it was clearly very difficult for the breeders to keep producing new cultivars, with new and different vertical resistances, to replace those cultivars whose older resistances had failed. During the 1960s, several potato breeders, who had spent their entire careers working with vertical resistance to potato blight, reached retiring age with a sense of despair, and a tragic feeling that their careers had been a waste of time. The breeding programs for blight resistant potatoes had failed, and this is why we still spray our potato crops in order to control blight.

Sex in the Blight Fungus

When the blight fungus was first discovered in Europe, the German mycologist Heinrich Anton deBary was studying reproduction in microscopic fungi. He showed that most fungi similar to *Phytophthora infestans* had two entirely different methods of reproduction. One method is sexless, or vegetative, reproduction in which the fungus buds off microscopic spores in vast numbers. This kind of *r*-strategist reproduction enables the fungus to multiply very quickly, and cheaply, whenever weather conditions favour it. This rapid reproduction produces a population explosion of the blight fungus, and it explains why potato blight epidemics can develop so rapidly, and cause so much damage, over such a wide area.

The other method of reproduction is sexual and, in potato blight, is the result of two different mating types fusing their cells together to produce a new genetic combination. Technically, these types are both hermaphrodite (i.e. each has both sexes) but self-sterile. Consequently both types must be present for sexual reproduction to occur. This kind of reproduction produces spores, called oospores, which are resting spores that enable the fungus to survive adverse weather during a temperate winter or a tropical dry season. This sexual reproduction also leads to genetic recombination. The spore will be genetically different from its parents. In particular, its combination of vertical parasitism genes is likely to be different from either of its parents. This provides a wild fungus population with the maximum genetic diversity at the start of the next epidemic. This is the time that it needs diversity most, in order to overcome the system of locking of the gene-for-gene relationship.

When deBary studied *Phytophthora infestans*, however, he could not find any sexual reproduction, or resting spores, at all. This discovery baffled him, and it continued to baffle scientists all over the world for about a century. Then a Mexican scientist, Jorge Galindo, discovered that there were two mating types of *Phytophthora infestans* in Mexico, and that the resting oospores were common in that country.

It then became clear that the blight fungus had originally been taken to New York, and from there to Europe, and to all the rest of the world, as one mating type only. And a single mating type cannot have sexual recombination with itself. It also became obvious that this single mating type had probably been taken from Mexico only once, because it is most unlikely that it could have been taken out more than once, as only one mating type, and the same mating type.

The accident which meant that Europe had only one mating type of *Phytophthora infestans* was to have profound effects on the development of crop science and, more specifically, on the breeding of plants for resistance to their parasites. With only one mating type, the blight fungus could overcome vertical resistances only by producing new strains by genetic mutation. The rate of mutation is rather slow, compared with the rate of production of new strains by sexual recombination. This meant that a vertical resistance to blight would remain unmatched, and effective, for several years, and this encouraged the breeders to use this kind of breeding, and this kind of resistance.

In Mexico, where the resting spores of blight are common, vertical resistance fails quite soon, because the many resting spores produce many different strains of the fungus, and the vertical resistance is matched quickly. Had both mating types of blight been present in Europe, and the rest of the world, breeding potatoes for vertical resistance to blight would never have started, because the resistance would usually have failed within one screening season. The breeders would have been compelled to use an entirely different breeding technique designed to accumulate polygenically inherited, horizontal resistance, and the influence of this potato work on the breeding of all other crops would have been profound.

Quite recently, the second mating type of blight was accidentally, but very carelessly, introduced to Europe and, from there, it has spread on seed potatoes to many other parts of the world. This means that vertical resistance to blight is even more futile than it was before. Furthermore, if blight is to be controlled by horizontal resistance, rather higher levels of this kind of resistance will now be required. This is because the resting spores increase the initial inoculum, which is the amount of the blight fungus at the start of each epidemic. The vary name of this potato disease may also have to be changed. In temperate countries, potato blight is usually called ‘late blight’ to distinguish it from another disease (called early blight) that occurs rather earlier in the season. With a wealth of oospores in the soil, late blight will start much sooner each season, and it will no longer be ‘late’.

This second mating type has also had a profound effect on tomato cultivation. When only one mating type was present, the blight fungus could survive a winter only in blighted potato tubers, and these were somewhat rare. This meant that the initial inoculum was small, and that tomatoes could get blight only from potatoes.

But now they can get blight directly from oospores in the soil, and the tomato epidemics start earlier and are much more severe.

Tuber-Borne Diseases of Potato

It was mentioned earlier that virus diseases of potatoes are transmitted by the vegetative propagation of seed tubers, but not by the sexual propagation of true seeds. This meant that virus diseases would gradually accumulate within a clone of potatoes until the yield of that clone was severely depressed. So far, the only method of solving this problem has been to produce seed tubers that have been inspected in the field, and which have been certified free from viruses. However, these tubers are expensive.

The key point about this problem is that these virus diseases spread quite slowly within potato crops. Without any artificial control of the viruses, a potato clone can usually be cultivated for about a decade before the accumulation of viruses renders it unprofitable. In fact, the viruses spread so slowly that a potato breeder rarely sees any evidence of them in his screening populations. This is a situation that is comparable with the breeding of potatoes after the discovery of Bordeaux mixture. It is impossible to select for disease resistance if that resistance cannot be seen. And it is impossible to measure disease resistance if the disease is absent. Furthermore, the disease must be universally present. That is, every individual in the screening population must carry the disease, otherwise individuals which have escaped infection will be disease-free, and will be mistakenly identified as resistant.

These potato viruses are European in origin. In theory, the foreign potato should have accumulated resistance to them after centuries of breeding in Europe. But that resistance can accumulate only during the breeding process, with its sexual reproduction, and genetic flexibility. Resistance cannot accumulate during the cultivation process, with its sexless reproduction, and genetic inflexibility.

Because the viruses spread so slowly, they appear only rarely in a breeder’s screening population. Consequently, there is no selection pressure for horizontal resistance to them. Like the loss of blight resistance under the shield of Bordeaux mixture, we have been losing rather than gaining resistance to these viruses. This trend has been perpetuated during the present century by the fact that the Mendelian breeders were unable to find a genetic source of resistance to these viruses. In modern potato cultivars, the level of horizontal resistance to these viruses is probably close to the minimum.

In eighteenth century England this problem of the ‘decline’ of potato stocks was well known. A group of farmers in eastern England decided to breed for resistance to ‘decline’, by using the oldest surviving clones as parents. This was in the days when farmers did their own plant breeding, and they knew exactly what they wanted. Unfortunately, someone else discovered that seed tubers brought from the Yorkshire Moors did not exhibit ‘decline’. This was the birth of the certified potato seed industry. Later, seed tubers from Scotland were shown to be even better. We now know that the aphids that spread the viruses are absent from cold climates such as the Yorkshire Moors and Scotland. But, at that time, using cold climate seed tubers was a much easier alternative to breeding, and the breeding stopped.

As a result this problem has now been with us for more than two centuries. Potato breeders have been ignoring resistance to virus diseases since before the appearance of blight in Europe, during the forty blight years before the discovery of Bordeaux mixture, during the forty years of breeding under the protection of Bordeaux mixture, during the forty years of breeding for vertical resistance, and ever since. The problem is still with us.

Modern potato breeders would have been happy to incorporate virus resistance in their varieties but, unfortunately, they could not find a ‘genetic source’ of resistance. What they should have been doing was to inoculate every single seedling in their screening population with these viruses. But suggest such a thing to a modern potato breeder, and he would be horrified. The viruses would make a frightful mess of his beautiful seedlings. Most of the seedlings would probably be killed, and only a few of them would survive as hideously distorted cripples. But these cripples would have some resistance. And they could produce true seed. And the next generation would be a little more resistant. Less than a dozen generations of this degree of selection pressure is all that would be required to reduce these viruses to unimportance. And the same is true for other potato diseases which are spread by seed tubers. There are quite a few of them, and they have picturesque names like wart, scab, root knot, scurf, black leg, ring rot, gangrene, jelly end rot, soft rot, and dry rot.

Why is this important? Certified seed tubers are expensive. In fact, the cost of this certified seed is the largest single input in the commercial production of potatoes. This cost is passed on to the consumer, and it should not be necessary.

This point is well illustrated by potato cultivation in non-industrial countries. Subsistence farmers cannot afford certified seed. Nor can they obtain it, because few of the non-industrial countries have an effective seed certification scheme. As a result of my own horizontal resistance breeding work in Nairobi, Kenya now has a couple of potato varieties, called *Kenya Akiba* and *Kenya Baraka* (*Akiba* is Swahili for a store of food, and *Baraka* is Swahili for blessings), which can be grown without any spraying against blight, and without the use of expensive certified seed. Because there are two potato crops each year in Kenya, these cultivars have now been cultivated for some seventy vegetative generations without any detectable loss of vigour.

Unfortunately, my breeding work came to an abrupt halt when an irresponsible, visiting, foreign scientist, speaking out of turn, expressed the view that there was no such thing as horizontal resistance, and that my work was a waste of time. I was invited to leave the country. However, my two cultivars are the main contributors to a potato acreage in Kenya that has expanded more than thirty times to an estimated 750,000 metric tonnes. The staple diet in the highlands of that beautiful country is now changing away from traditional maize and beans, towards a much more nutritious diet of potatoes and milk. It should be mentioned also that the Mexican variety *Sangema*, described in a moment, is being cultivated in Rwanda, in central Africa, without any spraying, and without any use of certified seed. But, sadly, these two, small, African countries are the exceptions that prove the rule, when it comes to this inexpensive and unpolluted potato cultivation. But they do suggest that a comparable freedom from certified seed and spraying is a realistic research target in every potato growing country, in spite of the fact that countries in Europe and North America have a more complex pattern of potato parasites.

Potato Breeding in Mexico

In the Toluca valley, in Mexico, which is the home of the blight fungus, John S. Niederhauser, of the Rockefeller Foundation, was the first modern crop scientist to work with the biometricians' many-gene resistance, which we now call horizontal resistance. Niederhauser started working on potatoes, as a mere sideline of his work on cereals, in 1947. Initially, he used the vertical resistance which, at that time, was the foundation of every potato breeding program in the world. However, the Toluca valley differed from the rest of the world in having both mating types and an abundance of blight oospores. This has two important effects on the blight epidemics in Mexico.

First, the epidemics are much more severe, because large numbers of oospores ensure that the initial inoculum of the blight is very high. This means that there is plenty of the blight fungus around, particularly at the beginning of the epidemic.

Second, the great diversity of oospores produces an equally great diversity of blight races. This means that vertical resistance breaks down very quickly in Mexico, and this is especially true of foreign cultivars which have only one or two genes for vertical resistance. Niederhauser showed that vertical resistance was useless in Toluca, because it was usually matched almost as quickly as the potato sprouts appeared above the ground.

Edible potatoes from the Andes were introduced to Mexico by the Spanish in the eighteenth century, but it was immediately discovered that they were very difficult to grow. As we now appreciate, this was because of blight, which was not even known, scientifically, at that time. Mexican farmers discovered that they could grow potatoes in the high *sierras*, where it is too cold for the blight fungus. They could also grow them at low altitude, under irrigation, during the dry season, when blight epidemics could not develop. But this kind of cultivation is limited, and the country was deprived of a valuable food crop over much of its agricultural area.

John Niederhauser showed that it was possible to grow potatoes in the blight areas if they were sprayed with a fungicide. But there was a difference. In Europe, a potato crop had to be sprayed about five times in order to control blight. But, in the Toluca Valley of Mexico, where John Niederhauser was working, the same potatoes must be sprayed up to twenty five times, if the blight is to be controlled.

Niederhauser's great discovery was that potato cultivars differed very considerably in the amount of blight that developed *after* the vertical resistance had failed. This was because of the second line of defence, which Niederhauser called “partial” (i.e., incomplete) resistance to blight, and which Vanderplank later re-named horizontal resistance, when he recognised that the concept applies to all plant diseases. As we now know, it was the same kind of resistance that led to the decline in the severity of those first blight epidemics in Europe, during the Hungry Forties. It was also the resistance that accumulated during forty years of potato breeding in the absence of Bordeaux mixture, and was largely lost again, during forty years of breeding in the presence of this fungicide. It is also the resistance that invariably remains in any plant after vertical resistance has been matched, even if it is at a very low level in many modern crop varieties.

Niederhauser was the first scientist who both recognised *and used* horizontal resistance. He deliberately abandoned vertical resistance, and he bred potatoes for higher and higher levels of the quantitatively variable, many-gene resistance. Perhaps his best known cultivar is *Atzimba*, which needs little spraying. When Niederhauser left Mexico, in 1972, his breeding work was continued by Mexican scientists, and they now have even better cultivars, including *Sangema*[*], mentioned above.

The most popular potato in Mexico is still the old Dutch cultivar *Alpha* which, as we have seen, was bred during the forty year period when potato breeders were using the protection of Bordeaux mixture. And its level of horizontal resistance to blight is low. As already mentioned, when grown at Toluca, it has to be sprayed with a fungicide up to twenty five times each season in order to control the very severe blight of that area. By way of comparison, a modern Mexican cultivar, such as *Tollocan*, or *Sangema*, has so much horizontal resistance to blight that it needs to be sprayed with a fungicide only once or twice each season, in Mexico. By way of further comparison, the wild potatoes of Toluca are never sprayed at all, yet they get so little blight that scientists often have difficulty in finding it for research purposes.

---

[*] This name is derived from the first names of the three Mexican scientists who bred this cultivar; thus *San*tiago Delgado Sanchez, *Ge*lasio Perez Ugalde, and *Ma*teo A. Cadena Hinojosa.

(Unfortunately, these Mexican potato cultivars cannot be utilised in temperate countries because they are short-day, tropical plants).

This indicates the importance of Niederhauser’s work, and it is a very real indication of what can be achieved with horizontal resistance. One would think that plant breeders the world over would have rushed to copy his work, in other potato areas, and in other crops. And did they? Well, no, they did not.

In most of the plant breeding during the twentieth century, horizontal resistance was ignored because it was unknown and unrecognised. Consequently, instead of being increased, it tended to be lost, and most modern cultivars, of most species of crop, now have levels of horizontal resistance similar to Alpha’s horizontal resistance to blight. It is probable that, when we start breeding other species of crop for horizontal resistance, we will achieve levels of horizontal resistance similar to *Tollocan* and *Sangema*, or even higher.

During the past forty years, scientists working with other crops have gradually concluded that breeding for vertical resistance was unsatisfactory. What they should have done was to imitate the work of John Niederhauser, and worked with horizontal resistance.

But they did no such thing. Many of them failed even to recognise the existence of horizontal resistance. Others refused to believe that horizontal resistance could provide an adequate control of crop parasites. Yet others declined to use it on the grounds that working with it was too difficult. They wanted to breed for horizontal resistance using their Mendelian breeding methods and, under these circumstances, this kind of resistance is indeed difficult to accumulate.

When the Rockefeller Foundation sent John Niederhauser to Mexico, it also sent Norman Borlaug to the same area to work on wheat. These two brilliant scientists had closely parallel careers. Norman Borlaug produced the ‘miracle’ wheats of the Green Revolution (Chapter 19) but, because breeding for horizontal resistance was so novel, and so difficult, he failed to produce wheats with horizontal resistance. The miracle wheats have vertical resistances, and they are still vulnerable to new strains of various parasites. On the other hand, John Niederhauser did produce horizontal resistance but, because this kind of breeding was so novel, and so difficult at that time, he failed to produce a green revolution in potatoes, comparable to the green revolutions in wheat and rice.

Norman Borlaug has saved millions of people from death by starvation, and hundreds of millions more from malnutrition. It could be said that he has redressed the horror of the potato blight famine, many times over. For this achievement, among the greatest in the twentieth century, he was awarded the richly deserved Nobel Peace Prize.

But, in the long run, John Niederhauser's achievement is likely to be deemed even more valuable, because he discovered a crucially important scientific principle that can now be applied to all crops. And, when it is, we may well see a completely new green revolution in every one of them. It is John S. Niederhauser who is likely to earn that ultimate accolade, "a paragraph in the history books". It is pleasing to add that, in 1991, John Niederhauser was awarded the World Food Prize.

Potato Breeding in Scotland

More than thirty years ago, N.W. Simmonds, in Scotland, attempted an interesting experiment. He wanted to prove that modern potatoes (*Solanum tuberosum*) really were derived from the *Solanum andigena* potatoes of South America. He also wanted to show that horizontal resistance to blight could be accumulated in these very susceptible potatoes. Using recurrent mass selection, and selecting for both the agronomic characteristics of modern potatoes, and quantitatively variable resistance, he was able to report very considerable progress after only four generations of breeding. This progress occurred in yield, long-day tolerance, tuber qualities, and blight resistance. Many of his selections compared favourably with commercial cultivars, and Simmonds called this material "neo-tuberosum".

Quite apart from making him one of the early pioneers of horizontal resistance, Simmonds' work is of relevance to Part III of this book. It provides an interesting illustration of what the members of a plant breeding club might accomplish.

Colorado Beetle

The Colorado beetle, named after the State of Colorado in the U.S.A., where it was first found, is a beetle that looks like a large ladybird. It is about half an inch in length and has characteristic orange and black stripes on its wing cases. As American pioneers moved West, their potato crops eventually came into contact with this new encounter parasite, and it then transpired that these cultivated potatoes had very little resistance to it. The greatly expanding beetle populations began to spread eastwards. During the 1860s, they reached Illinois and Iowa, and they were so numerous that they were a nuisance in the streets and houses. By the 1870s, they had reached Canada, Vermont, and New York.

Farmers in North America began to protect their potato crops with an insecticide called Paris Green. This was a powder consisting of copper aceto-arsenite. Its insecticidal ingredient was arsenic, and the substance was extremely poisonous, and very dangerous to both people and the environment. However, it was the best available insecticide at that time.

In 1877, the beetles were found, but exterminated, in Germany and various European governments became very alarmed. For the first time in history, they enacted legislation to prevent the arrival of a new crop parasite, and the Colorado beetle became a topic of major concern. During World War I, there was even a suggestion that the Allies should drop live Colorado beetles from airplanes over the potato crops of Germany. This was possibly the first recorded example of an attempt at biological warfare. Fortunately, wiser councils prevailed and this outrageous idea was abandoned.

In 1922, Colorado beetles were found in the South of France, established beyond any hope of eradication. The beetles spread northwards, and the farmers of Europe began to spray their crops with lead arsenate, which was doubly poisonous, and doubly dangerous.

The beetles have not yet reached Britain. E.C. Large, in his book *The Advance of the Fungi* (1940), stated that anyone who found a Colorado beetle in Britain should send it to the Ministry of Agriculture, stating where he had found it, and giving his name and address. He should then “stand by, and watch what happened, as one who has pulled a fire alarm near a gunpowder dump”.

The tiny island of Jersey, only fourteen miles from the Normandy coast, grows early potatoes for the British market. It too is still free of Colorado beetles, and it must remain that way if it is not to lose that British market. For this reason, the French Government ensures that the potato crops of nearby Normandy are given extra insecticidal sprays in order to protect the Jersey potato crops from flying beetles, which can easily cross fourteen miles of sea. This is a wonderful example of international goodwill which, sadly, has remained virtually unknown to the world at large.

With the discovery of DDT (Chapter 16), the protection of potato crops became much easier, and much safer. By the time that DDT was banned, there were other insecticides to replace it. Nevertheless, in those areas where it is a pest, we still spray our potato crops against Colorado beetle. It seems that no one has ever attempted to breed potatoes for resistance to this insect. The reason, of course, is obvious. No one could find a source of resistance. Vertical resistances to this parasite do not exist, at least in its known hosts that have been studied in this regard. And, it appears, no one has ever attempted to breed potatoes for horizontal resistance to Colorado beetle. But, as the new edition of this book was going to press, David Fisher, in the United States was reporting the results of his attempt to do just this.

No one knows whether horizontal resistance could be accumulated in potatoes to a sufficient level to control Colorado beetle. Anyone who expresses an opinion on this matter can only be guessing, because it has never been scientifically investigated. Needless to say, it should have been investigated, decades ago. And it deserves to be investigated now, pretty damn quick, as they say in the military.

Chapter 19

Why Did the Green Revolution Run Out of Steam?

Farmers often distinguish between intensive and extensive crops. Apples, for example, are an intensive crop because the fruit is valuable, and the crop justifies considerable work and investment. Cereals, on the other hand, are extensive crops which must be grown on large acreages, with relatively little work and investment devoted to each acre, because there is relatively little profit to be obtained from each acre.

Before the days of artificial fertilisers, farmers manured their crops exclusively with 'muck', the excrement of their cattle, pigs, and horses, otherwise known as farmyard manure, or F.Y.M. The work of spreading this manure over the fields was known as 'mucking out' and, as people who live in the country know well, it is a smelly business. However, this method of manuring crops has two drawbacks, quite apart from the stink. First, there is always a strict limit to the amount of farmyard manure that one mixed farm can produce, and it is never enough. Second, it is a labour intensive, and expensive, method of manuring crops. For these reasons, in the old days, farmers only manured their intensive crops, and their extensive crops had to get by with manure residues left in the soil from an earlier crop. One of the many reasons for crop rotation was to ensure that each field received a dose of manure every few years.

The purpose of manuring was to provide crops with the three main nutrients of plants, which are known as N, P, and K, these being the chemical symbols for nitrogen, phosphate, and potash. Some of the more important discoveries of nineteenth century chemistry revealed that these are the main nutrients of plants. Unlike animals, which have to eat organic plant or animal tissues, plants absorb their nutrients as inorganic chemicals. For this reason, it is possible to manure plants with inorganic or ‘artificial’ fertilisers.

One of the first of the so-called artificial fertilisers was, in fact, a natural product, and it was called guano. This material was quarried from tropical shorelines, mainly in Peru, and it consisted of the accumulated droppings of millions of sea birds that fed on fish. Guano is rich in phosphate and nitrogen. Another natural product is rock phosphate. Later, artificial fertilisers began to be produced in factories, and it was the demand for these that first led to the growth of the bigger chemical corporations. The manufacture of nitrogenous fertilisers is closely similar to the manufacture of explosives. Various nitrogen compounds are the basis of explosives such as nitro-glycerine, and ammonium nitrate. The big chemical corporations grew really big, and really rich, from the demand for explosives during two world wars.

One of the few good things to come out of World War II was an enormous surplus of factory space, in all the industrial nations, for the manufacture of explosives. When the war ended, the demand for explosives disappeared, and these factories were suddenly superfluous. The only thing they could be used for, without being entirely rebuilt, was the manufacture of nitrogenous fertilisers for agriculture. This manufacture requires large amounts of energy, in order to combine atmospheric nitrogen with hydrogen to form ammonia, which is the starting point of the industrial process.

In addition to the surplus explosives factories, for nearly thirty years following World War II, there was also a period of cheap oil, and cheap energy. As a consequence, the production of nitrogenous fertilisers increased to a state of glut, and prices fell dramatically. For the first time in history, it became economic to apply nitrogenous fertilisers to extensive crops, such as wheat.

Dwarf Varieties

Traditionally, wheat had long straw. Pieter Bruegel the Elder (1525-1569) painted a scene of wheat reapers, called *August* or *Wheat Harvest*, in which the wheat is nearly as tall as some of the men who are cutting it. In those days, this meant that the straw would be about four or five feet long. Long straw was desirable for several reasons. It was easier to cut by hand, and to tie the wheat into sheaves which were then propped together in stooks to dry. The straw also had a value of its own and, indeed, was almost as desirable as the grain itself. This was because of the many farm animals, particularly cattle and horses, which needed straw for bedding.

Wheat with long straw has a serious disadvantage, however. It is liable to be blown over when it gets wet, and heavy, with the wind and rain of a storm. This flattening of a wheat crop is known as ‘lodging‘, and it makes the harvesting difficult and, occasionally, impossible. Applying farmyard manure to wheat was dangerous, quite apart from the adverse economics of this practice, because rich nutrients increase the straw length, the ear weight, and the likelihood of lodging.

Now that horses have been replaced with machines, the need for long straw has largely disappeared, and the dangers of lodging have also disappeared. This is because the modern trend has been towards the exact opposite of long straw. The so-called dwarf and semi-dwarf wheats have very short straw. These dwarf wheats have the advantage that they can be given heavy doses of fertilizer with little danger of lodging. As a result, their yields can be increased very considerably.

This was the basis of the Green Revolution. In the 1940s, the Rockefeller Foundation decided to undertake agricultural research for non-industrial countries and, with the cooperation of the Mexican Government, they started in Mexico. One of their scientists was Norman Borlaug who was breeding improved varieties of wheat. He was aware of the falling prices of fertiliser, of the yield increases that could be obtained from this fertiliser, if there were no lodging, and of the possibility of developing dwarf wheats that were resistant to lodging. This became the basis of his research.

The dwarf character in wheat originated in Japan, and it was incorporated into American wheats by O. A. Vogel. Borlaug took Vogel's dwarf wheats to Mexico in 1954. He bred new dwarf wheat varieties from them, and they yielded so well that it was economic to grow them with artificial fertilisers, on irrigated land, in northwest Mexico. The increase in wheat production was dramatic. Within a few years, Mexico became self-supporting in wheat. The next development was that scientists in India heard about these new varieties and, after a few experiments, they imported bulk quantities of seed from Mexico. Very soon, India changed from being a wheat importing nation to being a wheat exporting nation. Similar, increases in production occurred in Pakistan, China, and various countries of the Middle East and North Africa.

In the meanwhile, other scientists of the Rockefeller and Ford Foundations were copying Borlaug's work in the Philippines, except that they were working with rice. They too produced new dwarf varieties that could be grown with cheap fertiliser, and which then had greatly increased yields. Quite quickly, countries such as The Philippines, India, Indonesia, and Thailand, increased their rice yields as much as the wheat growers had increased their wheat production.

The public relations people of these two Foundations coined the terms ‘miracle wheat’, ‘miracle rice’, and ‘green revolution’. We can forgive them for their euphoria, and their Madison Avenue terminology. The effects of the green revolution really were stunning. Here, at last, was technical aid, from the Industrial World to the Non-Industrial, that really meant something. Millions of people were saved from starvation, and at least one billion people were saved from serious malnutrition. And, as we saw in the last chapter, Norman Borlaug was given the Nobel Peace Prize. It was possibly the most richly deserved Peace Prize ever awarded.

International Research Centres

It was at this point that various governments and charitable organisations decided that the world needed more green revolutions, in more crops, and more countries. The governments of industrial nations had already agreed that they should each aim at spending 0.7% of their annual budgets on assistance to non-industrial countries. To this end, many of them set up their own overseas aid organisations. None of these governments reached their 0.7% targets but, even so, most of the aid organisations failed to spend all the money that was allotted to them. They all seemed to end their financial years with budget surpluses. Obviously, the best way to utilise these surpluses was to finance new green revolutions.

A body called the Consultative Group for International Agricultural Research (CGIAR) was set up, with headquarters in New York. Its function was to allocate these surplus funds to agricultural research in the non-industrial world, and it funded various international research centres. A list of the more important centres includes CIMMYT, with headquarters in Mexico, which now looks after wheat and maize, and IRRI, in the Philippines, which looks after rice. CIAT in Colombia is responsible for cassava, beans, and other tropical crops. IITA in Nigeria has a similar mandate for the wet tropics. CIP in Peru is responsible for potato research. ICRISAT in India does research on crops in the semi-arid tropics, and ICARDA specialises in dry area agriculture, particularly in the Mediterranean region. In total, there are sixteen centres, and their collective budget is around $400,000,000 a year.

The CGIAR made two mistakes when setting up these large and expensive international research centres. First, they deliberately created scientific monopolies in the non-industrial world. All the money available for research on a particular crop would go to a single research centre. If two centres, such as CIAT and IITA, had over-lapping areas of research, they were carefully controlled to ensure that they did not compete with each other. The justification for this was to avoid unnecessary duplication. Research is expensive and, it was argued, duplication makes it doubly expensive.

But, in fact, duplication in research is essential, because it provides the competition which is so necessary for good science. Nothing stimulates a scientist more than the thought that a rival scientist may anticipate him, and publish first. And nothing dulls a scientist more than the knowledge that he has no rivals. The scientists at the International Research Centres have no rivals.

The second mistake was fundamental. It was the hope was that these International Centres would produce new green revolutions. They did not. Indeed, they are a classic illustration of the completely false idea that you have only to throw enough money at enough scientists, in order to get new scientific breakthroughs.

The original inspiration for good science comes from the scientists themselves, and usually from an individual scientist who is likely to be grossly under-funded, and working in a basement laboratory that has been due for demolition for decades. Scientific inspiration does not come from money. Nor does it come from politicians, administrators, or bankers.

The CGIAR produced no new green revolutions for one very simple reason. All the plant scientists employed by the international centres had been trained in the Mendelian tradition. They believed that, when breeding plants for parasite resistance, you must first find a genetic source of resistance. If no source of resistance could be found, the resistance breeding could not even begin. You then had no choice. You had to use crop protection chemicals. For these Mendelians, there were really no other possibilities.

The International Potato Centre (CIP) was possibly the worst in this respect. For years its scientists were telling the world that there was no such thing as horizontal resistance. Vanderplank's writings were ignored. John Niederhauser's work in Mexico was ignored. My own later, and much less important, potato work in Kenya was also ignored. John Niederhauser who, by rights, should have been in charge of CIP research, was rigorously excluded from its affairs. On the one occasion that I visited the place, I was shouted down during a scientific meeting. In fairness, however, I must comment that this was many years ago, and that CIP is now greatly improved. Nevertheless, the CGIAR Centres, as a group, continue to neglect horizontal resistance.

Secondary Problems in the Green Revolution

The miracle wheats and rices both ran into what the Mendelians called ‘secondary problems’. There are vertical resistances in the miracle wheats, and they fail periodically. On one occasion in Mexico, many tons of special fungicide had to be air-lifted in from Europe, at huge expense, as an emergency measure, to save a large area of wheat whose vertical resistance had broken down. Equally insidious, the miracle wheats have proved to be abnormally susceptible to a few diseases which were previously quite unimportant. They have little resistance to *Septoria* diseases, for example, apparently because these fungi have a low epidemiological competence in Mexico, where the wheats were bred and selected. These diseases are now of major importance in other parts of the world where the fungi have a considerably higher epidemiological competence. The same is true of diseases which do not (or did not) occur in Mexico, such as ‘karnal bunt‘ in India.

The miracle rices were selected in the Philippines and they too had abnormal susceptibility to parasites which either do not occur, or which have a low epidemiological competence, in that area. For example, some of the miracle rices could not be grown in India because of a bacterial blight, and a virus disease called ‘tungro‘.

Rice has vertical resistance to one of its diseases, called ‘blast‘ (*Piricularia oryzae*), and one of its insect pests, called the brown plant hopper (*Nilaparvata lugens*). Blast disease has proved an intractable and recurring problem because of endless failures of vertical resistance. The brown plant hopper has proved even worse because, when the vertical resistance to it failed, the miracle rices were so susceptible that there were unheard of population explosions of this pest. There were so many hoppers around that they invaded neighbouring, resistant rice crops in huge numbers. These crops were often old, local landraces which had an adequate level of horizontal resistance to control normal infestations of brown plant hoppers. But their resistance was entirely inadequate to control this parasite interference, and the abnormal, and artificially high, levels of infestation. It was at this sad and sorry point that subsistence farmers in the non-industrial world were advised, for the first time ever, to start spraying their rice crops with crop protection chemicals.

No new green revolutions

Interestingly, the entire Green Revolution was based on two characters, the short straw of wheat, and the short straw of rice, which are both inherited in a Mendelian fashion. This, of course, was a tremendous boost for the Mendelian school of plant breeding. Suddenly, for the first time in half a century, the Mendelians had found inherited characters, other than resistance to parasites, that were of major economic and agricultural significance. In spite of the secondary problems, the dwarf wheats and rices were undoubtedly the two most important agricultural developments of the second half of the twentieth century, and they were the result of Mendelian inheritance. More than ever, pedigree breeding methods became ‘mainstream’ science.

This simple fact has had two very profound consequences. First, it confirmed and prolonged the Mendelian domination of plant breeding. The Green Revolution was claimed as a new triumph of the Mendelian school. It should, perhaps, be regarded as the last gasp of the Mendelian school.

It is possible, although rather unlikely, that a Mendelian character of major agricultural importance has still to be discovered. Crop science has had nearly a century in which to find such characters and, bearing in mind that virtually every crop geneticist was a Mendelian, they have not found many. Just short straw in wheat and rice, and vertical resistances. All other single-gene characters, such as seed and flower colour, are of quite minor economic significance.

Secondly, no new green revolutions were produced by the expensive, monopolistic, International Centres because no one could find even one new Mendelian character that could make such a revolution. If we are to have new green revolutions as, indeed, we probably can, and will, they are more likely to emerge from quantitative genetics, and from breeding plants for quantitative resistance which is durable, complete, and comprehensive.

There have been other green revolutions, in the past, although they were never called this. The development of sugar beet from fodder beet (Chapter 2) in the nineteenth century created an entirely new crop, and entirely new beet sugar industries, in many temperate countries. The breeding of sugarcane, which started in the late nineteenth century, had just as dramatic an effect on sugarcane production as did short straw on wheat and rice cultivation. The development of hybrid maize in the United States, and later most of the world, was even more important. Similarly, the breeding of new soybean varieties transformed an insignificant crop into the second largest crop in the United States. These developments all depended on quantitative genetics. On the few occasions when Mendelian characters were employed, they were a positive nuisance, because they provided vertical resistance to parasites, and nothing else.

Genetic Conservation

Finally, the Green Revolution, and the Mendelian school of genetics on which it was based, has led to another misconception. The centre of origin of wheat is in the Middle East, in the area that archaeologists call the ‘Fertile Crescent‘. This area used to be full of small farmers cultivating an incredible diversity of different wheat lines. When the wheat breeders needed new vertical resistance genes, to replace those that had failed, they usually searched for them in the wheats of these small farms.

The miracle wheats, however, yielded so much more than these old wheats that they quickly began to replace them. The small farmers of the fertile crescent, and elsewhere, discarded their old wheats in favour of the new. A side effect of this improvement was that genetic diversity began to be lost. There was a great outcry about this loss of diversity, because there was a fear that valuable resistance genes would be lost for ever. A new scientific discipline, called genetic conservation, was born of this fear, and wheat ‘gene banks‘ were established to ensure the survival of this diversity. Soon, gene banks were being set up for many other crops also, and a lot of research was undertaken to discover how best to store huge numbers of seeds in a viable condition for long periods of time.

Genetic conservation has now become part of the received wisdom of both crop scientists and green activists all over the world. But no one seems to have questioned just what we are trying to conserve. Mendelian genes? Vertical resistance genes? This is what the original wheat conservation was all about. It concerned vertical resistance genes and nothing else, other than some vague and ill-defined unknowns. And it was copied uncritically in most other crops, irrespective of whether they possessed vertical resistances or not, and regardless of whether we need vertical resistances or not.

If the world eventually abandons Mendelian genetics, and moves to quantitative genetics, we will not need these huge gene banks. Quantitative genetics does not depend on single genes. It depends on numerous polygenes which can vary in their frequency but which are always present in a mixed population. Obviously, we must have *some* genetic conservation, even with quantitative genetics. But we will need far less than the Mendelians suppose. Each quantitative breeding program will need a reasonably wide genetic base, but no more. In practice, that genetic base will normally consist of a range of modern cultivars, and the farming system itself will often maintain an adequate genetic diversity. If greater changes are required, a gene bank could be useful. But even if the old cultivars and primitive archetypes have been lost, the breeders can usually go back to the wild progenitors to find genetic diversity, if absolutely necessary. So, it can be argued that our current gene banks are something of a white elephant, and a rather expensive white elephant at that. (This topic is discussed further in Chapter 21).

Many organic farmers, who cannot obtain the seeds they need from the existing commercial seed suppliers, are concerned about the conservation of old crop varieties. They speak of ‘Heritage Seeds’, and ‘Heirloom Seeds’, which date from before the days of crop protection chemicals, and which are consequently resistant to many parasites. While this conservation is admirable, an even better idea is to create new, superior cultivars through the work of plant breeding clubs (Chapter 24) .

Chapter 20

Maize in Tropical Africa

On his return from the New World, Columbus took maize to Spain. From the Iberian Peninsular, the Portuguese then took maize to West Africa and, soon after, to the countries of the Indian Ocean. Maize has thus been in Africa since the early sixteenth century, and it has been the staple food of most of Africa ever since.

There is a disease of maize called ‘tropical rust’ caused by a microscopic fungus named *Puccinia polysora*. It is called ‘rust’ because the fungus produces spots of rust-coloured spores on the leaves, in a manner closely similar to coffee rust (Chapters 4 & 21). And it is called ‘tropical’ rust because it has epidemiological competence (i.e., it is able to cause epidemics) only in the tropics. For this reason, the disease could not survive in the Iberian Peninsular (assuming it ever got there, which is doubtful) and, consequently, it did not reach Africa, which remained free of this maize parasite for about four centuries.

Tropical rust apparently arrived in Africa as a result of the development of trans-Atlantic air transport. It is thought that the rust was accidentally introduced, in the 1940s, on green corn cobs flown from tropical America to West Africa. The rust then became a ‘re-encounter parasite’, because it had been separated from its host for some four centuries, and then it re-encountered it again, in a new area.

The disease in equatorial Africa was devastating, and it ruined the maize crops, in much the same way that blight ruined the potato crops of Europe, during the hungry forties. This was another example of crop vulnerability, resulting from an extreme susceptibility in the absence of a foreign parasite. When the parasite was inadvertently introduced, the susceptibility was revealed, and the vulnerability was manifested. Potential damage became actual damage.

Tropical rust reached East Africa, in Kenya, in 1952. As a young plant pathologist, straight out of university, I arrived in Kenya in 1953, and this disease proved to be one of the formative experiences of my career. On my arrival, I found government officials in a state of considerable alarm, because there were real fears of a very serious famine.

Based on earlier experience gained in West Africa, a team of scientists in Kenya had launched a breeding program for resistance to tropical rust. They used the accepted procedures of the day, and they first looked for a genetic source of resistance. They could not find a source of resistance in Africa, and they had to use resistant lines imported from Central America. Inevitably, this was vertical resistance and, as it happens, vertical resistance to tropical rust of maize breaks down extremely quickly. In Kenya, the tropical rust fungus produced new strains so rapidly that each new vertical resistance failed while the breeding work was still in progress.

I myself was too junior to be involved in this work, but no one could prevent me from observing it with a lively curiosity. On my first visit to Coast Province, I was shown the disease. The maize crops resembled scrap metal in junk yards, with many leaves showing little but the colour of rust, with scarcely a speck of green to be seen anywhere. Many of the plants were killed before they could even form flowers, let alone produce seed. It was a depressing sight. However, matters soon began to improve.

The first good news was that the disease lived up to its name. It really was confined to a hot, tropical climate. The equator runs right through the middle of Kenya and, at the equator, the disease loses epidemiological competence at altitudes above 4000 feet. At sea level, it lost epidemiological competence at the latitudes of the tropics of Cancer and Capricorn. The fears of a major famine receded rapidly when it was realised that the Highland maize crops were safe. The majority of the population of Kenya, and the bulk of the agriculture, are located in the Highlands, which are all above 4000 feet in altitude.

The next good news was that the severity of the disease appeared to be slowly declining, and it continued to decline until, about six or seven years after its first appearance, it ceased to have any importance whatever. The problem solved itself. It did so without any help from either plant breeders, or plant pathologists. As we now know, the problem solved itself naturally, by the operation of normal biological processes. These processes led to a steady accumulation of horizontal resistance until the disease was no longer important. If we analyse just what happened during these processes, we can learn some important lessons on how to breed plants for horizontal resistance.

These are those lessons.

Lesson 1: The bankruptcy of the Mendelians' resistance

Perhaps the first lesson was that the traditional approach to breeding crops for resistance to their parasites was useless. The Mendelian breeders used genetic sources of single-gene resistance in maize imported from Central America, and they employed gene-transfer techniques to incorporate them into the local maizes. Obviously, these were vertical resistances. Unfortunately, the parasite was able to match them so quickly that the use of this kind of resistance was futile. Being in Kenya at that time, I shared the dismay of the breeders when their first resistance gene, named *Rpp*1, was matched in field trials, well before any seed was available for farmers. The second resistance gene, named *Rpp*2, was matched in the research greenhouse, at an even earlier stage than the first gene. Then the combination of both genes was matched. By this time, it was apparent that tropical rust was no longer a serious disease, and the breeding program was abandoned.

With this disease, the resistance produced by the Mendelian breeding method proved to be unusually short-lived, because the rust is able to produce new strains so quickly. I know of only one disease in which vertical resistances are matched more quickly. This is potato blight in Mexico, where foreign commercial cultivars with vertical resistances are matched in their first season, almost as soon as the sprouts appear above the ground (Chapter 18).

When we look at all the vertical resistances of crops, there is thus great variation in the durability of those resistances. With tropical rust of maize, it fails so quickly that it has no agricultural value at all. At the other extreme, a few examples of vertical resistance have endured for most of the twentieth century, and they are very valuable (Chapter 16). The majority of vertical resistances fall between these two extremes, and are of limited value. For example, after nearly half a century of wheat breeding in Kenya, it was calculated that the average commercial life of a new, vertically resistant, wheat cultivar was four and a half years. It takes about eight years to produce a new wheat cultivar, using the Mendelian breeding methods.

Lesson 2: The vindication of the biometricians

The accumulation of polygenic resistance in the African maize landraces was a total vindication for the biometricians.

However, no one recognised this at the time. In the late 1950s, we in Kenya knew that the tropical rust of maize had declined to insignificance, but we had no explanation for this. We knew that the official resistance breeding program had failed, but we were having similar experiences in our breeding of other crops, such as wheat and potatoes, in which valuable resistances were repeatedly being lost. The difference was that the tropical rust of maize was no longer a serious disease, while the various parasites of wheat and potatoes continued to be very serious indeed.

This accumulation of resistance in maize went largely unnoticed in the world at large, and many crop scientists are still unaware of it. This is understandable because things that happen in Africa tend to remain unknown, unless, sadly, large numbers of people happen to die. Nevertheless, this accumulation of resistance in maize was among the most important crop science events of the twentieth century. It was important because it both demonstrated the value of horizontal resistance, and it taught us exactly how to breed other crops for horizontal resistance. However, this importance did not became fully apparent until Vanderplank started publishing his highly original and innovative books on plant diseases. Only then did it become possible to extract a slew of lessons from the maizes of tropical Africa.

It was soon after the arrival of Vanderplank‘s first book, in 1963, that it dawned on me that the best way to breed our crops for parasite resistance was to imitate the behaviour of the African maize landraces, following the appearance of tropical rust. I have been trying to persuade others of this ever since, with very little success. The Mendelian tradition dies hard.

Lesson 3: The erosion of horizontal resistance

When maize was being cultivated in Africa, in the absence of tropical rust, it had no need for resistance to this parasite. There was negative selection pressure for resistance, and the resistance was gradually lost. This was an excellent example of the erosion of horizontal resistance. Because this erosion resulted from genetic changes in the host population, it is termed a host erosion of horizontal resistance (Chapter 13). It was also a massive erosion. There was very little resistance left. This is why the African maize was so susceptible to the rust when it first appeared. Furthermore, because subsistence maize crops are genetically diverse, and genetically flexible, this erosion occurred during the *cultivation* process (Chapter 8).

A comparable erosion has occurred in many modern cultivars, which are genetically inflexible. But, here, the erosion occurred during the *breeding* process. These cultivars have been subjected to about a century of breeding with negative selection pressures for horizontal resistance. These negative selection pressures usually occurred because of a functioning vertical resistance, or because of the use of crop protection chemicals, during the breeding process. When cultivated in the absence of crop protection chemicals, many modern cultivars are now as susceptible to some of their parasites as the African maizes were when tropical rust first appeared. These maizes in tropical Africa can tell us a lot about our own crops, and the way we have been breeding them. And just how susceptible our modern crops are now. And precisely why it is that we now have to use crop protection chemicals in such huge quantities.

Lesson 4: Genetic flexibility

Next, we must enlarge on the concepts of genetic flexibility, and selection pressure. As we have just seen, the African maize crops could respond to selection pressures during the cultivation process, because they were open-pollinated, genetically diverse, and genetically flexible. They could not only lose horizontal resistance, because of negative selection pressure in the absence of tropical rust. They could also gain horizontal resistance, because of positive selection pressure in the presence of the rust. And both of these processes occurred during cultivation.

Most modern cultivars are genetically uniform, and genetically inflexible. As we saw in Chapter 8, we positively want them that way in order to preserve valuable agricultural characteristics. For precisely this reason, these cultivars do not gain or lose horizontal resistance during the cultivation process. They can gain or lose it only during the breeding process.

The fact that modern cultivars need so much protection from crop protection chemicals suggests that they have lost a lot of horizontal resistance. And this further suggests that there is something very wrong with the breeding methods that we have been using for most of the twentieth century. Equally, these modern cultivars cannot gain horizontal resistance during the cultivation process. They can gain it only during the breeding process. If they are to do this, we must change our breeding methods in order to ensure that they include positive selection pressures for horizontal resistance.

Lesson 5: Population breeding

It will be recalled from Chapter 2, that the biometricians had developed their own method of plant breeding, known as population breeding. This method involves recurrent mass selection, in which only the best individuals of each generation are allowed to become the parents of the next generation. This is exactly what happened with the maize landraces that were exposed to tropical rust. When the rust first appeared, many of the maize plants were killed by it. Relatively few plants survived long enough to produce flowers. And only some of those were resistant enough to produce a few seeds. It was this minority of very susceptible but *relatively* resistant plants that became the parents of the next generation.

Had this disaster happened to modern commercial farmers, they would have rejected the cultivar, and replaced it with a different one. This, after all, is precisely what happens with the twentieth century boom and bust cycle of breeding vertically resistant cultivars. But the farmers in Africa were much closer to nature. They had confidence in their treasured landraces, and they resolutely refused to abandon them. They kept the few seeds produced by their devastated crops, and they cherished them. There was no question of eating them. Subsistence farmers eat their seed only the very worst of famines and, in this famine, the Government had provided food relief. So the farmers could keep their precious seeds, and these seeds became the parents of the next generation.

These farmers were all peasants. They had small, subsistence farms, and they were poor. Most of them were uneducated and illiterate. But they displayed great wisdom. This wisdom involved hope, patience, and, above all, a complete trust in nature. And their trust was magnificently vindicated as their prized landraces slowly accumulated more and more resistance, and yielded more and more food, of the quality they liked best.

Lesson 6: The nature of the resistance

The resistance that accumulated was undoubtedly horizontal resistance. Some scientists have attributed the decline in the tropical rust to the official breeding program for vertical resistance. One author (who, in charity, need not be named), discussing maize breeding programs, and the use of single-gene resistance to maize diseases, used the phrase "...the most spectacular was obtaining resistance to *Puccinia polysora* in Africa." He really believed the tropical rust problem has been solved by the vertical resistance breeding program, and he was totally ignorant of what a fiasco that program had been.

Other scientists suggested that the resistance was really vertical resistance, because they secretly believed that this is the only kind of resistance that exists. However, the resistance has now endured for more than forty years without any suggestion of a failure. It must be remembered that, in the Mendelian breeding program, three vertical resistances failed so quickly that the breeding process could not even be completed.

Other scientists have suggested that the resistance might result from a mixture of many different vertical resistances. But, were this so, the Mendelian breeders would have had no difficulty in finding resistance genes in the African maizes when the rust first appeared. In fact, they found none at all.

All the evidence is clearly in favour of this being horizontal resistance. But this evidence is circumstantial only. No one has done any research on this matter for a very simple reason. These countries in Africa are poor countries. They cannot afford academic research. They can afford research only for the most pressing of problems. And tropical rust is no longer a problem.

Lesson 7: Transgressive segregation

When the rust first appeared in the tropical maizes, there was an immediate, and very strong, positive selection pressure for resistance. As we have seen, the mechanism of this selection pressure was that the most susceptible individuals were killed. Less susceptible individuals managed to survive but failed to produce pollen or seed. The least susceptible individuals managed to produce pollen, and a few seeds, and they became the parents of the next generation.

The next generation was changed genetically because all the individuals in it were the progeny of a very small minority of relatively resistant parents. The new generation had more resistant individuals in it than did the previous generation. Even more important, the most resistant individuals in the new generation had a higher level of resistance than any of their parents. As we have seen (Chapter 12), this phenomenon is called transgressive segregation.

This fact of transgressive segregation is essential to the accumulation of horizontal resistance and, indeed, to the accumulation of any quantitative variable. The explanation of how it works is so important that it is briefly repeated here. Suppose that, among the surviving plants that become parents, which are highly susceptible, each has only 10% of the alleles contributing to horizontal resistance. But, if they each have a *different* 10% of alleles, some of their progeny will have more than 10% of the total available alleles. These individuals will be more resistant than either of their parents. Under a strong positive selection pressure for resistance, these more resistant individuals will have a reproductive advantage, and will become the parents of most of the next generation. In the next generation, the process of transgressive segregation is repeated. And the accumulation of resistance continues until all the individuals in the population possess most of those resistance alleles, and no more resistance is needed.

Lesson 8: On-site selection

On subsistence farms, each farmer keeps some of his own harvest for seed. He maintains a local landrace which is genetically flexible and has responded to the selection pressures in the local environment, just like an ecotype in a wild ecosystem (Chapter 8). Indeed, an open-pollinated landrace can be called an agro-ecotype. Consequently, a landrace is normally in a state of excellent balance with its own, local agro-ecosystem. In systems terminology, this is called local optimisation. However, if a landrace is taken to a different agro-ecosystem, it will perform less well. This is because various environmental factors will be different. These factors include the components of climate, such as temperature and rainfall, and various aspects of the soil, such as structure, nutrients, and microbiological activity. Many of the subsystems called pathosystems will also differ, because the epidemiological competence of the many different species of parasite will also be different. In the new environment, the foreign landrace will have too much resistance to some parasites, and too little to others.

For these reasons, when breeding plants for horizontal resistance, the screening must be done locally. As we have seen (Chapter 12), this is called on-site selection, which means that the screening is conducted in the *area* of future cultivation, in the *time of year* of future cultivation, and according to the *farming system* of future cultivation.

When the vertical resistance breeding was in progress in Kenya, the scientists concerned received a report that maize in Malawi was highly resistant to tropical rust. So they imported some of this maize for testing in Kenya. It proved to be just as susceptible as the Kenya landraces, and the scientists concluded (wrongly) that the strains of the fungus in Kenya were different from those in Malawi. Malawi is about 1000 miles south of Kenya, and it is much closer to the Tropic of Capricorn. Consequently, tropical rust has a greatly reduced epidemiological competence in Malawi. A level of horizontal resistance that was adequate in Malawi, was quite inadequate in Kenya, where the rust has a very high epidemiological competence. As we have seen (Chapter 13), this is called the environmental erosion of horizontal resistance. It indicates why on-site selection is essential when breeding for horizontal resistance.

Lesson 9: No source of resistance

The maize crops that were exposed to tropical rust were landraces. This is the technical term for crop varieties that were cultivated before the discovery of pure lines, and genetic uniformity. Subsistence maize crops in the tropics are some of the very few crops still being cultivated as landraces. Even though all the plants within a landrace are very similar in appearance, they differ genetically among themselves. This genetic diversity is not very great, but it is enough to embrace all the alleles necessary for the accumulation of a very high level of horizontal resistance (Chapter 12). Far more important is the fact that the African maizes accumulated high levels of horizontal resistance without the genetic source of resistance that is essential in the Mendelian breeding methods.

It follows that, when we breed for horizontal resistance, we must have genetic diversity, but we do not need very much diversity. And, above all, we do not need a Mendelian source of resistance.

Lesson 10: Selection pressures

When the rust first appeared in an area of high epidemiological competence in tropical Africa, it was extremely damaging. The selection pressure for resistance was then very strong. However, the selection pressure was less in West Africa than in equatorial East Africa, because the maize areas of West Africa are five to ten degrees north of the equator, and appreciably above sea level.

In either event, as resistance accumulated, the selection pressure declined. This happened because the least resistant plants were no longer being killed, or even prevented from flowering. They were merely suffering a reduced rate of reproduction. Eventually, all the maize had adequate resistance for its own agro-ecosystem, and the selection pressure for resistance was reduced to a mere maintenance level. That is, if a rare, susceptible individual happened to appear within a local landrace, it would be so severely parasitised that it would have few progeny.

This steady reduction in selection pressure has two warnings for plant breeders. First, the initial selection pressure may be so high that the entire screening population will be killed off entirely. If this total destruction appears likely, it is entirely reasonable to use crop protection chemicals towards the end of the screening process. This will enable the least susceptible individuals to form a few seeds.

The second warning is that, as resistance accumulates, and the selection pressure for resistance declines, the rate of breeding progress, or genetic advance, will also decline. This decline can be prevented by artificially intensifying the epidemics with spreader rows or surrounds. Spreader rows intersect the screening population at regular intervals, while surrounds are planted all around it. The spreader rows or surrounds are planted with susceptible plants in order to generate large numbers of parasites that then move into the screening population. However, great care must be taken to ensure that these susceptible spreader plants are not allowed to introduce any undesirable pollen into the screening population. There are various techniques for ensuring this (Chapter 25).

Lesson 11: The number of screening generations

Initially, the maize in Africa had a very low level of horizontal resistance to tropical rust, but it accumulated enough resistance to control the disease in 10-15 generations. This indicates the probable duration of a horizontal resistance breeding program. There are two generations of maize each year in most of tropical Africa, and adequate resistance thus accumulated in 5-7 years. In temperate climates, with only one growing season each year, this period would be doubled. However, the duration of the program can be reduced by beginning with plants that have a rather higher level of horizontal resistance than the African maizes started with, and by increasing selection pressures with artificial inoculation. Conversely, more time may be required if the breeding involves resistance to several different species of parasite, as will usually be the case. In general, therefore, a horizontal resistance breeding program is likely to require some 5-10 generations to produce worthwhile results. But it can probably be continued with profit, producing diminishing returns, but cumulative improvements, for some time.

The duration of the breeding program is also governed by the generation time, which determines the breeding cycle. One breeding cycle is the period from cross-pollination of the parents until the following cross-pollination. When breeding maize in tropical areas, it is possible to have two breeding cycles in each year. When breeding potatoes in high-altitude, equatorial Nairobi (Chapter 18), I was also able to process two breeding cycles each year. However, in temperate countries that have a winter, only one breeding cycle is possible each year, when working with crops that are either open-pollinated or vegetatively propagated. Late selection (Chapter 25) is necessary with self-pollinated crops, and the breeding cycle is then likely to require two years in temperate areas. However, various techniques can shorten the breeding cycle. Obviously, if the duration of a breeding cycle can be halved, the results will be achieved twice as quickly.

Lesson 12: The holistic approach

Many crop scientists like to study the mechanisms of resistance, which are many and varied, but two examples of resistance mechanisms will be sufficient for our purposes. A common resistance mechanism is called hypersensitivity, and it is a form of extreme sensitivity to the presence of a parasite. When a parasite penetrates host tissue, all the host cells surrounding it die very quickly, and the parasite dies with them. This happens mainly on a microscopic scale, and the dead tissue shows as a minute, necrotic fleck which is just visible to the naked eye. This mechanism is often, but by no means exclusively, the mechanism of vertical resistance.

Another mechanism is hairiness. Very hairy plants are resistant to a range of small insect parasites, such as aphids, white flies, and leaf hoppers. This mechanism confers horizontal resistance.

It is a feature of Mendelian plant breeding that the breeder usually prefers a single, prominent resistance mechanism, and preferably one whose inheritance is controlled by a single gene. Tropical rust of maize has taught us otherwise. This lesson comes mainly from a comparison with another rust disease of maize caused by the fungus *Puccinia sorghi*, and known as the common rust of maize. Unlike tropical rust (*Puccinia polysora*), the common rust is not confined to the tropics, and it occurs wherever maize is grown. It has been in Africa for as long as anyone has known. Apart from this, the two parasites are physically so similar that it takes a specialist to recognise which is which.

The maize landraces that were so susceptible to tropical rust were, at the same time, highly resistant to common rust. Some 10-15 generations later, these maize landraces were highly resistant to tropical rust as well.

It is obvious, first of all, that the horizontal resistance to one rust is entirely different from, and independent of, the horizontal resistance to the other rust. Furthermore, there are no visible differences between the resistant and susceptible maizes. The plants look the same, and the seeds look, cook, and taste the same. And there are no obvious resistance mechanisms. It is thought that the resistance to each rust is the result of many different mechanisms and that, very probably, each mechanism is quantitatively inherited, and quantitatively variable. We have no idea what these mechanisms are. Nor do we need to know. *It is entirely feasible to breed for horizontal resistance without knowing anything about the resistance mechanisms involved.*

In addition to the multiplicity of mechanisms to each parasite, there was also a multiplicity of parasites. Maize has many different leaf blights, stalk, cob, and root rots, and other diseases, as well as a wealth of insects that eat, suck, or tunnel through its tissues. With the one special exception of streak virus (see below), maize landraces have high levels of resistance to all of these local parasites. It could be said that the many species of the parasites of maize are so numerous that we do not normally attempt to catalogue all of them. And, it could be said also that they normally cause so little damage, that we do not even notice them. And the resistances to all of them result from so many different mechanisms that we cannot even begin to explain how they work. Nor do we need to do so.

This is the holistic approach, operating at the highest systems level. It is the converse of ‘reductionism‘, which focuses entirely on details in the lower systems levels. To breed for one single resistance mechanism, which operates against one single species of parasite, is to operate at too low a systems level. This, it will be recalled (Chapter 10), is called sub-optimisation. In systems analysis, sub-optimisation leads to false conclusions and, in systems management, it leads to material damage to the system.

Nature knows better. In wild ecosystems, in wild pathosystems, and in genetically flexible crop pathosystems, the selection pressures operate at the highest systems levels, and there is no sub-optimisation. When we breed crops for horizontal resistance, we should do the same. We too must have the holistic approach.

Lesson 13: Parasite interference

The effects of parasite interference must be taken into account when screening plants for resistance in a horizontal resistance breeding program. This interference operates between individual plants within the screening population. The most resistant plants will normally be surrounded by plants that are less resistant. Allo-infection from the susceptible to the resistant plants will ensure that the most resistant plants will have a level of parasitism that is considerably *higher* than if there were no interference. Even though they are the most resistant plants in the entire screening population, they may well look awful.

When screening, therefore, it is important to select the *least* parasitised plants, regardless of how severely parasitised they may be, or how terrible they may appear. In other words, all measurements of resistance must be *relative* measurements. Only the best plants are kept, however dreadful they may look. In the early stages of the program, even these best plants are likely to look frightful. In fact, a Mendelian breeder would probably abandon the entire program, on the grounds that it was futile. But those best plants represent the first stages of a gradually changing, and very important, process of quantitative improvement.

Lesson 14: Size of the screening population

In the 1950s, the average size of a subsistence farm in Kenya was about eight acres, which is roughly the area that can be hand-cultivated by one family. The whole farm would normally be planted to the same mixture of crop species, which usually included maize, sweet potatoes, cassava, various species of peas and beans, bananas, papaya, and so on, all jumbled up together. One farm thus constituted a single maize screening population which probably contained several thousand maize plants. However, when farms were within about 100 metres of each other, there would be a significant degree of pollen exchange between farms.

This indicates the size of screening population necessary for effective recurrent mass selection for horizontal resistance. The population should be numbered in thousands rather than hundreds and, depending on the size of plant, the land available, and the number of people cooperating, may be as high as some hundreds of thousands. The exact size is not critical, but a general rule is that the larger the population, the smaller is the proportion of that population that need be selected as parents of the next generation, the greater is the selection pressure, and the more rapid is the genetic advance.

Lesson 15: The range of levels of horizontal resistance

There is a very large difference between the lowest and the highest levels of horizontal resistance to tropical rust. With a very low level of resistance in Africa, the maize crops were largely destroyed. With a very high level of resistance, the tropical rust is controlled to the point of causing no significant loss of crop. This difference is far greater than most Mendelians are prepared to credit.

However, we have reason to believe that the total range of differences is even greater.

The low level of horizontal resistance to tropical rust, at the time of the first re-encounter, was considerably more than the minimum level. For a variety of reasons too complex to discuss here, negative selection pressures fade away well before the minimum level of horizontal resistance is reached. The only way to discover the minimum attainable level of horizontal resistance is to conduct an experiment in which there is powerful selection pressure for susceptibility. Obviously, the test plants would have to be protected with a fungicide, once their susceptibility had been determined, but, apart from that, this would not be a difficult experiment to conduct.

The same is true of the upper levels of horizontal resistance. The African maize populations which are no longer susceptible to tropical rust probably have considerably less than the maximum level of horizontal resistance. This is because the selection pressures for resistance faded away, once the reproductive ability of the maize was no longer affected by the rust. A fairly simple experiment would determine just how much more resistance could be accumulated before the maximum attainable level was reached.

To the best of my knowledge, these experiments have never been done, and we can only speculate as to what the results might be. But we can be confident that a level of horizontal resistance that is somewhat above the minimum level, is a very high susceptibility. The destruction of the African maize crops was not total. Even in the worst years, the farmers got at least enough seed to sow their next crop. But in terms of practical farming, the destruction of their harvest was complete.

From this we can conclude with complete assurance that most modern cultivars have rather more than the minimum levels of horizontal resistance. We can think of a few cultivars that would be a total loss if they were not treated with protective chemicals. Any European potato cultivar, when grown in a Mexican blight epidemic (Chapter 18), is a case in point. But even these cultivars have more than the minimum level of horizontal resistance. This should encourage anyone planning to breed for this kind of resistance, because even the most susceptible cultivars still have enough horizontal resistance to initiate a breeding program.

Equally important, the African maizes have shown that a level of horizontal resistance that is somewhat less than the maximum will provide a complete control of a parasite, without any use of crop protection chemicals. This should encourage breeders who may believe, perhaps incorrectly, that they might reach the limits of horizontal resistance breeding without actually controlling the parasites in question.

Lesson 16: Comprehensive horizontal resistance

Subsistence farmers in tropical Africa cultivate their maize without any use of crop protection chemicals, and without any serious pest problems. This means two things. First, their maize landraces have *comprehensive* horizontal resistance to all the local maize parasites. We can be confident of this because, if resistance to only one species of parasite was inadequate, that parasite would cause significant damage. No parasite causes significant damage, therefore none of the many horizontal resistances is inadequate (but see maize streak virus, below).

Second, we can turn this argument the other way round, and contemplate any parasite, of any crop, that does cause significant damage. That damage occurs because that crop has an inadequate level of horizontal resistance to that species of parasite. In other words, we can argue that *any* serious parasite of *any* crop is serious only because there is an inadequate horizontal resistance. If we can increase that horizontal resistance sufficiently by breeding, we can control all serious crop parasites with horizontal resistance. However, only time will tell how universally this argument is valid.

Lesson 17: Selection pressures for other qualities

Apart from their resistance, the new maizes that emerged from the devastation of the tropical rust slaughter were indistinguishable from their susceptible progenitors. Obviously, enough horizontal resistance had been accumulated to control the disease, without any sacrifice of yield, quality of crop product, or agronomic suitability. This indicates that, when breeding for horizontal resistance, we should use the best available cultivars as parents. That is, we should use the best available cultivars in terms of yield, quality of crop product, and agronomic suitability. These cultivars will have major susceptibilities to a number of parasites, and our task is to accumulate horizontal resistance to these parasites without sacrificing those other qualities. That means we must exert selection pressures for all of those other qualities throughout the entire duration of the breeding program. In practice, this should not be difficult as we are merely preserving existing qualities. We have to ensure that they do not become eroded in the course of our breeding for resistance. In practice, some slight erosion is likely to occur but it will easily be restored in the later stages of the breeding program.

Lesson 18: Seed screening

We saw in the introduction that crop losses can occur both before and after harvest. Post-harvest losses can be caused by various storage insects and rotting agents, and some cultivars are more susceptible than others to these parasites. This means that it is possible to screen the harvested product for horizontal resistance to storage parasites. With some crops, such as fresh fruit and vegetables, the prospects of such work are obviously poor. With many cereals and grain legumes, the prospects of accumulating useful levels of resistance are somewhat better. In general, however, storage pests are better controlled with environmental controls. For example, storage rots will not occur if the grain is dry. And storage pests cannot survive if the grain is stored without oxygen. Equally, refrigeration will delay the development of storage pests and rots.

A more important aspect of screening seed concerns the laboratory screening of cereals and grain legumes, in which the harvestable product is the seed itself. Yield is measured by the total weight of all the seeds coming from one plant, but it is important that these seeds have the optimum size. For example, several hundred grains that are small and shrivelled are less valuable than a few tens of grains that are large and fat. For this reason, it is necessary to both weigh and count the seeds harvested from each plant. It then possible to calculate the 'hundred seed weight' or the 'thousand seed weight', depending on the species of crop. The plants that have the highest yield of the optimum seed size are the ones to keep as parents for the next generation. However, there is an important caveat to this rule. In the early stages of the breeding program, all the seed is likely to be shrivelled and small, simply because even the best plants were severely parasitised. Once again, all measurements must be relative measurements.

Seed can also be screened for other qualities, such as colour, hardness, and specific gravity. The specific gravity can be measured by putting the seeds into a salt solution of known concentration, and separating the ‘floaters’ from the ‘sinkers’. Alternatively, a machine called a gravity separator can be used. It is clear, however, that destructive tests (e.g., cooking) can be employed only after a certain bulk of pure line seed has been accumulated.

Lesson 19: Demonstration of horizontal resistance

As we saw in Lesson 6 (above) the horizontal nature of the resistance to the maize in tropical Africa has not been conclusively demonstrated, and our evidence is circumstantial only. Breeders working with horizontal resistance, however, will want a more definite indication of the nature of the resistance.

The best proof of the horizontal nature of resistance is to demonstrate the polygenic control of its inheritance. This is done by making an experimental cross with a susceptible plant, and measuring the resistance of each individual in a progeny of about one hundred plants. When the frequency of each category of resistance is plotted on a graph, there should be a bell-shaped curve, which indicates a normal distribution, and is clear evidence of a polygenic inheritance. Conversely, if there is a Mendelian ratio of resistant to susceptible individuals in the progeny, the inheritance of the resistance is controlled by a single gene, and the resistance will almost certainly be vertical.

Lesson 20: Measurement of horizontal resistance

The African maizes also showed us the best measurement of horizontal resistance. If there is no significant parasitism in farmers' crops, there is enough resistance. If significant levels of parasitism occur (i.e., enough to have an economic effect on either the yield and/or the quality of the crop product), then the resistance breeding should continue. However, these field measurements should be made under conditions in which there is no parasite interference, and in which all biological controls (Chapter 14) are functioning fully. Both of these criteria have now applied in the subsistence maize crops of tropical Africa since the late 1950s.

Lesson 21: Maize streak virus

There is a virus disease of maize called ‘Streak’ which is interesting because, at first glance, it appears to contradict some of these lessons. The maize host evolved in the Americas, but the virus has an African origin. This is consequently a new encounter disease. The virus is transmitted by insects called leaf hoppers (*Cicadulina* spp.). This discovery was one of the first demonstrations of an insect transmission of a virus disease, and it was made by my old friend and mentor, H.H. Storey, whom I met on my first arrival in Kenya. The virus normally kills an infected maize plant and, incredibly, the maize populations do not develop resistance to it.

The explanation lies in the leaf hoppers. These insects are gregarious, and they like to congregate in colonies. In ecological terms, they have a patchy distribution. And not all the insects are carrying the virus. In practice, only about three percent of maize plants both carry the insects, and become infected with the virus. This is a classic example of a low frequency of parasitism (Chapter 9). This is not a high enough frequency to exert selection pressure for resistance and, as a direct consequence, the maize landraces are highly susceptible to the virus. Infected plants die. This is also a classic example of a high injury from parasitism. This is in sharp contrast to the tropical rust situation in which every plant in the population is exposed to approximately equal levels of infection, and the frequency of parasitism is maximal. The lesson of this is that we must achieve a uniform distribution of parasites, and a maximum *frequency* of parasitism, within our screening populations. Patchy distributions lead to escapes from parasitism, and a false appearance of resistance.

My colleague Ivan Buddenhagen (who developed the very useful concepts of old encounter, new encounter, and re-encounter parasites) showed that the plant hoppers can easily be disturbed, and they are then likely to settle on a different maize host. By disturbing the plant hoppers every day, with two men lightly dragging a bamboo pole across the tops of the plants, he soon obtained a 100% occurrence of streak in his screening population. And he showed that, in a few generations of screening, it was possible to obtain high levels of resistance to the streak virus. However, this resistance cannot be maintained in open-pollinated maize crops. With only a three percent natural infestation of leaf hoppers, there is negative selection pressure for resistance, and the maize soon becomes susceptible again because there is a host erosion of horizontal resistance. A genetically diverse, and genetically flexible crop clearly has disadvantages, as well as advantages.

High levels of resistance to maize streak can be maintained in a hybrid maize seed production program, simply by ensuring that all the parents are infested with leaf hoppers. Any parent plants that show severe symptoms of streak are then removed.

It is perhaps worth commenting that the very high susceptibility of the African maizes to streak virus is, in fact, an *adequate* level of horizontal resistance. So long as only 3% of the plants are infected and killed by the virus, the disease is quite unimportant, because a 3% loss of plants is usually not significant, and it is usually made good by improved growth in the surviving plants. Consequently, a higher level of horizontal resistance is not necessary. Occasionally, a freak season can so favour the leaf-hoppers that the loss of plants can be as high as 30%. In areas where this happens frequently, it justifies a resistance breeding program.

In terms of wild plant pathosystems, this very patchy distribution is a survival advantage for the parasite. By confining its parasitism to a small minority of host individuals, it exerts no selection pressure for resistance. It then has a host with a very low level of resistance. If necessary, it can even consume those few host individuals entirely, without threatening the host's ecological and evolutionary competitive ability.

Maize streak has another lesson for us. I once met a maize breeder in Africa who had recently arrived from Europe. He was breeding maize for resistance to streak virus, which he did not fully understand. In his screening population, he removed all the plants that showed symptoms of streak, on the grounds that they were susceptible. And he kept all the plants that showed no symptoms, on the grounds that they were resistant. But he made no progress because, obviously, he was not screening for resistance at all. He was keeping susceptible plants which had merely escaped the disease, and which only appeared to be resistant. When we breed plants for horizontal resistance, therefore, we must be quite sure that our selections really are parasitised. They must be truly resistant, and not just apparently resistant.

Lesson 22: Hybrid maize

There is a very important lesson about maize breeding that was not illustrated by the maize in tropical Africa, and this is a suitable moment to discuss it. American plant breeders first tackled the problem of breeding seed-propagated crops that are open-pollinated. Self-pollinated crops, such as wheat, rice, and beans, can be genetically manipulated into pure lines (Chapter 7) which breed true. But cross-pollinated crops cannot be treated in this way, because the process of self-pollination, which is essential for the production of pure lines, is detrimental to them. When maize is self-pollinated, it exhibits ‘in-breeding depression‘ in which the vigour and yield are severely reduced. This phenomenon in plants was first observed in England, in 1876, by Charles Darwin, famous for his theory of evolution.

Darwin also observed the converse of in-breeding depression, which is called ‘hybrid vigour‘ or, technically, *heterosis*. If two strongly inbred, and severely depressed, maize lines are crossed, the progeny exhibits hybrid vigour, and it yields about twenty percent more than the best open-pollinated maize crop. Such a progeny is called a ‘hybrid variety’ and the crop is known as ‘hybrid corn’ or ‘hybrid maize’.

William James Beal, in Michigan, was the first person to attempt maize improvement by exploiting heterosis. In 1908, George Harrison Shull, at Cold Spring Harbor, New York, showed that the progeny of two inbred lines of maize would produce a uniform crop, with yields superior to any open-pollinated variety. However, it proved impossible to produce adequate quantities of seed of such hybrids for commercial purposes.

In 1918, Donald F. Jones solved this problem with his research at the illustrious Connecticut Agricultural Experiment Station, in New Haven, where vitamins were first discovered. Jones used a ‘double hybrid’ method. He produced a cross of two single crosses, using a total of four inbred lines. His double hybrid is usually represented as (A x B) x (C x D). It produced a hybrid variety that was uniform, and which yielded twenty percent more than the best open-pollinated maize.

Jones’ double hybrid method solved the problem of commercial seed supply, and it became the basis of one of the most productive advances in the entire history of agriculture in the United

States. The first hybrid corn seed was sold by the Connecticut Experiment Station in 1921.

A second hybrid was developed by Henry Agard Wallace, who launched his own hybrid seed production firm, and later entered politics to become Secretary of Agriculture and then Vice President of the United States. Within fifteen years of Jones' discovery, double hybrid maize was economically important and, by 1950, virtually all the corn of the corn belt was planted to double hybrids. By 1970, virtually every commercial maize crop throughout the industrial world was a double hybrid. In 1999, Wallace's seed firm was sold to a chemical corporation for $7.7 *billion*.

The double hybrid maize had a secondary effect on plant breeding that was both profound and important. The progeny of a hybrid variety does not possess any hybrid vigour, and it reverts to the lower yields of open-pollinated maize. This means that new hybrid seed must be purchased for each new crop, but farmers are happy to do this because the additional cost of hybrid seed is such an excellent investment. This rapid loss of hybrid vigour also means that a plant breeder, who produces a new and superior hybrid variety, is protected from unlawful commercial competition. No unauthorized person can produce seed of that hybrid, because only the breeder possesses the original inbred lines that produce the double hybrid.

The production of hybrid corn seed led to a surge of private enterprise in maize breeding in the United States. Many companies, which grew wealthy on the proceeds of hybrid corn seed, re-invested much of this wealth in research designed to produce even better hybrids. This private enterprise prompted an entirely new idea called ‘plant breeders’ rights’ that is highly relevant to this book, as Part Three will reveal.

Many countries now have legislation designed to protect a new crop variety, in the same way that an author’s copyright protects his writing. A registered crop variety can then earn royalties, just as a book earns royalties. And a plant breeder can hope to produce a ‘best seller’, just as an author can hope to write a best selling book.

Plant breeders’ rights are not necessary in hybrid varieties of open-pollinated crops, such as maize, cucumbers, water melons, and onions, because the hybrid vigour is lost in the next generation. But they are very necessary in all other crops, where they are as essential to private enterprise in plant breeding, as copyrights are to private enterprise in writing, painting, sculpting, photography, and music. The same is true of patents for private enterprise in inventing.

Lesson 23: Other things we did not learn from the maize in Africa

There are two other aspects of modern population breeding that were not emphasised by a study of the African maizes. These are the technique of family selection, otherwise known as 'head-to-row' screening, and the technique of late selection. The details are given in Chapter 25.

Chapter 21

The Loss of Resistance in Coffee

The Origins of Coffee

In spite of the fact that coffee is an old world crop, there are no early historical references to it. There is no mention of coffee in ancient Egyptian, Sumerian, Greek, or Roman records. Nor is coffee mentioned in the Bible or the Koran. It seems that the first historical reference to coffee is an Arabian one, dating from the ninth century A.D.

The Swedish taxonomist Carolus Linnaeus (1707-1778) believed coffee to have originated in Arabia and, more specifically, in *Arabia Felix* (Southern Yemen). He accordingly gave it the Latin name *Coffea arabica*. This area is the source of the world's finest coffee, known as the *Mocha* variety which, sadly, is now virtually unobtainable.

In fact, Linnaeus was mistaken. We now know that coffee originated in Africa, in the eastern, equatorial highlands. *Coffea arabica* was probably an accidental hybrid between two wild species and, somewhat tentatively, we can both date the time of this accident, and locate where it occurred.

Arabica coffee must have appeared at least a century before its first historical record in 850 A.D., and the earliest possible date can be determined by the spice trade of the ancient Romans. In his book *The Spice Trade of the Roman Empire* (1969), J.I. Miller has described how the Romans obtained cinnamon (*Cinnamomum zeylanicum*). At that time, this spice was being produced only in the general area of lowland, tropical S.E. Asia, and its source was a well kept trade secret.

The Romans believed cinnamon to come from Africa but, in fact, it was taken to Madagascar by ancient Austronesian people, who used to sail from Indonesia, straight across the Indian Ocean, as early as the second millennium before Christ. These people also brought the banana, rice, turmeric, and an Asian species of yam, from Asia to Madagascar. The present day inhabitants of Madagascar, the Malagasy, are descended from them. Their language is not one of the African languages, and it belongs to the Austronesian family of languages. Unlike any other people in

Africa, the Malagasy have also cultivated paddy rice, in the Asian manner, since antiquity.

It seems that these Austronesian sailors relied entirely on the monsoon winds to make this 6,500 kilometre journey across open ocean, and that, for this reason, their journeys were strictly seasonal. It is probable also that they relied on the coconut to provide them with both fresh water to drink, and vitamin C to prevent scurvy. One of their items of trade was the scented bark of the cinnamon tree, and the principal market for this bark was the city of Rome.

From Madagascar, the cinnamon was taken by canoe to the east coast of Africa, to an area near the modern border of Kenya and Tanzania which, in ancient times, was called Rhapta. From there, the trade route went overland. This was possibly because the sea journey round the Horn of Africa, to the Red Sea, was too hazardous, or too difficult in the ships of that time. The land caravan would also be greatly enriched in the course of its travels. By the time it reached the Mediterranean, the caravan would have gained wild animals for the Roman circus, Nubian slaves, ebony, ivory, frankincense, gold, and other rare African luxuries.

The overland route went through the area of modern Kenya to southern Ethiopia where it forked. One fork went northwest to the Blue Nile, then by river boat to Alexandria and then, by sea, to Rome. The other fork went northeast to Assab, on the Red Sea coast, where the remains of an ancient Roman port still exist, and then by sea, with a short overland journey at Suez, to the Mediterranean and Rome.

The point about this trade route is that it went right through the heart of the traditional coffee growing areas of Ethiopia, and yet the Romans never knew about coffee. It is inconceivable that the Roman spice trade, which was so sophisticated that it included Indonesian cinnamon, would have remained unaware of such a stimulating and important beverage as coffee, had it been present in Ethiopia at that time. We must conclude, therefore, that coffee was not present in Ethiopia during the period of the Roman spice caravans. The Roman spice trade collapsed with the fall of Rome, and we can accordingly date the appearance of coffee at not earlier than 450AD, and not later than its first historical mention in 850AD. For convenience we can set a tentative date of about 650AD.

The origins of arabica coffee can be determined from botanical data with a fair degree of confidence. There are some sixty species of wild coffee in Africa and India. These wild species are all diploids. That is, they have two sets of matching chromosomes, with one set coming from the male parent and the other from the female parent. Each set has eleven chromosomes and diploid coffees thus have twenty two chromosomes. (a chromosome is a microscopic bundle of the DNA genetic code that controls all things inherited).

Arabica coffee differs in that it is a tetraploid. That is, it has four sets of chromosomes. It is thought, but not finally confirmed, that this is a new species that arose when a rare hybrid was formed between two different wild diploids. Such a hybrid would normally be sterile, because the two sets of chromosomes would not match each other. However, a spontaneous doubling of the number of chromosomes can sometimes occur, and a sterile hybrid then becomes fully fertile, because it now has two double sets of chromosomes, and the two doubled sets match each other. It is highly probable that arabica coffee was formed in this way.

An immediate question is where did this accidental hybridisation occur? One of the more notable botanical features of

Ethiopia is that no wild diploid coffees occur in that country. We can be confident of this because many botanists, myself included, have searched for them without success. A second question, related to the first, concerns the identity of the wild parents of arabica coffee.

The late and little known scientist, I. R. Doughty, is reputed to have hybridised two wild diploids, *Coffea eugenioides* and *Coffea canephora*, at the Lyamungu Research Station, on the slopes of Mount Kilimanjaro, in Tanzania. He did this in the late 1930s, and he obtained a sterile hybrid. However, one lateral branch underwent a spontaneous doubling of its chromosomes, and it became tetraploid and fertile. Apparently this fertile branch was indistinguishable from *Coffea arabica*.

Unfortunately, World war II interrupted his research and, when Doughty returned to Lyamungu after the war, the hybrid tree had disappeared. Unfortunately also, Doughty, who was in many ways a brilliant scientist, disliked writing, and he published little. Doughty died many years ago, and his experimental records are lost. I met him on several occasions but, alas, it never occurred to me to discuss his coffee work. His colleague, who remembered this work, and told me of it, has also died. This evidence is consequently hearsay evidence only, and Doughty's work on identifying the wild progenitors of Arabica coffee must obviously be repeated.

A few of the wild diploid coffees are cultivated, but they all produce coffee that is inferior to arabica, and they all occur wild in Western Africa. This natural distribution would explain why these coffees also remained unknown to the Romans. One of these cultivated diploids is *Coffea canephora* which produces the 'robusta' coffee of commerce, and was used by Doughty in his hybridisation experiment.

The eastern limits of the natural distribution of this species are in Uganda or, possibly, western Kenya, but well to the west of the cinnamon trade route. Doughty's other species, *Coffea eugenioides*, is an East African species, of no culinary value, that also extends into Uganda. If these two species are indeed the progenitors of arabica coffee, the centre of origin must be in the area where their natural distributions coincide. That is, in the general area of modern Uganda.

The hypothesis, then, is that arabica coffee is a tetraploid species, derived by hybridisation between *Coffea eugenioides* and

Coffea canephora, in Uganda, in about 650AD. New tetraploids often have characteristics that are considerably different from either of their parent species. Quite frequently, they have different climatic requirements from either parent and, for this reason, they often flourish in a new area, called the centre of diversification, which may be quite distant, and considerably different, from the centre of origin. Apparently, this happened with arabica coffee. Uganda is too warm and moist for arabica coffee, which probably died out there soon after it was formed. In the meanwhile, however, it was taken to Ethiopia, which became its centre of diversification.

The relatively cool highlands of Ethiopia are separated from the more lush and humid, tropical environment of Uganda by an arid and forbidding arm of the Sahara Desert, that extends from southern Sudan to the Horn of Africa. We must presume that seed of arabica coffee was taken from Uganda to Ethiopia by travellers, possibly as a gift from one king to another. We have good reason to believe this because, it seems, a disease of the wild coffees was left behind. I shall return to this point in a moment.

Coffee obviously became popular in Ethiopia, and its cultivation spread widely. By the ninth century it had become an important item of trade with the Arabs living across the Red Sea in the Arabian peninsular. It will be remembered that the Prophet had forbidden his followers to drink alcohol, and Muslims consequently had only water, fruit juices, and milk to drink. Coffee became a very important beverage for them but, after a war had interrupted the supply of Ethiopian coffee, the Arabs decided to produce their own. They started cultivating coffee in the province of Yemen in southern Arabia. As we have seen, Linnaeus believed that coffee originated in this area and, following centuries of selection and improvement by Arab farmers, these crops became famous as Mocha coffee, the finest of them all.

During the seventeenth century, coffee became popular in Europe. The first coffee house in London was established in the early part of that century, and coffee houses soon became important meeting places for social, political, literary, and business activities, in both Europe and America. Samuel Pepys mentions coffee houses frequently in his London diary (1660-1669) where they were usually known by the name of the owner. Lloyd's coffee house became famous as an insurance exchange, and Boodle's and White's became famous London clubs. In France, coffee houses became so important that they gave their name, *café*, to most of the languages of the world, and the word ‘cafeteria’ is a derivative of this French word.

The world distribution of coffee

Arabian production was inadequate for these rapidly expanding markets of Europe, and coffee became increasingly expensive. In its turn, this stimulated production in other parts of the world. The Arabs were probably the first to take coffee seeds from Arabia to India and Sri Lanka. The Dutch took coffee seed to the island of Java, in modern Indonesia. In 1706, they took one coffee tree from Java to Amsterdam and, as a gift, sent one of its progeny to the *Jardin des Plantes* in Paris. The French sent seed taken from their single tree to Martinique in the West Indies. Attempts to maintain a French monopoly failed, and the crop was soon being cultivated in various parts of Central and South America. Four points about this world distribution of coffee are of interest.

The first concerns the narrowing of the genetic base. Arabica coffee is most unusual, among tree crops, in being self-pollinated. This means that all the seeds coming from one tree tend to be the same. They ‘breed true to type’. As we saw in Chapter 1, the technical term for this is homozygous. Every time coffee was moved from one country to another, transported usually as a single tree, or as only a few seeds taken from one tree, there was an increase in homozygosity, a narrowing of the genetic base. This meant that the coffee that finally reached the New World was a pure line. It was genetically uniform, and all the trees were effectively identical.

This uniformity has considerable agricultural and commercial advantages, but it makes coffee breeding very difficult, because genetic improvement depends on crossing differing types to produce variation. Coffee breeding was impossible in the New World until other coffee lines were introduced, and this happened only to a very limited extent, and only during the twentieth century.

The second point of interest is that, when coffee was moved from one country to another, its pests and diseases tended to be left behind. By the time coffee reached the Americas, it was virtually free of parasites. This freedom from parasites gave the New World an enormous commercial advantage over the Old World, where coffee parasites were common. Until quite recently, the control of coffee parasites was extremely difficult, because modern insecticides and fungicides did not exist. The New World advantage was thus a crucial one, and it led to a commercial domination, in which the Americas now produce about eighty percent of the world's coffee. This happened in spite of the fact that, for about 250 years, the entire coffee crop of Latin America consisted of only one pure line. This degree of monoculture, and genetic uniformity, positively invites ruinous epidemics.

This brings us to the third point, and an even less attractive aspect of this situation. All this coffee in the Americas is free from parasites, but it is also very susceptible to those parasites, should they ever reach the New World. As we have seen (Chapter 20), this situation is called crop vulnerability, which means that the crop is susceptible to an absent, epidemiologically competent species of parasite. When the parasite arrives in the area of cultivation, the susceptibility is revealed, and the vulnerability is manifested.

A major coffee vulnerability in the New World was due to coffee leaf rust, caused by the fungus *Hemileia vastatrix*, which has already been described (Chapter 4) in the discussion on auto-infection and allo-infection. This parasite was blamed for the failure of several old world coffee cultures. When it reached Brazil in 1970, it caused something of a panic in the world coffee trade. It has since spread to all the coffee producing nations of South and Central America. Fortunately, it proved to be seriously damaging only on coffee grown in hot, humid climates and, because most of the new world coffee areas are relatively cool and dry, the rust is easily controlled. But we shall return to this problem in a moment.

The fourth point of interest, arising from the international movement of coffee, concerns the resistance of the coffee itself to its pests and diseases. When the new hybrid of arabica coffee was first formed in Uganda, about fourteen centuries ago, it had as much resistance to coffee parasites as its wild progenitors. This natural level of resistance is a very high level, because all wild plants must have adequate levels of resistance to all their parasites. This is axiomatic, because any individual plant, or species of plant, that had poor resistance would be unable to survive ecological and evolutionary competition, and would have been destroyed long ago.

As we saw earlier, the new hybrid coffee was taken to Ethiopia in about 650AD, and, as we now believe, one of its parasites was left behind in Uganda. This was the microscopic fungus *Colletotrichum* (pronounced 'colley-tot-tree-coum') *coffeanum*, which causes a disease called coffee berry disease (see below). The new coffee hybrid was then cultivated in Ethiopia for some fourteen centuries in the absence of this fungus. Plants which grow in the absence of a parasite tend to lose resistance to it. They become highly susceptible and, possibly, highly vulnerable as well. However, all the other coffee parasites were present in Ethiopia and the coffees of the Ethiopian highlands have remained resistant to all of them.

There is one exception to this rule of resistance in Ethiopia. In eastern Ethiopia, there is a relatively dry province called Harrar. The coffee of Harrar has been grown for centuries in an area where most coffee parasites have a greatly reduced epidemiological competence, due to the dry atmosphere, and the relatively dry soils. The Harrar coffee has consequently lost resistance and, when it is cultivated in wetter environments, such as southwest Ethiopia, it is highly susceptible to many coffee parasites, including both coffee rust, and coffee berry disease.

The susceptible Harrar coffee was almost certainly the coffee taken in the thirteenth century to the Southern Yemen by the Arabs, where it was grown for several centuries in a climate that is even drier than Harrar. The coffee of this area probably lost even more resistance. This was the coffee that was taken to Indonesia and, later, to Europe, and the New World. There seems to be little doubt that the coffee of the Americas is both a narrow gene base coffee, and is a very susceptible coffee. Indeed, all the arabica coffee of the world, outside of Ethiopia, has suffered a major erosion of horizontal resistance to many of its parasites.

This is a ludicrous situation. If the Dutch had taken coffee from southwest Ethiopia to Java, instead of from Yemen, there would be *no serious pest or disease problems of arabica coffee anywhere in the world,* apart from coffee berry disease (see below). In other words, all the serious parasite problems of arabica coffee are due to an erosion of horizontal resistance. Three points about this erosion merit discussion.

First, this comment is not a criticism of those early, and very courageous, Dutch explorers, because there was no way they could have understood this complex situation. Equally, there was no way they could have reached southwest Ethiopia which, in those days, was a completely inaccessible part of the entirely unknown, and very dangerous area known as Darkest Africa. South Yemen was close to the sea and, for all that these Dutch explorers knew, it was the only place in the world where coffee was cultivated, or even existed. As we have seen, Linnaeus believed it was the home of arabica coffee.

Second, this situation indicates just how important an erosion of horizontal resistance can be. Eighty percent of the world's coffee production is in the New World because this area is free of so many coffee parasites that were left behind in the Old World. This indicates how serious these parasites really are, because coffee is so much more difficult to produce, and it has such a competitive disadvantage, when it is cultivated in the Old World.

Third, the extent of this erosion indicates the potential of horizontal resistance in a crop such as arabica coffee. Eventually, it should be possible to breed arabica coffee with enough horizontal resistance to permit its cultivation anywhere in the cool tropics, without any crop protection chemicals, and without any loss of either yield or quality. Indeed, such coffee varieties already exist, as we shall see in a moment.

Because the coffee in the New World is so susceptible, it is clearly also vulnerable to many Old World, re-encounter parasites. This is a dangerous situation, but there is one clear advantage. There is obviously tremendous scope for breeders who are working with resistance to coffee pests and diseases.

Coffee berry disease

At the end of the last century, the British started coffee cultivation in Kenya, using the narrow gene base of susceptible coffee. After World War I, they initiated a large coffee expansion project in western Kenya, near to the Uganda border. For the first time in about fourteen centuries, arabica coffee came into physical contact with its wild progenitors in its centre of origin, and the inevitable happened. *Colletotrichum coffeanum* moved into the cultivated coffee, and it caused a devastating disease, now known as coffee berry disease. This disease was new to science, but it was not new to nature. As we have seen, it occurred on the wild coffees all the time, and it had been inadvertently left behind when the new hybrid was taken to Ethiopia, in about 650AD.

As its name implies, coffee berry disease is a disease of the green, unripe, coffee berries. Although the parasite can survive non-parasitically in the bark of the coffee tree, it can only parasitise the berries, and it does not harm any other part of the tree. The berries, of course, contain the coffee beans, and they are the harvestable product. In a very susceptible tree, all the berries are destroyed by the disease several months before harvest time. Obviously, the disease can be a very damaging one.

As we have seen also, this kind of parasite is a 're-encounter' parasite. The crop was taken by people to another part of the world, and the parasite was left behind. The crop then lost resistance to the parasite. Eventually, when this susceptible crop and the parasite re-encountered each other, the parasitism was very damaging because of the loss of resistance. Coffee berry disease is a typical example of a re-encounter parasite. And it is a very damaging disease. Indeed, the coffee expansion project in western Kenya was a complete failure, and many farmers, who were mostly World War I veterans, were ruined financially.

Coffee berry disease was first described in Kenya by J. Macdonald in 1926 and, observing that some trees were more resistant than others, he recommended the use of resistance as the best means of control. But Macdonald was not believed, mainly because coffee breeding was a long term project. It was also thought that the resistance would be temporary, and would fail when a new strain of the parasite appeared. Even in those days, it was already beginning to be believed that *all* resistance to crop parasites was bound to break down sooner or later. The resistance was also quantitative and this too was considered a bad sign at that time. There was no good source of resistance, and the breeding was believed to be difficult, if not impossible. The work on resistance breeding was stopped, and the research in Kenya turned to fungicidal chemicals. Ironically, Macdonald's best coffee selections, which have useful levels of horizontal resistance to coffee berry disease, were used successfully in other parts of Africa, where the disease had a lower epidemiological competence. And, although susceptible, most of the coffee in Kenya is now considerably more resistant than the most susceptible coffees from Harrar.

I met Macdonald, when I first went to Kenya, in 1953, and when he was an old man. Sadly, his percipience concerning resistance to coffee berry disease was recognised only long after his death.

Coffee berry disease soon started to spread inexorably through the cultivated coffees of Africa. In 1970, the disease reached Ethiopia, where coffee provided 60% of the country's exports. It was apparently taken there by people trying to improve Ethiopian coffee production with seed from Kenya. Coffee berry disease is not normally carried in coffee seed, but it seems that this batch of seed was dirty, and it contained many dried remains of diseased fruit tissues. Unfortunately, these foolish people distributed this dirty seed among many friends throughout the country, and the disease erupted all over the coffee areas of southern and western Ethiopia. The disease was soon threatening to destroy up to forty percent of the already low coffee yields.

In those days, coffee in Ethiopia was being cultivated according to centuries-old traditions, using centuries-old germplasm. The coffee was not planted in neat rows, to permit mechanical cultivation, nor was it manured, or pruned. The crops were a genetic mixture, with most of the trees being different from each other. And the only cultivation involved the weeding of the dense tropical vegetation, once a year, so that the pickers could reach the trees. The average yield was 10% of the best commercial yields in neighbouring Kenya. Under these circumstances, coffee berry disease was ruinous, and there could be no question of fungicidal spraying being either a practical, or an economic, proposition.

At that point, the good people of the Food And Agriculture Organization of the United Nations (FAO) were asked to help, and they invited me to go Ethiopia to direct the research on what appeared to be an insoluble problem. In fact, they had great difficulty in persuading me to undertake such a difficult task. However, once in Ethiopia, my colleagues and I soon discovered that, although the coffee crops as a whole were highly susceptible to coffee berry disease, there was great variation among the individual trees. The most susceptible trees lost all their berries several months before harvest time, while the most resistant trees had lost none of their berries at the time of harvest.

As already mentioned (Chapter 20), this range indicates just how great the difference can be between the minimal and maximal levels of horizontal resistance. Some of the more conservative Mendelian plant breeders argue that the total range of variation of horizontal resistance is so slight, that breeding for it is a waste of time. But this argument is clearly refuted by coffee berry disease.

Approximately one coffee tree in a thousand had a very high level of resistance. By travelling all over the country, and looking at about half a million coffee trees, my team of FAO and Ethiopian scientists eventually identified 640 resistant trees.

Coffee in Ethiopia normally ripens in November. In January of 1974, my Ethiopian counterpart, Dr Teklu Andrebahn, and I, were taking a shortcut across a coffee plantation at Agaro, near Jimma, when we found one tree that was loaded with ripe cherries. This was a serendipitous discovery as exciting as Donald Johansson's discovery of the hominid fossil "Lucy" in the Afar Desert. Indeed, Johansson's equally serendipitous discovery was quite close,[1] in both space and time.

This single coffee tree was obviously an abnormal type which ripened some 8-10 weeks later than usual. For this reason, the pickers had ignored it, because all the berries were unripe when they were harvesting the crop. Equally obviously, this tree was highly resistant because it was carrying a huge yield of healthy berries, in spite of the fact that it was surrounded by susceptible trees, and was growing in an area where coffee berry disease was specially severe.

---

[1] Johansson's discovery was made on November 30th, 1974, in the Afar Desert, only a few hundred miles away.

Every resistant tree that we found was numbered in chronological order of discovery, with the first two digits indicating the year of discovery. This tree thus became 741, being the first resistant tree to be identified in 1974. It was unusual in another respect also. Instead of being bright red, when ripe, the berries were yellow. Tree 741 turned out to be the best of all the resistant selections. It has now become the principle coffee variety of Ethiopia and I am told that it has been planted on many thousands of hectares.

However, we did not know this at that time and, in the meanwhile, we had many other selections to evaluate. The first harvest of newly identified, resistant trees was kept for seed, and about a thousand seedlings were produced from each resistant tree. Coffee seedlings usually take three years to produce their first berries. During this period, the parent trees were repeatedly visited, and tested for resistance, yield, and cup quality. The progenies from the worst trees were discarded while those from the best trees were retained for further development. These progenies were also tested for homozygosity, and only those that were breeding true to type (i.e., those that were already pure lines from natural self-pollination) were kept. And, when the seedlings came into fruit, their resistances to coffee berry disease, and other parasites, were tested, and the horizontal nature of those resistances was demonstrated.

I left Ethiopia, to take up other FAO work, at the end of 1974, and my assistant, N. A. Van der Graaff, took charge of the project. As a result of his efforts, about a dozen, highly resistant, high yielding, and high quality, new varieties were released to farmers only eight years after the disease had appeared. This was an unprecedented achievement in tree breeding, in which it takes many decades to produce useful results, using Mendelian breeding methods.

These new cultivars have provided a clear demonstration of what horizontal resistance can achieve. They have produced a control of coffee parasites that is permanent, complete, and comprehensive. They have also shown that these high levels of horizontal resistance are not in conflict with high yields, a high quality of crop product, and good agronomic suitability.

All the coffee in other parts of the world is susceptible to many different parasites, because horizontal resistance was lost during centuries of cultivation in the dry climates of Harrar and

Southern Yemen. All that susceptible coffee can eventually be replaced, in the course of normal replanting, with new cultivars that are as resistant as the new Ethiopian coffees. The widespread use of crop protection chemicals, that now occurs throughout the coffee growing areas of the world, will then cease. This change-over will doubtless require many decades to complete and, before it can even be started, a lot of tests will have to be done. But, in principle, there is no reason why all coffee crops should not eventually have maximum yields, a very high cup quality, and be entirely free of both pests and pesticides.

These new Ethiopian cultivars are likely to be extremely valuable to other countries in Africa, where coffee berry disease prevents the cultivation of coffee, particularly by the smallest and poorest farmers, who generally lack both the expertise, and the money, to spray their crops.

Coffee is close to being economically synthesised by chemists in factories. The coffee crop would then be ruined, just as the linseed oil crop was destroyed by plastic paints, and various fibre crops, such as Manila hemp and sisal, were destroyed by the manufacture of nylon. The coffee producing nations should not regard each other as competitors. Their real competitors are the big food and chemical corporations, which are close to producing a synthetic coffee. Coffee producing nations should help each other as much as they can, and keep the world price of coffee as low as they economically can, for as long as they can.

Genetic Conservation

Eventually, all the cultivated coffee of Ethiopia will have been replaced with new, disease-resistant varieties. In the process, the genetic variability that exists in these old coffee crops will be lost, just as much of the variability in wheat crops has been lost (Chapter 19). This raises the issue of genetic conservation which is a major concern among some crop scientists. If genetic variability is lost, plant breeding will become more difficult. In theory, if there is no genetic variability at all, plant breeding is impossible. For this reason, it is argued that we must conserve existing variation in ‘gene banks‘ which are either carefully stored collections of seeds of annual crop species, or botanic gardens of tree crop species.

When the prospect of replacing all the old Ethiopian coffee crops first arose, genetic conservationists were concerned that the variability should not be lost. A controversy developed, and it emphasized that the issue of genetic conservation is much more complex than may appear at first sight. Several arguments suggest that genetic conservation is often an expensive and, perhaps, an unnecessary luxury.

The first and very obvious argument is that farmers cannot be expected to carry the burden of genetic conservation. If superior new varieties threaten the loss of genetic variability, no farmer should be penalised, and expected to cultivate the old, inferior varieties, merely to conserve that variability.

Second, there is often some doubt whether the old varieties are worth conserving anyway. In the case of the Ethiopian coffees, the old landraces are susceptible to coffee berry disease. This material is of very doubtful value in a breeding program. Only Mendelians would argue that this material may carry valuable resistance genes which must be conserved. But single gene resistances are vertical resistances, and they are liable to fail. Resistance failures can be disastrous in a tree crop that is normally replanted, somewhat expensively, only once in fifty years. As far as we know, there are no other single gene characters in coffee that are worth preserving.

A third argument against conserving the Ethiopian coffees is that very considerable variation will remain in the semi-wild coffee that occurs in the uninhabited forests of Kaffa, which is the main coffee-producing province, located in S.W. Ethiopia. This coffee consists of the self-sown remnants of abandoned cultivation. However, this coffee population will slowly change as it responds to selection pressure from coffee berry disease, because the susceptible trees will produce so much less seed than the resistant trees. The susceptibility will gradually be reduced, and it will eventually be eliminated from the population, just as the susceptibility to tropical rust was eliminated from the maizes of tropical Africa (Chapter 20). But, as one coffee generation requires three years, and most coffee trees live for about fifty years, this process will require several centuries.

But perhaps the most important argument arises from L. R. Doughty‘s work, already described. Possibly the best way to produce new coffee varieties is by re-synthesising *Coffea arabica* from its wild, diploid progenitors. It is here that the real variability exists, and these populations of diploid wild coffees are not threatened. Furthermore, new tetraploids will be both genetically stable, and highly resistant to all coffee parasites. So, it seems, genetic conservation is not necessary, at least in arabica coffee.

Vertical Resistance in an Evergreen Perennial

Observant readers may have noticed an apparent contradiction in this discussion. It was stated earlier (Chapter 6) that vertical resistance required both genetic diversity, and a discontinuous pathosystem, in order to function as a system of locking. For this reason, a gene-for-gene relationship can evolve only in an annual species, or against the leaf parasites of a deciduous tree or shrub. Coffee is an evergreen perennial, and the rust pathosystem is apparently continuous. But, in spite of this, there is vertical resistance to leaf rust.

The explanation of this anomaly lies in a neat biological trick which suggests that the deciduous habit in trees has as much to do with parasitism as it does with the onset of an adverse season, such as a temperate winter or a tropical dry season. Rust spores must have free water on the coffee leaf in order to infect it. This means that the rust can infect its host only during the rainy season. During the dry season, infection cannot occur. During the dry season also, the coffee host sheds every leaf that has any rust fungus in it. These fallen leaves die, and the rust dies with them. This makes coffee functionally deciduous with respect to rusted leaves only, and the pathosystem is discontinuous. With the start of the new rains, the tree is entirely free of rust, and it can only be allo-infected. The effectiveness of its vertical resistance is renewed each dry season.

This loss of leaf during the dry season explains why leaf rust can such a damaging disease on cultivated coffee. We cultivate our arabica coffee as genetically uniform pure lines, and this intensifies the rust epidemics very considerably. Furthermore, as we saw earlier, all the arabica coffee cultivated outside Ethiopia originated in the Yemen, and it is abnormally susceptible to rust. During the dry season, in other coffee growing areas, these cultivated trees are liable to lose so many leaves that their very survival is jeopardised. They have to be regularly sprayed with a fungicide if they are to retain their leaves, and survive, quite apart from yielding well.

Indeed, in the old days, in Kenya, coffee used to be sprayed with a copper fungicide solely for its ‘tonic effect’. It was thought, incorrectly, that the copper had nutritional value, and that this helped the tree to retain its leaves. In fact, the fungicide was controlling invisible rust infections that would otherwise have caused the trees to shed leaves during the dry season.

Conclusions

From our experience in Ethiopia, it is now quite clear that arabica coffee can easily possess enough horizontal resistance to control all its parasites. And this resistance need not conflict with either the yield or the quality of the coffee beans. Furthermore, the coffee in S.W. Ethiopia has so much horizontal resistance to rust that the disease is extremely rare. And this level of horizontal resistance is possible even when there is a vertical subsystem superimposed on the horizontal subsystem.

Incredible though it may seem, coffee scientists the world over are still working with vertical resistance to coffee rust. With the notable exceptions of A. B. Eskes in Brazil, and the FAO team in Ethiopia, they are apparently all Mendelians, and they have continued to ignore horizontal resistance to this disease. Most coffee breeding in the world is now based on a series of back-crossing programs, using the apparently immune ‘Hibrido de Timor’ as a source of resistance. This source of resistance is a natural hybrid between arabica and robusta coffees, and it has both vertical resistance, and a very high level of horizontal resistance, to rust. Unfortunately, its yield, cup quality, and agronomic suitability are poor, and this is why the back-crossing is necessary. However, back-crossing reduces both horizontal resistance and separates vertical resistance genes. When the vertical resistance of these new coffees fails, there may be little horizontal resistance left.

Chapter 22

Sugarcane

A Very Ancient Crop

There are four reasons for thinking that sugarcane (*Saccharum officinarum*) is of very ancient domestication. First, the cultivated canes are very different from their wild progenitor, particularly in their domestication characteristics of juiciness and sweetness. Second, sugarcane, like modern wheat and maize, cannot survive on its own in the wild. It is dependent on cultivation by people for its survival. Third, sugarcane has lost the natural ability to propagate itself by seed. Except on research stations, it can be propagated only vegetatively, by cuttings. Lastly, there is an astonishingly wide range of varieties of cane in the centre of origin, which is in the general area of Papua New Guinea.

It is thought that an accidental hybridisation occurred in northern India between a sugarcane and a wild relative called *Saccharum spontaneum*. This produced a new species called *Saccharum barberi* with thinner, harder stems. These hybrid canes were better suited to the subtropics, and to high altitudes, where the original, or noble canes do poorly. Although they produce less sugar, they are more hardy, and more resistant to pests and diseases, than the noble canes. It was one of these hybrid canes that was taken to China in ancient times and, later, another was taken to Persia (modern Iran) and, from there, to Europe.

Many of these events can be dated from historical records. Alexander the Great saw sugarcane, and sugar, during his conquest of northern India in 326BC. The Greeks called sugar "honey from reeds". In the first century AD, Dioscorides wrote of "a honey called sakkharon, collected from reeds in India and *Arabia felix* (modern Yemen), with the consistency of salt, and which could be crunched between the teeth". The Greeks, of course, knew only about brown, or honey-coloured, sugar. This 'sakkharon' was traded in Alexandria at that time, but the sugarcane plant itself did not reach the Mediterranean until the Arabs conquered Egypt, and introduced it in 641AD. This was the period of the lightening Arab conquests, and they took sugarcane with them all the way across north Africa, into Spain where, five hundred years later, some 75,000 acres of sugarcane were still being cultivated.

The Portuguese took sugarcane to Madeira, the Canary Islands, the Azores, and to West Africa. On his second voyage, in 1493, Columbus took sugarcane to Hispaniola (now the Dominican Republic and Haiti) where, however, both the cane and the Spanish colonizers that he left behind, were exterminated by native Caribs. West Indian sugar was first produced in Hispaniola in 1506 and, by 1550, it had been taken to most of the tropical New World.

Re-encounter Parasites

In the course of this transfer of sugarcane from India, across Eurasia, Africa, and the Atlantic, to the New World, two quite typical things happened. The first was that virtually all the pests and diseases of sugarcane were left behind. The sugarcane industry of the New World then had an enormous commercial advantage over the Old World because, being pest-free, it was much more productive.

The second typical happening was an extreme narrowing of the genetic base. In the centre of origin of sugarcane, there is a bewildering variety of different sugarcane clones. But, it seems, only one clone was taken to the New World. It still exists and, in

India, is called ‘Puri’. It is also known as ‘Yellow Egyptian’ and, in Spain, it is called ‘Algarobena’. In the New World, it is called ‘Creole’, or ‘Cana Criolla’, which is Spanish for ‘native cane’. The extraordinary thing about ‘Creole’ was that it was the only clone of sugarcane present in the New World for more than 250 years.

‘Creole’ is a variety of *Saccharum barberi*, and it is a very tough cane, which can be grown almost anywhere in the tropics and subtropics. In this sense, the New World was fortunate in its very narrow base of genetic material of sugarcane because, largely by chance, it received some of the best genetic material available, and it received it free of parasites.

Towards the end of the eighteenth century, a noble cane (i.e., pure *Saccharum officinarum*) was taken from the Far East to the New World, and it was found to have a higher yield of sugar than the old Creole cane. This new cane is believed to have been collected by the French admiral Bougainville, after whom one of the Melanesian group of Pacific islands, and the ornamental plant *Bougainvillea*, are named. He collected this new cane when he circumnavigated the world in 1766-68.

Bougainville took this cane to the French island of Bourbon (now called Réunion), in the Indian Ocean, and the cane became known as ‘Bourbon’ when it was taken to Martinique, Guadeloupe, and Haiti. The original name of this cane was ‘Otaheite‘ and Captain Bligh, famous because of the mutiny on his ship, the ‘Bounty’, also carried it to the West Indies in 1793.

Because of its superior yield, Otaheite (or Bourbon) rapidly replaced Creole and, once again, the entire cane industry of the New World became dependent on a single clone. This was a dangerous situation because, as more and more transfers of crop varieties were made around the world, so more and more pests and diseases began to be spread to places where they had never been seen before.

Otaheite turned out to be very susceptible to what is believed to have been a new encounter parasite. This created a grave crop vulnerability. In the French islands of the Indian Ocean, Otaheite failed suddenly in the 1840s and had to be replaced with other, inferior varieties. This was about the time of the great Irish potato famine (Chapter 18) and no one in those days knew anything about plant diseases. Crop failures were attributed to such ill-defined things as evil fumes and miasmas. For this reason, we do not know what parasite of cane destroyed ‘Bourbon’ in the French Indian Ocean islands. In 1860, Otaheite failed in Brazil. Equally suddenly, it failed in Puerto Rico in 1872 and, one by one, in all the other West Indian islands between 1890 and 1895.

Sugarcane Breeding

In 1888, a singular discovery was made simultaneously in Barbados and in Java. The British scientists Harrison and Bovell, in Barbados, and the Dutch scientist Soltwedel, in Java, discovered that it was possible, after all, to grow sugarcane from true seeds. This meant that sugarcane breeding became a practical possibility for the first time. A wave of cane breeding followed, and this had such a dramatic effect on cane production that it has even been suggested that this was the first ‘green revolution’.

Cane breeding stations were set up in all the major cane growing countries. A convention developed in which a new cane variety was named with the initials of its breeding station followed by figures. Thus, all ‘Co’ varieties come from Coimbatore in India, all ‘B’ varieties from Barbados, all ‘H’ varieties from Hawaii, and all ‘POJ’ from the Dutch Proefstation Oost Java. Without the slightest doubt, the most famous new cane variety of all was POJ.2878. This variety was so successful that it was eventually grown in just about every cane producing country of the world, and it became an ancestor of every modern cane variety.

In spite of the magnificent example of sugar beet breeding, every one of the new sugarcane breeding stations adopted the Mendelian breeding approach. It turns out that there is not a single Mendelian character in sugarcane that is of any agricultural significance, and the biometrical, or quantitative, breeding approach would have been more suitable.

The Mendelian breeders working with sugarcane believed very firmly in the importance of pedigrees. They were convinced that the only way to obtain new cultivars was to cross a high quality, high yielding 'father' with a high quality, high yielding 'mother'. They even spoke of good and bad 'blood' in sugarcane, and they believed it was imperative to know the pedigree of a cane for as many generations back as possible. Their research records resembled the stud books and pedigrees of race-horse breeders.

The chief characteristic of this procedure in plant breeding is that the breeder keeps looking backwards, to the parents, grand parents, great grand parents, and so on. This is the precise opposite of natural evolution. In the process of evolution, the past is quite literally dead and gone for ever. Evolution looks forwards, not backwards. It is the fittest of the present generation that are going to have the most offspring in the next generation. The population breeding of the biometricians imitates natural evolution in that it looks forwards to the progenies, not backwards to the parents. Population breeders are not interested in pedigrees.

However, plant breeding is a continuing process and it is not easy to switch methods in the middle of that process. Once all cane breeding stations had adopted pedigree breeding methods, they stayed that way to this day. This is not to say that pedigree breeding is useless in sugarcane. It has produced some outstanding results. But population breeding can be expected to produce even better results, and more of them, in a shorter time.

The one exception to this rule of pedigree breeding in sugarcane is in Hawaii, where the cane breeders decided to launch an entirely new breeding program, using a population breeding methodology that they called the ‘melting pot’ technique. They took pollen from about twenty good male parents, and used it to randomly pollinate millions of flowers of some twenty good female parents. They produced enough true seed to grow three million seedlings. These were screened by eye and reduced to about 600,000 selections that had the purely visual appearances of a good cane cultivar. These selections were screened for sucrose content, and only those with very high sucrose contents were kept for further growth and screening. With each screening, there was a drastic reduction in the number of survivors, and a corresponding increase in the complexity of the screening tests became feasible.

The best selections of one screening generation became new cultivars. They also became the parents of the another screening generation, with another three million seedlings. This approach, of course, is recurrent mass selection, and it is the basic method of population breeding. It emphasizes the transgressive segregation of continuously variable characters that are polygenically inherited, such as sucrose content, total yield of cane at the time of harvest, horizontal resistance to pests and diseases, and so on.

As a result of some decades of this kind of breeding, Hawaii now has a wealth of outstanding cane cultivars which, however, are not often useful in other parts of the world because of differing environments, and differing patterns of pests and diseases.

Apart from protecting the cut surfaces of cane ‘setts’, or pieces of stem, used for planting a new crop, Hawaiian cane farmers do not use insecticides or fungicides, and they have no important pest or disease problems. They also have the highest sugar yields in the world, with double the yield of any other country. No doubt, these high yields are due, at least in part, to the magnificent climate of these beautiful islands. But the best climate in the world will not produce high yields unless there is magnificent plant breeding as well.

Because sugarcane is derived from a continuous pathosystem (Chapter 6), all of its resistance to pests and diseases is horizontal resistance. The vertical resistances, that have caused so much trouble in crops derived from discontinuous wild pathosystems, such as potatoes, tomatoes, wheat, rice, peas, and beans, do not occur in sugarcane.

The durability of resistance in sugarcane is well established. For example, in the early part of the present century, a new encounter virus disease, called mosaic, appeared in the sugarcane of

South Africa. All the existing varieties were highly susceptible, except one called ‘Uba’, which was of such poor quality that it was described as being more like a bamboo than a sugarcane. The South African sugar industry faced ruin. It was eventually saved by POJ.2878, and varieties bred from it, which are resistant to mosaic. This disease has never again been serious in that area.

A similar story can be told of every cane producing area when the mosaic virus first appeared. There have been occasional subsequent outbreaks of mosaic virus, but only because the disease was controlled so totally by the use of resistant varieties, that breeders sometimes forgot to test new varieties for resistance to it, and they inadvertently released a susceptible variety to farmers. This error has often been wrongly interpreted as a breakdown of vertical resistance, resulting from the appearance of a new, matching strain of the parasite.

In 1936, in his presidential address to the American Phytopathological Society, G. H. Coons spoke about controlling plant diseases by breeding crops for disease resistance. In those days, it was considered essential to first find a source of resistance, to use single gene resistances, and gene-transfer breeding methods, leading, as we now know, to vertical resistance which is usually temporary in its effects. In those days also, scientists working in crops such as wheat, potatoes and beans, were already beginning to think that all disease resistance was bound to fail sooner or later, because of new strains of the parasite. Coons believed otherwise. In his presidential address, he described how the historic sugarcane industry of Louisiana was ruined during the years 1923-1927 due to three recently introduced diseases. These diseases were mosaic, red rot, and root rot, to which all the old cane varieties were highly susceptible.

When the old varieties were replaced with resistant new ones, these diseases virtually disappeared, and the State average yield of sugar increased by fifty percent. Coons believed that this resistance was durable. And he was right. It has now endured for some seventy years, and no one seriously suggests that the resistance is going to break down to new strains of these parasites. Perhaps the pedigree breeders of wheat, rice, potatoes, peas, and beans, should take a more careful look at sugarcane. Perhaps all the vertical resistance breeders of the world should visit Hawaii, to see how the sugarcane breeders of that island did it.

It is safe to assume that all resistance to sugarcane pests and diseases is horizontal resistance. In theory, this means that a sugarcane cultivar should last for ever. It should never have to be replaced because of a failed resistance. In practice, however, there are two situations in which the horizontal resistance of a cane cultivar can apparently fail, or can become inadequate.

As already mentioned, a new cane cultivar may not be tested carefully enough before being released to farmers. It might be very susceptible to, say, mosaic virus, but this susceptibility has not become apparent because of faulty or inadequate testing. Because all the cane of the area is resistant, this virus is rare. It is only later, when the new cultivar is established as a crop, that there is a flare-up of the disease, and the susceptibility of the new cultivar becomes obvious. It is then very easy, and very tempting, for the crop scientists to blame nature, and to claim that the resistance was vertical, and had broken down, rather than to admit to their own carelessness. As we have seen (Chapter 13) this apparent loss of resistance is called a false erosion of horizontal resistance.

The second apparent failure of resistance occurs when a crop vulnerability is manifested, as also happened repeatedly, with mosaic virus. In the 1970s, two additional re-encounter sugarcane diseases finally reached the Caribbean, more than four hundred years after the crop itself had been introduced there. The first of these diseases was ‘smut‘ caused by a microscopic fungus called *Ustilago scitaminea*. This is a spectacular disease in which the entire shoot of the cane is transformed into a smut ‘whip’, up to six feet long and covered in black microscopic spores which are like a very fine soot. It has been estimated that one smut whip may produce as many as one hundred *trillion* spores. This is *r*-strategy reproduction at its most extreme.

The second disease was sugarcane rust, *Puccinia erianthi*, which is a close relative of the rusts that have caused so much trouble on wheat (Chapter 19) and maize (Chapter 20). It produces rust red pustules on the leaves and, in a susceptible cultivar, the plant is killed because of the loss of leaf.

Throughout the Caribbean, there were sugarcane cultivars that were susceptible to one or other of these re-encounter diseases. They were susceptible only because they had been bred and selected in the absence of the diseases. These susceptible cultivars had to be replaced with resistant ones, and then the problem was not only solved, it was permanently solved.

However, the susceptibility was occasionally a very serious one, at least for a time. Cuba, for example, is the second largest sugarcane producer in the world (after Brazil), with an annual production of up to eleven million tons of extracted sugar. When rust appeared in this island, one third of the entire cane crop was planted to a rust-susceptible cultivar and, until it could be replaced several years later, Cuba suffered crippling losses in production.

At about this time, the sugarcane scientists in Barbados were anticipating the arrival of both smut and rust, because these diseases were already present in mainland South America. Barbados has its own cane breeding station, and it has a wealth of cultivars to choose from. The Barbados scientists decided to test as many of them as possible in South America, so that they would know in advance which cultivars were susceptible. The idea was to remove any susceptible cultivars from cultivation, as part of the routine replanting process, and to do this before the diseases appeared in the island. This is quite the best way of solving problems of crop vulnerability.

Barbados sent 1,600 potential new cane cultivars to Guyana for testing. Each cultivar had to be tested twice because there were two diseases. Guyana is a very small, and a very poor, country. It has few scientists, and those it does have are over-worked. The task that these scientists undertook was a heavy one, but they knew that their results would be of immense benefit, both to Barbados, and to the whole of the Caribbean. This was a magnificent example of international goodwill, and of the assistance that non-industrial countries can give to each other.

The results were impressive. When smut and rust finally arrived in Barbados, all the susceptible canes had been replaced, and these diseases caused no damage whatever.

Chapter 23

Ancient Clones

There are a number of crop plants that can be propagated by vegetative methods only, using cuttings, grafts, tubers, setts, bulbs, corms, or rhizomes. This method of propagation means that these crops exist as clones. Except for the occasional mutation, or 'sport', all the individuals within a clone are genetically identical. A clonal population is thus genetically uniform, and genetically inflexible (Chapter 8). Because propagation by true seed is impossible, usually because it leads to a complete loss of crop quality, it follows that most of these clones have been carefully preserved and nurtured by generations of farmers since ancient times. In the study of horizontal resistance, these ancient clones are of interest in a number of ways.

The first point is that these ancient clones are highly resistant to all their old encounter parasites. Any clone that was susceptible to even one of its parasites would have been abandoned centuries ago.

A second point is that all this resistance must be horizontal resistance. Had the resistance to even one parasite been vertical resistance, it would have broken down centuries ago, and that clone would then have been abandoned. The mere survival of these clones until the present demonstrates both the durability, and the utility, of horizontal resistance.

A third point is that the levels of resistance were high enough to permit an economic cultivation without any use of crop protection chemicals. The first highly effective fungicide, Bordeaux mixture, is little more than a century old. And DDT, the first highly effective insecticide, is only half a century old. Any clone that was unduly susceptible, before the discovery of these chemicals, would have been abandoned. For all practical purposes, their resistance was complete.

A fourth point is that the horizontal resistance was comprehensive, in the sense that all the old encounter parasites were controlled. Even one major susceptibility would have doomed a clone to rejection and extinction.

A fifth point is that many of these ancient crops are very difficult to breed, and modern plant breeders are usually unable to improve on the work of the unknown, ancient, cultivators. In spite of this, many of these crops have hundreds, sometimes thousands, of surviving clones. The production of so many clones must have required a long period of history. This is a further indication of both the antiquity of the clones, and the durability of their resistance.

A sixth point is that many of these clones have very high yields and quality. With modern plant breeding, it has proved impossible to improve on either the yield or the quality of, say, the classic wine grapes, olives, dates, hops, bananas, or pineapples. This indicates that high levels of horizontal resistance are not incompatible with high yields, and high quality of crop product.

A last point is that some of these crops have pathosystems that are discontinuous, and they have evolved gene-for-gene relationships, and vertical resistances. These vertical resistances must have ceased functioning at the time of the first clonal cultivation. This indicates that high levels of horizontal resistance are possible in species that were normally protected by a system of locking, based on vertical resistance, and genetic diversity.

We should also consider the antiquity of these clones. There are four categories of evidence for antiquity.

The first category of evidence involves written records which, in the case of some Egyptian, Sumerian, Indian, and Chinese records, go back as much as five thousand years.

The second category concerns the wild progenitors of crop plants. Every cultivated species of plant was derived from one or more wild species and, usually, we can identify these wild progenitors with complete confidence. Occasionally, however, there seems to be no wild progenitor, and it appears to have disappeared. The most likely explanation is that hunter-gathering people exploited it to extinction. The domesticated forms survived because farmers are always careful to preserve propagating material of their crops. But food gatherers are often careless about wild plants and, in the course of a few human generations, they would never notice the decline in numbers that was occurring because of their activities. Among ancient clones, this loss of wild progenitors has occurred with black pepper, garlic, ginger, olive, saffron, and turmeric (see below). Among other crops, a loss of wild progenitors also occurred with apple, broad bean, cassava, chillies, peanuts, soybean, sweet potato, and tea.

In many crops, the changes that domestication have made are so profound that the modern crop plant bears little resemblance to its wild progenitors. Crops such as wheat, maize, sugarcane, and tobacco, have been changed so much that their wild progenitors are difficult to identify. In the hands of primitive cultivators, who did not understand plant genetics, these changes could only have occurred slowly, over long periods of historical time. Profound alteration is another indication of the antiquity of domestication.

The next category of evidence concerns the loss of seed production, or even flower production, so that vegetative propagation becomes essential. Ancient cultivators would have known that you can increase the yield of the vegetative parts of a plant if you remove the flowers. This is because the flowers and, to an even greater extent, the seeds, constitute a physiological 'sink', which takes the lion's share of nutrients away from other parts of the plant. If those cultivators came across a clone which did not form seeds or, even better, did not form flowers, they would preserve that clone very carefully. Other things being equal, such a clone would save a lot of labour. If the cultivators had many of these seedless clones to choose from, they would discard the seeded forms which would then become extinct. Among ancient clones, a loss of flower or seed formation occurred with banana, garlic, ginger, horseradish, pineapple, and yams.

Ancient cultivators could not always find lines that did not flower, or did not set seed. Nor did they always want to, because, in some crops, it was the seed itself that was the harvestable product. This was true of all the cereals and the grain legumes, for example. Here, the prime consideration was to find plants that did not disperse their seeds at maturity, as is natural for all wild plants. Obviously, any plant that retained its seeds until after harvest was highly valued by farmers, and was preserved. And any plant that scattered its seeds on the ground was difficult to harvest, and it would be discarded as soon as seed-retaining plants became available. The loss of seed shedding is also a sign of an ancient domestication.

A final category of evidence concerns the diversity of ancient clones. If there is a great diversity of clones, in spite of the loss of seed production, the production of that diversity must have required a long period of historical time. This is because of the sheer difficulty of producing new clones, let alone of producing good new clones, when the crop in question does not normally produce true seed. This is particularly true of crops such as banana, sugarcane, yams, ginger, and turmeric.

For ease of reference, the following list of ancient clones is in alphabetical order, rather than in any order of importance or interest.

Aroids

Aroids are tropical root crops that are largely unknown in temperate countries, because they have never become an item of international trade. There are several genera of edible aroids, of which *Colocasia*, originating in the Old World, and *Xanthosoma*, originating in the New World, are the most commonly cultivated. Aroids have a number of vernacular names, such as taro, tannia, eddo, dasheen, and coco-yam. All the cultivated aroids are ancient clones whose ages should probably be measured in millennia rather than centuries. Some modern plant breeding has been attempted, but it has not produced any new cultivars.

The cultivation of aroids requires considerably more labour than either maize or sweet potato. For this reason, aroids do not compete well, and the production of aroids has not increased very much during the past century. Nevertheless, the world production of aroids is estimated at about four million tons annually. The only serious parasite is a new encounter disease of *Colocasia* in the South Pacific, caused by the fungus *Phytophthora colocasiae*. However, the importance of this disease declines within a few decades of its first appearance, as the more susceptible clones are eliminated, and more resistant clones replace them.

Banana

Many people speak of the banana ‘tree’ (*Musa* spp.) but this is botanically incorrect. The banana plant has no woody tissues and, for this reason, it must be described, botanically, as a herb. However, it happens to be the largest known herb, and some plants grow to a height of twenty five feet. Like garlic (see below), the cultivated clones of banana do not set seed, and they are of ancient origin. They also have excellent levels of horizontal resistance to all their old encounter parasites.

The banana originated in lowland, tropical S.E. Asia, and it was taken to Madagascar and East Africa by ancient Austronesian peoples who sailed directly across the Indian Ocean in the second millennium before Christ (Chapter 21). From Madagascar, the banana was taken to East Africa, and then overland to West Africa where the Portuguese were the first Europeans to encounter it.

One clone, called *Pisang ambon* in Malaysia and Indonesia, was taken to Martinique in the early 1800s, where it was renamed *Gros Michel*. This name means “Big Michael” and it probably has a scatological origin. *Gros Michel* is now regarded as the finest eating banana in the world, and it was cultivated in many tens of thousands of acres, for many decades, by the United Fruit Company, in the so-called ‘Banana Republics‘ of the Caribbean.

This was an incredible monoculture. A monoculture means that a single species of crop, often a single clone of that crop, is cultivated continuously, without rotation, and without any mixing with other crops. Monocultures provide the best conditions for really damaging epidemics. Being a herb, with soft and succulent tissues, we might expect the banana to have many parasites, and the danger of damaging epidemics in this monoculture was aggravated in several ways. The banana is a perennial, evergreen plant, and its epidemics are continuous. Being a tropical plant, growing in an environment that is continuously warm and wet, it invites population explosions of parasites, with little chance of population extinctions.

And *Gros Michel* was cultivated for decades, producing some five million tons of fruit annually, from about 250,000 acres, as a single clone, with every plant genetically identical to every other plant. And yet, there were no epidemics. At least, there were no epidemics of old encounter parasites.

It is interesting to compare this ancient clone of banana with the modern clones of potatoes, in Europe. These modern clones cannot be cultivated at all without the use of expensive seed certified free from viruses and other tuber-borne parasites, and without routine spraying with insecticides and fungicides to control leaf parasites. There is something seriously wrong with these potatoes.

Eventually, a serious epidemic did develop in the New World bananas, but this was the result of a new encounter parasite, a fungus called *Fusarium oxysporum* f.sp. *cubense*, which causes a wilt called Panama disease. This new encounter parasite is native to the new World, and it came from wild botanical relatives of the banana. However, other banana clones were found to be resistant to them, and bananas are still cultivated in huge areas of complete genetic uniformity, in a climate that is very conducive to disease.

Subsequently, other new encounter diseases, such as Moko disease, and Sigatoka, have become serious. It should also be noted that it has not proved possible to develop large banana plantations in tropical Africa or S.E. Asia, probably because of old encounter parasites which become serious only under conditions of extensive monoculture.

Gros Michel is still being cultivated, under its original name of *Pisang ambon*, in its centre of origin, where these new encounter diseases do not occur. And hundreds of other ancient clones are being cultivated by subsistence farmers throughout the tropics, without any use of crop protection chemicals, and producing an estimated fifteen million tons of highly nutritious food each year.

Black Pepper

Black pepper (*Piper nigrum*) originated in India, and seed propagation is not normally feasible, both because true seedlings lack the desired agricultural and culinary qualities, and because the seeds remain viable for only a few days. The crop was taken to various parts of Southeast Asia as clones. There are relatively few of these clones, and they are all ancient.

Pepper was in great demand in medieval Europe for preserving meat. In those days, farmers had no means of feeding their farm animals during winter, because this was before the days of fodder crops, such as turnips and fodder beet. Consequently, farmers had to slaughter all but their breeding stock in the Fall. Unfortunately, they had no really effective method of preserving meat, because this was before the days of refrigeration. The meat would be either smoked or salted, and then it would be liberally laced with garlic and black pepper to disguise its poor taste. The many varieties of traditional sausage, that are typical of various countries in Europe, date from those bad old days.

The pepper trade was a monopoly. In fact, it was a double monopoly. The Arabs controlled both the sea and the land routes from India to Europe, and the Venetian navy controlled the sea routes within the Mediterranean. In those days, pepper was so valuable that it became the main incentive for both Vasco da Gama and Christopher Columbus to find alternative routes to India. When the Portuguese found their way around Africa, they sent a naval task force to grab the monopoly, and the wealth of both Venice and Arabia began to decline. Since that time, black pepper clones have been taken to all parts of the wet tropics, but they have been largely supplanted by the red peppers (*Capsicum* spp.) of the New World. The development of new fodder crops in Europe, to feed farm animals in winter, further reduced the demand for this spice.

The world production of black pepper is now based on a very small number of clones, and they are all ancient. Parasites are occasionally damaging in modern black pepper crops but this is usually because of inappropriate cultivation methods (i.e. the crop likes a soil that is rich in humus, with plenty of organic mulch), or because of a new encounter parasite, such as a *Fusarium* or *Verticillium* fungal wilt.

Citrus

Some citrus clones are modern, and ancient clones were often propagated by nucellar seed. Nevertheless, the ancient clones of citrus were cultivated for many centuries without crop protection chemicals, and even a tree produced from a nucellar seed lives for many decades. Such cultivation would have been impossible if these clones had been susceptible to even one species of parasite. These days, new encounter parasites, and commercial considerations, such as freedom from blemishes, increased yields of perfect fruit, an environmental erosion of horizontal resistance, dense stands, monoculture, inappropriate stock-scion grafts (graft incompatibilities), etc., have all led to an increasing use of crop protection chemicals in this crop.

Dates

The date palm (*Phoenix dactylifera*) is unusual among plants in that an individual palm is either male or female, but never both. The technical term for this is *dioecious* (Greek = two houses). Being dioecious means that self-pollination is impossible. The only possible pollination is cross-pollination. In its turn, this means that pure lines are also impossible. Indeed, date palms are extremely heterozygous. They do not “breed true to type” and, although seed propagation is possible, it is not practical. Date palms produced from true seed normally produce fruit that is of such poor quality that it is fit only for feeding camels. This means that the only practical method of propagation is vegetative but, unfortunately, this too is difficult because basal suckers must be used, and these are produced only by mature palms at a rate of only three or four a year.

To produce a large clonal population from one palm thus requires many decades of propagation.

Breeding dates is equally difficult. How, for example, do you select a male parent on the basis of fruit quality, when fruits occur only on female plants? It can be done, but it requires a lot of very patient experimental work. This sort of work is not made any easier by the long generation time in dates, which is 6-7 years from seed to flowering.

Given all these difficulties, we must recognise that the prehistoric farmers who domesticated dates did a fantastic job. Dates are cultivated in the desert belt that stretches from Morocco in the west, to Pakistan and India in the east. Throughout this area, there are hundreds of different clones. Each one of these clones has been selected, and carefully preserved, from among hundreds, probably thousands, if not tens of thousands, of useless palms that were grown from seed. While it is possible that a few clones are relatively modern, the majority are ancient. A few may even have survived from Neolithic times. We can conclude this because, in spite of the slow rate of vegetative propagation, and the even slower rate of producing new clones, there are about 100,000,000 cultivated date palms in the world.

Dates have excellent levels of horizontal resistance to all their old encounter parasites. However, in Morocco and Algeria, a new encounter disease called *Bayoud*, caused by the microscopic fungus *Fusarium oxysporum* f.sp. *albedinis*, is killing thousands of high quality palms a year, and is spreading inexorably across the Sahara Desert to the East. No one knows where the disease came from, but its relatively recent arrival on the west coast of Morocco suggests a New World origin. Seedling palms are mostly very resistant, but the high quality, cultivated clones are mostly very susceptible. However, a few resistant clones of reasonably good quality are known.

Figs

In Turkey, a clone of the edible fig (*Ficus carica*) called *Sari Lop* has been grown for at least two millennia. In his botanical writings, the ancient Roman author Pliny the Elder (**A.D.** 23-79) mentioned the clone *Dottato* by name, and this clone is still widely cultivated in Italy. Another clone, *Verdone* has been grown in the countries of the Adriatic for many centuries.

These ancient clones of figs have many species of parasite but none of them is serious. Furthermore, fig trees are deciduous, and it is thought that gene-for-gene relationships may occur with some of their leaf parasites. Nevertheless, these clones have been cultivated for many centuries without any use of crop protection chemicals, and there has never been any suggestion of a resistance failure. They have horizontal resistance that is durable, complete, and comprehensive, and which is in no way compromised by an original, additional protection from vertical resistance.

Garlic

Garlic (*Allium sativum*) is one of the oldest cultivated plants of all, being widely recorded in ancient Chinese, Indian, Sumerian, and Egyptian cultures. Garlic never sets seeds. It can be propagated vegetatively, from individual ‘cloves’, and from inflorescence bulbils, but in no other way. No one knows when garlic lost the ability to form true seeds, but it was probably thousands rather than hundreds of years ago. Equally, no one has been able to identify the wild progenitor of cultivated garlic with any certainty. This indicates quite clearly that all the existing clones of garlic are very ancient indeed. There are many of these cultivated clones, differing widely in their agronomic and culinary qualities. They are all ancient and, for centuries, they were cultivated without any crop protection chemicals whatever. Every clone has high levels of horizontal resistance to all its parasites, and these resistances have endured for millennia.

Modern garlic farmers often treat their crops with crop protection chemicals in order to obtain improved yields and quality. However, it is likely that many of these clones have suffered an environmental erosion of horizontal resistance (Chapter 13), by being cultivated in an environment that differs considerably from the original. There may also be some new encounter parasites involved.

Ginger

The origin of ginger (*Zingiber officinale*) is unknown. It has been cultivated in tropical Asia since antiquity, but no wild forms are known. This is the most important spice in Chinese cuisine, and it is a major component of Indian curries. Ginger was known to the ancient Greeks and Romans, and it has long been an important spice in Europe, where it was originally used to disguise the taste of rancid flour, hence the term gingerbread. It is now cultivated throughout the tropics. Propagation is exclusively vegetative, and only a few clones are known. There are no serious parasites of ginger but, in modern commercial cultivation, crop protection chemicals are sometimes used to control minor pests and diseases.

Grapes

There are more than twenty five million acres of vineyards in the world, producing mostly wine, but also table grapes and raisons. All these grapes (*Vitis vinifera*), without exception, are clones, and the great majority of them are ancient. It is thought that there may be as many as ten thousand different clones, but a mere dozen clones are responsible for the great wines of the world. And most of them have been cultivated for centuries, if not millennia, without any use of crop protection chemicals. These clones quite obviously had horizontal resistances that were durable, complete, and comprehensive.

Then, in the nineteenth century, a new encounter parasite was introduced to Europe from North America. This was a root-infesting aphid traditionally called *Phylloxera vitifoliae*, but now the taxonomists have most irritatingly re-named it *Daktulosphaira vitifoliae*. European grapes were so susceptible to it, that the European wine industry was threatened with ruin. The problem was solved by introducing American species of grape to Europe. Scions of the classic wine grapes were then grafted on to rootstocks of these American grapes, which are highly resistant to the *Phylloxera*. It should perhaps be added that this resistance is horizontal, and that it has now endured in Europe, without any suggestion of failure, for more than a century.

Soon after the discovery of resistant rootstocks, large quantities of American vines were imported into Europe and, inevitably, other new encounter parasites were imported with them. The worst of these was the downy mildew (*Plasmopora viticola*) which threatened the wine industry with ruin for a second time. As we have seen (Chapter 18), this problem was solved by Millardet when he discovered Bordeaux mixture.

These grape parasites emphasise the importance of making a clear distinction between old encounter and new encounter parasites. Viticulture has been so plagued by new encounter parasites, for more than a century, that people tend to forget that, for several millennia, it was a parasite-free crop, and a pesticide-free crop as well.

Perhaps more than any other crop, the classic wine grapes indicate that there need be no conflict between high levels of horizontal resistance, and a quality of product which, at its best, is so exquisite that it is impossible to envisage improvement.

Hops

Throughout the Northern Hemisphere, only about eight cultivars of hops (*Humulus lupulus*) are cultivated. The figure is not clear because some cultivars are mixtures of different, but very similar, clones. Nevertheless, hops are propagated vegetatively, and the clones are mostly ancient. In Britain, the Golding hop has been cultivated for at least 250 years, but the very popular Fuggle hop, which was a new seedling discovered by chance in 1861, now occupies about 80% of the total acreage. In continental Europe, the

Hallertauer type dominates southern Germany, and the Saaz type is predominant in Czechoslovakia. The traditional beers of these various regions differ accordingly.

The only serious parasites of hops appear to be either new encounter parasites, or to occur on new cultivars that were inadequately tested for resistance during the breeding process. Hop fields, with their expensive systems of supporting wires, are regarded as permanent installations, because the hop plant is a long lasting perennial. Nonetheless, the above ground parts of the plant have discontinuous pathosystems, because they die back to ground level each Fall. Incredible though it may seem to us, with our modern knowledge, some hop breeding in the past has involved vertical resistance. It is almost beyond belief that anyone should want to breed a long-term perennial crop for temporary resistance. This is yet another indication of how the Mendelian school of genetics has dominated the whole of crop science.

Horseradish

When grated, and mixed with oil, vinegar, and salt, the roots of *Armoracia rusticana* produce a hot condiment known as horseradish sauce. This crop has to be propagated vegetatively because fertile seeds are very rare. Apparently, horseradish has a hybrid origin, and this may explain why most of its seeds are sterile. Even if a fertile seed does occur, it does not breed true to type, and it will produce a plant of dubious agricultural value. Consequently, most clones of horseradish are many centuries old, and they have been successfully cultivated without crop protection chemicals for the whole of their history.

Olives

An olive tree (*Olea europaea*) lives for many centuries, and it is thought that a few trees that were planted by the ancient Romans may still be alive. When olives are grown from true seed, the variation is so great that it is almost impossible to obtain a tree superior to existing cultivars. This means that olives must always be propagated vegetatively, using suckers that develop at the base of the trunk. However, these suckers occur infrequently, and olive propagation is a slow process. For this reason, many of the older olive orchards contain a mixture of clones. This propagation problem has recently been solved by rooting cuttings in mist propagators.

Most olive clones are very ancient indeed, and the age of some of them should be measured in millennia rather than centuries. They have been successfully cultivated for all of this time without any use of crop protection chemicals. More recently, some growers have started to use crop protection chemicals, and have obtained yield and quality increases that are economic. However, this does not detract from the fact that all olive clones have sufficient horizontal resistance to permit an economic cultivation without pesticides, and that this has been true for the whole of their long history.

Pineapple

Like bananas, pineapples (*Ananas comosus*) are normally seedless, and they must be propagated vegetatively. The clones are somewhat unstable, and tend to produce mutants with some frequency. As a consequence, many clones are known. However, one clone, consisting of a number of closely similar mutants, dominates pineapple cultivation, worldwide. This is ‘Cayenne’ which was first taken to Europe (for greenhouse cultivation) in 1820, but is believed to have originated in Venezuela many centuries earlier. Modern cultivators complain that this clone is susceptible to several parasites, particularly the mealy bug wilt, which results from the destruction of the roots by the insect *Dysmicoccus brevipes*. It is now thought that much of this susceptibility may result from an environmental erosion of horizontal resistance, or from a loss of biological controls. ‘Cayenne’ dominates world production because of its excellent yield and quality, and its slight susceptibility to parasites does not prevent this domination. Most other cultivars have considerably higher levels of resistance to the few known parasites of pineapple.

Saffron

Saffron (*Crocus sativa*) is one of the finest spices of them all, and is the basis of French *bouillabaisse*, Spanish *paella*, English saffron buns, Jewish *gilderne*, Russian *challah*, Indian *zaffrani chawal*, and Persian *sholezard*. Saffron is also the most expensive spice of them all, because it consists of the dried anthers of a crocus flower, and it is the most labour-intensive of all crops to harvest.

The saffron crocus originated in India. It does not occur in the wild, and this is an indication of its antiquity. Like garlic, the cultivated crocus does not set seed, and it can be propagated only by corms. Multiplication of the crop is a very slow process because only two or three new corms are formed each year at the base of the old corm. It is not known how many clones exist but it is quite clear that all of them are ancient, and that they have been cultivated for millennia without any use of crop protection chemicals.

Sisal

Sisal (*Agave sisalana*) occurs wild in the semi-arid areas of Mexico, and other parts of Central America, where it has a natural vegetative propagation, and a very limited seed production. This crop was introduced to East Africa in 1893 and, until the world demand for its fibre collapsed with the appearance of nylon, this area was the largest commercial producer. It is thought that the entire crop of East Africa consisted of a single clone or, at most, two or three indistinguishable clones. There are no important parasites of this clone, in spite of the fact that it was grown in a wide range of environments within East Africa, where it could be expected to have suffered an environmental erosion of horizontal resistance. However, the clone, which is still cultivated on a reduced scale, may be vulnerable to re-encounter parasites.

Turmeric

This tropical plant (*Curcuma longa*), which is a botanical relative of ginger, produces yellow underground stems that are used for dyes and spices. The spice is the basis of all curries. Wild turmeric does not occur, and the cultivated clones never form seed. Like garlic (above), the cultivated clones are of very ancient origin, and were derived by vegetative propagation from an unknown wild progenitor. There are not many of these clones, and they are usually named after their place of cultivation in India. Although several parasites of turmeric are known, none of them is serious enough to hinder cultivation, and crop protection chemicals are unnecessary.

Vanilla

This spice (*Vanilla planifolia*) is the only orchid that is cultivated for purposes other than providing ornamental blooms. It is a native of Mexico, and it was being cultivated by the Aztecs when the Spanish arrived in 1520. The crop is propagated vegetatively and it is thought that only a few, very ancient clones exist. There are no serious parasites of vanilla.

Yams

The botanical family of yams is so old, in evolutionary terms, that it had spread to all the main continents before they were separated by continental drift. Consequently, this is one of the very few crops that was domesticated in the Americas, Africa, and Asia, although different species were domesticated in each continent. Yams are cultivated for their starchy tubers. About twenty million tons of tubers are produced annually, with about two thirds of this coming from West Africa. The present discussion concerns the West African yam (*Dioscorea rotundata*).

Like the date palm (above), yams are dioecious. However, the male and female plants both provide tubers, and both are cultivated. Some of the clones never form flowers, and none of them form seed under the normal conditions of cultivation. Consequently, new clones of high yield and quality are likely to be discovered and preserved by cultivators only very infrequently. It follows that, like garlic, horseradish, and turmeric, these non-renewable clones are ancient. There are no serious parasites of yams. They have resistance which is durable, complete, and comprehensive, in spite of their tropical rain forest environment that is continuously warm and wet.

Part Three: Solutions

Chapter 24

Plant Breeding Clubs

Introduction

There were no professional plant breeders before 1900. Since the dawn of agriculture, some nine thousand years ago, all plant breeding was done by farmers. It was only with the recognition of Mendel's laws of inheritance that plant breeding became scientific and esoteric. Farmers were squeezed out of the new plant breeding, which made remarkable progress in some respects, but was positively detrimental when it came to breeding for resistance to crop pests and diseases. Throughout history farmers had worked with horizontal resistance. The scientific breeders preferred vertical resistance, possibly because it illustrated Mendel's laws of inheritance so beautifully.

It is useful to think of vertical and horizontal resistance in terms of space, profile, and time. Vertical resistance functions over a wide climatic range. It is thus ‘big space’. In the early days of the Green Revolution, the miracle wheats had a single vertical resistance all the way from Morocco to China. While it lasts, vertical resistance also provides a complete protection. For both these reasons, it is very prominent, and it has a ‘high profile’. The chief drawback of vertical resistance, of course, is that it is usually ephemeral, and it stops functioning on the appearance of a matching pathotype. It is thus ‘small time’.

Horizontal resistance, on the other hand, is the exact opposite in all three of these characteristics. The epidemiological competences of various parasites differ from one agro-ecosystem to another. Consequently, a cultivar that is perfectly balanced in one agro-ecosystem will have too much resistance to some parasites, and too little to others, when taken to another agro-ecosystem. A horizontally resistant cultivar is at its best only in its own agro-ecosystem. Compared with vertical resistance, it consequently has ‘small space’. This limitation, combined with the fact that horizontal resistance usually allows a low level of parasitism, means also that it is ‘low profile’. However, horizontal resistance is durable. It is thus ‘big time’.

Vertical resistance is big space, high profile, small time.

Horizontal resistance is small space, low profile, big time.

Breeding for Horizontal Resistance is Easy

Another difference between the two kinds of resistance is that breeding for vertical resistance is difficult. It requires a large and expensive institute with a team of highly specialised scientists. Breeding for horizontal resistance, on the other hand, is so easy that it can be undertaken by any group of determined amateurs who organise themselves into a plant breeding club. Breeding for horizontal resistance involves recurrent mass selection and three simple rules.

Recurrent mass selection means that a large and heterogeneous population is screened for the few best individuals which then become the parents of the next generation. This process is continued for as many generations as necessary, usually between five and fifteen. Obviously, the recurrent mass selection must be conducted in the absence of crop protection chemicals.

The three simple rules are as follows:

- Screen for yield, on the grounds that only resistant plants can yield well.

Use simple inoculation techniques (Chapter 25) to ensure that the high yields are due to resistance, and not to chance escape from infection or infestation.

Use the 'one-pathotype technique' (Chapter 25) to ensure that the resistance is horizontal, and not vertical.

The Functions of Plant Breeding Clubs

The amateur plant breeders who form themselves into a plant breeding club might be farmers, hobby gardeners, environmentalists, or any group of activists concerned about the world food problem, and the environmental and food pollution caused by pesticides. Plant breeding clubs would serve several important functions.

First, an abundance of clubs would collectively expose the whole subject of crop science to public scrutiny. Because of its technical nature, and a general lack of public interest, this branch of science has been left to its own devices for far too long. It is a fundamental requirement of science that every experimental result, and every idea, must be exposed to the widest possible public examination, doubt, criticism, and testing. Had the public at large taken more interest in crop science, it is unlikely that the Mendelian school of genetics could have dominated agricultural education, plant breeding, and the control of crop parasites, so totally, so unnecessarily, and so inappropriately, for more than ninety years. Crop scientists have had these ninety years in which to examine the possibilities that are postulated in this book. With a few notable exceptions, they have not done so. It seems indisputable, therefore, that this branch of science needs some stimulation from outside, and the fresh, clean, invigorating wind of competition. Such competition is most likely to come from plant breeding clubs.

Second, plant breeding clubs appear to be the only way of defeating the commercial certified seed producers that favour the *status quo*. These vested interests positively require susceptibility to crop pests and diseases, if their industries are to prosper. They sustain an unnecessarily high cost of food production, particularly with potatoes. These industries can be vanquished only by some very effective competition. To be effective, this competition must produce a wide range of new, high-yielding, high quality cultivars with parasite resistance that is durable, complete, and comprehensive. In its turn, this requires three things. We need (i) the formation of sturdily independent breeding clubs, (ii) made up of concerned and determined individuals who (iii) are free to breed crops in any way they choose. These new plant breeding clubs must also be efficient. And there must be many of them.

The third important function of plant breeding clubs is to reduce the crop loss form parasites. As we have seen, pre-harvest crop parasites are destroying an estimated twenty percent of all crop production, particularly food production. This loss of food is enough to feed about one billion people, and it occurs in spite of an extravagant use of crop protection chemicals. While plant breeding clubs cannot be expected to eliminate this loss entirely, they will reduce it very significantly. Furthermore, successful plant breeding clubs are likely to increase crop yields above their present levels, quite apart from reducing the losses due to parasites. Breeding clubs could thus be an important factor in alleviating the world food problem.

Fourth, these breeding clubs will have the general function of reducing or, in some crops, even eliminating, the use of crop protection chemicals. Without question, this appears to be the best way of reducing the environmental and food pollution that results from these chemicals. Like the vanquishing of the certified seed interests, this will necessitate very effective competition from plant breeding clubs.

Fifth, these clubs would make plant breeding democratic. During the twentieth century, virtually all plant breeding was in the hands a small group of professionals who had an autocratic monopoly, a scientific ‘closed shop’, because of the technical nature of their work. Support for this assertion comes from the currently widespread belief that amateurs cannot undertake plant breeding. Well, they can. And they should. And, when they do, plant breeding will become democratic, producing a huge increase in the breeding output, in the variety of new cultivars, as well as in their resistance to parasites. Their yield, quality of crop product, and agronomic suitability may also be enhanced.

Sixth, plant breeding would become self-organising (See *Self-Organising Agro-Ecosystems* available for download from this *Sharebooks* website). This is a relatively new term that emerges from modern complexity theory. The details are beyond the scope of the present book and it is sufficient to compare plant breeding with the whole system of food production and distribution. Consider the food production of a country. Many individual farmers grow whatever crops they please, and their choice is based mainly on climate, and market demand. Their produce is purchased by competing merchants who process it and distribute it. Retailers sell it to consumers, who also have a free choice, usually based on either cost or quality. There is some government control to ensure purity and free competition. But, in general, too much government control is damaging. This has been dramatically revealed by the failure of the collective agriculture in Soviet Russia, North Korea, and other authoritarian countries. The whole system of food production is thus self-organising in a manner that was first recognised by Adam Smith in his famous book *The Wealth of Nations*, published in 1776.

Self-organisation is a feature of all non-linear systems. These are systems that are too complex to be explained by basic scientific laws, such as Newton’s laws of motion. All living systems are non-linear systems, whether a single cell, an organism, a population, or an ecosystem. Many human systems are also non-linear, including the stock market, politics, horse racing, and agricultural production. The worst political system is one that is over-controlled, usually by a dictator and an authoritarian government. The best and safest political system is one that is allowed to self-organise. This process of self-organisation is called democracy. Our plant breeding should also be allowed to self-organise, and to become democratic. There should be thousands of plant breeding clubs around the world. Such a development would ensure that farmers got the cultivars they wanted, and that consumers got the food they wanted. This would be food that was of high quality, cheap, and free of pesticides.

Seventh, plant breeding clubs can be fun. They can also provide a sense of achievement for activists, a source of new friends with interests similar to one's own, and a new sense of purpose for amateur breeders. These amateur breeders may range from commercial farmers to hobby-gardeners who just love growing plants, but who were previously involved only in their own private gardens. Many other people of widely varying interests could also become members. Baby-boomers and retired people are likely to find plant breeding clubs particularly attractive.

Finally, plant breeding clubs have an added attraction in that they have the potential to earn large sums in plant breeders' royalties. The odds are far better than most lotteries.

University Plant Breeding Clubs

Plant breeding clubs in universities might have the following special features.

- Club activities would be part of the university teaching. Students who participate in the work of a plant breeding club for a full breeding cycle would receive course credits. The professor in charge of the club would receive teaching credits.
- Graduates would earn life-membership in the club, or clubs, that they had joined. This would entitle them to receive new lines coming out of the club for the rest of their lives. They could test these lines in their own locality, reporting results back to the club. They could also keep any lines they liked, and give them to farmer friends.

Graduates would be encouraged to start new breeding clubs in their place of work or, if farmers, in their home districts. The total breeding expertise would then increase rapidly, as would the total breeding activity.

If the club involved a crop with a two-year breeding cycle, it would run two parallel breeding programs that were out of phase by one year. The students would then experience all aspects of the breeding cycle in one year. Comparable arrangements would be made for crops with breeding cycles of more than two years.

Graduate members of a club could return to their universities in order to attend club meetings, giving the current student members the benefit of their experience and results.

University clubs could assist secondary schools to initiate and run their own breeding clubs, with special help for students who were planning either to enter university, or to form their own clubs, after leaving school. This ‘twinning’ would be of special benefit in rural areas where many of the secondary school students were the children of farmers. On the same basis, university clubs could assist and cooperate with amateur clubs.

Universities should allow outsiders to become temporary members of a club, in order to audit the club activities, just as they might audit any other course of study. This would be of special benefit to amateur breeders who were contemplating a new club of their own but were hesitating because of the intimidating nature of plant breeding.

The Problem of Intimidation

For someone who is computer-illiterate, the first use of a computer can be an intimidating experience. Equally, for someone who has never attempted plant breeding, the *mystique* of such a technical undertaking is also intimidating. People who are contemplating a new plant breeding club should bear this in mind, because the intimidation is often sufficiently powerful to destroy all inclination to persevere. The new club, and all its potential benefits, would then be stillborn.

The best way of overcoming this intimidation is by getting help from sympathetic experts who might even become club members. At the very least, they could become club advisors. These experts might be professionals from either a university or a research institute, or they might be life members of university clubs.

The Advantages of Plant Breeding Clubs

The advantages of plant breeding clubs, particularly university clubs, over institutional and corporate plant breeding, are so marked that they merit special emphasis:

A new approach to practical plant breeding. These clubs would take plant breeding out of the hands of the big institutes and the large corporations, ending their domination of this field. This would eventually make plant breeding self-organising and democratic, as free and productive as writing, inventions, and software design. This private plant breeding would be supported by intellectual property rights legislation, and it has the potential of transforming our crops through the widespread use of horizontal resistance.

Farmer-participation in research. University breeding clubs would be singularly appropriate to the original objectives of the land-grant colleges in the United States, and of similar institutions in other countries. These objectives were essentially to provide effective links between scientists and farmers. These links have been so diminished by institutional and corporate plant breeding that we now speak of farmer-participation in plant breeding as being something rather rare and rather special.

A new approach to teaching. A university club would provide students with hands-on experience in plant breeding for horizontal resistance. This would be an entirely new teaching activity for most universities and agricultural colleges.

A new approach to crop research. An advantage for the professor in charge of a university club is that he can undertake long-term research into horizontal resistance. Because this research would be part of a teaching activity, it would not be dependant on the more normal short-term research grants which have no guarantee of renewal.

A new approach to overseas aid. Donor agencies could adopt university breeding clubs as a new technique for agricultural improvement in non-industrial countries. This would involve no more than sending a consultant to the country concerned, to assist in funding and setting up club(s) in local universities. The consultant would re-visit the club(s) once or twice a year until no further support was necessary. This would provide a cheap but very effective assistance in agricultural training and crop improvement.

A return to resistance breeding. The current tendency among institutional and corporate breeders to abandon resistance, as a breeding objective, would cease. There would be a return to resistance breeding. And the repetition of vertical resistance failures would be replaced by the progressive and cumulative improvements that are possible when breeding for horizontal resistance.

The only means of reducing crop pesticide use. Horizontal resistance offers the best and, indeed, the only possibility of reducing both the use of crop protection chemicals, and the environmental and health hazards caused by these chemicals, while also reducing the damage caused by crop parasites.

The only means of defeating cultivar cartels. The existence of hundreds, possibly thousands, of independent breeding clubs, exploiting horizontal resistance, in many crops, in many areas, all over the world, offers the best and, indeed, the only possibility of defeating the cultivar cartels now being developed by large corporations (Chapter 17).

A Typical Plant Breeding Club

A plant breeding club would normally be formed by determined and dedicated individuals who are concerned about the world food problem, the environment, and food contaminated with pesticides. Most of the members would be either farmers or amateur gardeners who are prepared to undertake the actual work of breeding plants. However, a few members might be professionals, with expertise useful to the club, in fields such as science, farming, law, and accounting. Other members might have no expertise whatever in this area, other than a general interest. The club should have elected officials such as a president, secretary, and treasurer. And there should be a club constitution and club rules. Depending on the country concerned, the legal basis of a club might be a private club, a society, a limited liability company, a corporation, or a foundation.

Most clubs would specialise in one species of crop which would normally be an important food crop, and one that is commonly cultivated in their locality. The objective would be to produce high yielding, high quality, new cultivars of that food crop, with high levels of durable resistance to all the locally important pests and diseases. However, the emphasis must be on freedom. A plant breeding club has an absolute right to breed roses or petunias, if it so decides.

Aims and Objectives

Different clubs may well have different objectives. A club made up of farmers, for example, may want new cultivars simply because the farmers concerned are dissatisfied with the commercially available cultivars. A club made up of environmentalists might be primarily concerned about reducing the pollution caused by pesticides. Another club may be interested in helping the poorer, non-industrial countries. A university club might be concerned chiefly with teaching students by practical example. Some clubs may be interested mainly in gaining plant breeders' royalties. Most clubs would have a combination of these various objectives.

The ultimate aim of a breeding club should be to breed high quality, competitive cultivars that can be cultivated successfully and economically, without any significant losses from parasites, with no use of crop protection chemicals, and without any need of certified seed. The club would achieve this by accumulating high levels of horizontal resistance to all locally important parasites, while maintaining high yields, high quality of crop product, and high levels of agronomic suitability.

The club would recognise that this ultimate aim may be unattainable, and that it would, in any event, be a long-term objective. However, the components of this ultimate aim are all quantitative variables that differ in degree. In the shorter term, therefore, the club would aim to produce gradual improvements in of all these components. A new cultivar produced by the club would thus be superior to an older cultivar in most of its attributes, and not markedly inferior in any of them. The breeding process would be cumulative and progressive.

Hands-on Experience

It is now a *cliché* in the computer world that it is impossible to learn about computers from books and manuals. The only way to learn is with ‘hands-on’ experience. The same is true of plant breeding, particularly when breeding for horizontal resistance. Undoubtedly, there will be teething troubles and difficulties, but none of them will be insuperable. Club members who are absolute beginners should charge ahead anyway. They will quickly gain confidence as hands-on experience shows them how easy the biometricians’ plant breeding really is. They will also make mistakes but, at worst, these will only waste some time and money. And learning from mistakes is part of the hands-on experience. A perusal of all the techniques listed below will reveal that none of them is difficult. Every one of them can be mastered quite quickly, and with only a little practice, by any determined amateur.

Many people who are computer illiterate find that the prospect of learning to use computers is a daunting task. Those with the courage to tackle this challenge soon find that computers are easy to use, and are great savers of time and labour. Computers are also fun, and they can quickly become fascinating, and totally absorbing. They can also be very rewarding, in every sense of this word. The same is true of plant breeding.

Basic Organisation

One of the first decisions to be made by a breeding club should be a choice between either a centralised or a decentralised organisation.

The centralised organisation would require a field with enough land to grow a single screening population of 10^4-10^6 plants (depending on the crop species being improved), as well as various field trials, greenhouse work, etc. Such a centralised organisation could be operated by about a dozen active members who would have to devote full-time hard work at peak periods, such as sowing, inoculating, weeding, screening, and crossing. Active members would have to be willing to devote many evenings, weekends, and holidays to the club activities. All the active members would be jointly responsible for these club operations, and they would share the expenses, work, rewards, and satisfaction equally.

The decentralised organisation would involve perhaps one hundred active members, each with enough farm or private garden space to grow and screen one thousand or more plants in a corresponding number of small screening populations. Depending on the crop being improved, each active member may also require a small greenhouse, and various types of equipment. Each active member would then be independently responsible for the work of growing the screening population, selecting the best plant(s) from within it, and submitting selection(s) to the club jury. Each individual member who produced a winning cultivar would be entitled to a significant proportion of the rewards and satisfaction. The best selections of each screening generation (breeding cycle) would become the parents of the next generation.

The choice between the two strategies will depend on a number of factors. A centralised organisation will suit a small club with only a few members who enjoy working cooperatively, and who enjoy each other's company. This organisation is also better suited to extensive crops, such as wheat, which require relatively little attention to each plant. A decentralised organisation will be preferred by a large club with members who are individualists. This organisation is better suited to intensive crops, such as potatoes, or apples, in which each plant requires considerable individual attention.

Membership Fees

The club should have both entry fees, and annual membership fees. These fees should be calculated to cover the club costs until such time as breeders' royalties are earned. Membership fees are unlikely to exceed the sum that most people are prepared to spend on a cherished hobby. If the club is successful in producing one or more popular new cultivars that earn royalties, the membership fees can be abolished, and the club may also be in a position to pay its members their share of royalties.

Passive members should be required to pay membership fees that are considerably higher than those of active members. The difference should correspond roughly to the value of the work that each active member contributes each screening season. Active, farmer, professional, and research members, as well as club officers, would pay lower membership fees, commensurate with their non-financial contributions to the club. However, all members should have equal voting rights, equal ownership rights in club property, and equal rights to the general share of breeders' royalties.

Size of club

The number of active members in a club would vary with the species of crop being improved. Some of the larger clubs, of course, may decide to work on more than one species of crop, or on several categories of cultivar within one species of crop (e.g., white, red, and black haricot beans).

As we have seen, intensive crops would require many active members because all the plants of the screening population must be handled individually. Extensive crops, on the other hand, will need only a few active members, because much of the screening population can be handled in bulk until the final selections are made. Some crops, such as beans, are approximately halfway between these two situations and a choice of organisation, and club size, is then possible.

Categories of Member

A breeding club will normally have several categories of membership as follows:

Active members

Active members are those who undertake the actual breeding work, at their own expense, and possibly using their own facilities, such as farms, greenhouses, equipment, and gardens. The number of active members in a club will vary widely, depending mainly on the basic organisation (see above). It will also depend very largely on the species of crop, the amount of time that each member is able to devote to club activities, and the labour-saving facilities available to the club. Some clubs might have as few as half a dozen, while others might have 50-100 active members. The club as a whole should be able to screen many thousands of seedlings each summer. However, this figure is likely to vary considerably with different crops.

Club officers

Although elected, some of the club officers should preferably be professionals. Thus, a biologist, a lawyer, and an accountant could assume responsibility for scientific, legal, and financial affairs. However, the president, chairman, and secretary should normally be elected from the ranks of the unspecialised members.

Farmer members

Some clubs that are made up of amateur gardeners may choose to have a few farmer members. These would be one or two farmers able to contribute the use of field space and farm machinery far beyond the capacity of the private gardens of the many active members. Some of the more important functions of farmer members would be to multiply potential new cultivars, and to conduct field trials to make final selections among them.

Passive members

Passive members are members who lack the skill, time, or facilities to undertake actual breeding work, but who nevertheless wish to support the club with membership fees, and to earn a share of any royalties that the club may earn. Passive members would require several years of membership before being allowed to earn royalties. The primary function of passive membership is to provide the club with additional funds during the financially critical years before breeders’ royalties are being earned. Passive members should be regarded as benefactors or, if the club succeeds in earning royalties, as sleeping partners, and providers of venture capital.

Professional members

Professional members would each have an area of special expertise which may be scientific, agricultural, horticultural, legal, financial, mechanical, computational, or administrative. Their primary function is to ensure that the club is well run in all its professional and technical aspects.

Research members

Research members are those who prefer to investigate specific problems rather than undertake the more routine tasks of breeding. A club might have several research members, possibly working competitively, who are given problems of special urgency or acuity to solve. Research members might be scientists themselves or, alternatively, they should have useful scientific contacts. Their investigations might involve field or laboratory experiments, library research, or the locating and consulting of specialists.

Technician members

Technician members would have uncommon technical skills that enable them to undertake various specialised tasks (e.g., laboratory work) that is beyond the normal expertise of active members. A technician member need not necessarily be professionally qualified, and any active member may learn the skills involved, with a view to becoming a technician member. Technician members would normally rate as active members, in terms of membership privileges, but would be excused the routine breeding tasks of the active members. Their activities might include the identification and culture of crop pests and diseases, the ‘one-pathotype’ technique, and so on.

Labour-saving Techniques

Pedigree breeding is labour-intensive work and this is one of the reasons it is so expensive. For example, it employs cross-pollinations made by hand, and each pollinated flower or plant must be individually labelled with various data such as the identity of the male parent. A plant breeding club has only so-many person-hours available to it, and these hours should be used to the maximum advantage. One of the advantages of recurrent mass selection, and random cross-pollination, is that no labelling of individual plants is necessary. It is then possible to obtain vastly more cross-pollinations per person-hour.

Plant breeding clubs should use as many labour-saving techniques as possible. This is not because their members are lazy. It is simply because they want to screen as many plants as possible with the available person-hours. One of the most labour-economical methods of screening for horizontal resistance is to let the parasites do the work of screening for you. The plants you want are then alive, and forming seed, while all others have died and possibly disappeared entirely. This is a replication of the maize in tropical Africa (Chapter 20).

Constitution

Each club should have a constitution comparable to those of other private or professional societies. The constitution would be open to amendment and, with experience, it would gradually be improved. Eventually, it should be possible to publish examples of model constitutions that newly formed clubs can adopt as their own.

Obligations of Membership

The obligations of membership should be clearly stated in the club constitution, and the club rules. There should be a constitutional means of expelling members who conspicuously neglect their obligations.

Plant Breeders' Rights

The concept behind plant breeders' rights is the concept of a copyright, otherwise known as intellectual property protection. Most of the industrial countries now have legislation controlling plant breeders' rights. The general purpose of this legislation is to promote innovation, and private plant breeding, by protecting and rewarding private initiative with copyrights and royalties.

There is a widespread fear that modern plant breeding is so complex that it can be undertaken only by large institutes, staffed with many highly qualified scientists, and costing millions each year to run. Furthermore, until plant breeders' rights were established, there was no way in which these expensive institutes could recover the costs of their plant breeding. This has meant that virtually all plant breeding during the twentieth century has been undertaken by governments, or government-funded universities and research institutes. The only possible private plant breeding, therefore, has involved the production of hybrid seed in open-pollinated crop plants, such as maize, in which the hybrid seed can be used only once (Chapter 20). The spectacular progress of private research in producing hybrid maize seed has demonstrated the potential of private plant breeding.

Because of its expense and complexity, it is now feared that non-governmental plant breeding can be undertaken only by very large, and very wealthy, corporations, such as the big chemical firms. In its turn, this has led to a fear that the new plant breeders' rights will encourage restrictive cartels in crop varieties and farmers' seeds, rather than innovation in plant breeding. Another fear is that the non-industrial countries may be required to pay plant breeders' royalties to the rich industrial countries.

However, these fears result from Mendelian breeding methods, which do indeed require large and expensive institutes, and which produce cultivars that have 'big space, high profile, small time'.

But, if we use the biometricians' breeding methods, there is a very different picture. This quantitative plant breeding does not require large and expensive institutes, and it is well within the capability of a group of resolute amateurs who have organised themselves into a plant breeding club. Furthermore, this alternative kind of breeding uses on-site selection, and produces cultivars with local adaptation, and a limited climatic adaptation. This is the 'small space, low profile, big time' aspect of horizontal resistance. There is then no question of the poor countries having to pay royalties to the rich. These poor countries will have their own plant breeding clubs, producing their own local cultivars.

Depending on the country concerned, plant breeders' rights are granted by a government, with respect to a specified cultivar, to the owner of that cultivar, for a period that may vary between 15 and 22 years. These rights reward the private breeder for the initiative, expense, and work expended in breeding that cultivar. They do this by prohibiting anyone else from propagating and/or selling that cultivar, unless licensed to do so, and they entitle the owner to a royalty on the sale of all propagating material. Once the patent or copyright expires, the intellectual property enters the public domain. The comparison with book copyrights and royalties is a close one. In order to anticipate the eventual effect of plant breeder's rights, we have only to ask ourselves how many books would be written if there were no author's copyrights.

Just as private individuals are allowed to make photocopies of copyrighted writing, or tape recordings of copyrighted music, for their own private use, and not for re-sale, so a farmer can use some of his own harvested material of a protected cultivar for propagation purposes on his own farm. But he may not sell any of it, unless licensed to do so. This is the so-called ‘farmer’s privilege’. Equally, any breeder may use a protected cultivar as parent material in a breeding program. This is the equivalent of new writing being influenced by older, copyrighted writing, or of a scientific paper making reference to earlier papers. Intellectual property always has a parentage and, if it is any good, it produces a progeny as well.

Some owners of breeders’ rights in the United States have been selling seed with a restrictive clause by which the purchaser surrenders the farmer’s privilege. This is a practice that should, perhaps, be made illegal. Some countries also permit the patenting of a single gene, mainly with a view to protecting transgenic cultivars. However, this interferes with the right to use a patented cultivar in a breeding program. As most breeding programs require 5-10 years to complete, the owner of a gene used in a transgenic cultivar should be able to maintain a competitive edge on all rivals without patenting that gene.

Plant breeding patents are still being tested in practice, and many complications and difficulties have emerged. One of these is a clear recognition of the public domain. All old cultivars, and all wild plants must be in the public domain. So must any cultivar whose patent has expired. So too should any single gene that occurs in the wild.

The licensing authority registers all trade in protected cultivars, and controls the collection and distribution of royalties. In order to obtain plant breeders' rights, an applicant must supply a sample of the new cultivar to the appropriate authorities who will subject it to field and laboratory tests, in order to confirm that it conforms with the necessary requirements. The development of 'DNA finger-printing' has greatly facilitated this process.

Allocation of Breeders' Royalties

Each club must reach its own decisions concerning the sharing of any royalties that it may earn. In general, royalties should serve three functions within a breeding club. The first is the financial support of the club itself, including both the existing activities and possible expansion. Second is the incentive to individual club members. If there is a decentralised organisation (see above), the active member who actually discovered the winning cultivar should receive a significant proportion of the royalties as his or her own personal reward. Third, the remaining monies should be shared equally among all the members.

It must be remembered that an exceptionally successful cultivar can earn royalties amounting to millions each year. A successful cultivar could also earn royalties for many years running. It must also be remembered that, the more breeding clubs there are, the less will be the chances of earning royalties. But let us recognise also that, usually, money is not the primary motivation in the forming of a breeding club. And if the prospects of earning royalties have been greatly reduced, this can only mean that the whole idea of breeding clubs has been immensely successful.

Ownership of Cultivars and Breeders’ Rights

Any new cultivars produced by the club should be the sole property of the club. The club should also be the sole owner of the breeders’ rights, and to the royalties earned from its cultivars. However, the club would be legally required to share these royalties among its members, according to the club constitution.

Sustainable Agriculture

In the recent past, rapid growth in the human population has led to an emphasis on total agricultural production, with little regard to the methods of that production, or to the sustainability of the agricultural system producing it. With improving prospects of stabilising human population growth, there is now a new emphasis on LISA.

LISA is an acronym for *Low-Input Sustainable Agriculture*. LISAT is an acronym for such agriculture in the tropics. The low input refers to the costs of production, which should be minimal. These costs refer particularly to energy-extravagant cultivation practices, such as deep ploughing, and the wasteful use of fertilisers. They also refer to the expense of using susceptible cultivars, which require both crop protection chemicals and seed certified free from parasites.

The sustainable component refers to all aspects of the environment, which must not be damaged in any way. This means there must be no soil erosion, no undue depletion of soil nutrients, no damage to the soil structure, no build-up of harmful residues in the soil, no depletion of the ground water, no loss of biological controls, no damage to non-target organisms, no build up of crop parasites, particularly soil-borne parasites, no pollution from crop protection chemicals, herbicides, or fertilisers, no atmospheric pollution from the burning of crop residues, and so on. Sustainability also refers to the cultivars themselves. The failure of vertically resistant cultivars, whose resistances have been matched, does not represent sustainability.

The very foundation of LISA is obviously resistance to crop parasites that is comprehensive, complete, and permanent. In a word, it is the proper utilisation of horizontal resistance.

Organic Farming

Organic farming eschews all synthetic chemicals, including artificial fertilisers. Ultimately, the total amount of organic farming will be limited by the amount of organic manure available, and this is probably less than many people realise. Organic farming also eschews all synthetic crop protection chemicals and this places a very heavy reliance on resistant cultivars. There is a popular misconception that healthy plants, grown in a healthy soil will have more resistance than unhealthy plants. This is not true. Resistance is genetically controlled and the physiological state of nutrition of the plant host has very little influence on it.

Organic farmers rely on two key factors when they eschew crop protection chemicals. First, they prefer ‘heritage’ seeds, which are cultivars that were in use before the invention of synthetic pesticides. These cultivars are consequently more resistant than modern cultivars. Second, they rely on the fact that the farmers all round them differ in that they are using crop protection chemicals. This lowers the incidence of crop parasites, and provides a false impression of resistance in the organic crops. It is clear that, if the total amount of organic farming increases significantly, the countrywide use of pesticides will decline, and the incidence of crop parasites will increase. For this reason alone, breeding for horizontal resistance is essential to the expansion of organic farming. Organic farmers should be more interested than most in plant breeding clubs.

Breeding Strategy

The club would normally be breeding for horizontal resistance that is both complete and comprehensive. This will require the biometricians’ system of breeding, involving recurrent mass selection designed to produce changes in the frequency of polygenes controlling continuously variable characters.

If the crop is derived from a discontinuous wild pathosystem (e.g., an annual or biennial species, or a deciduous tree or shrub), gene-for-gene relationships may occur, and the vertical resistances must be genetically eliminated, or epidemiologically inactivated, during the screening process. This will normally be done with the one-pathotype technique (See Chapter 25).

If the crop is derived from a continuous wild pathosystem (e.g., an evergreen perennial), gene-for-gene relationships will not occur, and precautions against vertical resistance will not be necessary. (The only apparent exception to this rule is arabica coffee; see Chapter 21).

There will have to be on-site screening which is conducted in the *area* of future cultivation, during the *time of year* of future cultivation, and according to the *farming methods* of future cultivation. These future methods may be different from the current methods (e.g., changed fertiliser or irrigation use.).

Depending on the crop, it may be necessary to have a crossing generation and/or a multiplication generation between each screening generation. Single seed descent, family selection, and late selection are recommended for many self-pollinated, seed-propagated crops. (See Chapter 25 for detailed descriptions of these procedures).

Prepare for Disappointments

Do not expect any new cultivar to be perfect, however promising it may appear at first. Once a new cultivar is being cultivated, various defects are likely to become apparent. There may be an undue susceptibility to a very minor pest, which then becomes a nuisance. Or other characters of yield, quality of crop product, or agronomic suitability may be imperfect. Occasionally, a very promising cultivar will later prove to have a defect that is quite unacceptable commercially. What is important is that the club’s new cultivars will need less protection from crop protection chemicals, and possibly no protection at all. The whole point about horizontal resistance breeding is that it is cumulative and progressive. The earliest cultivars will be little more than a step in the right direction.

It will probably prove impossible to produce the perfect cultivar, ideal in every single respect. But the combined efforts of many breeders’ clubs will eventually get very close to it, in most species of crop, and in most areas.

Club Property

The club might either lease, or purchase, a small farm, using membership fees to pay rent, or to pay off a bank loan. This farm may need a greenhouse large enough to handle the basic club activities, such as cross-pollination, and the maintenance of designated hosts and parasites. The farm should also have enough land for screening activities (if there is a centralised organisation), and for field trials, multiplication plots, and similar activities.

The farm will also require equipment such as farm machinery, and a simple laboratory for culturing parasites will be desirable. The club might also own other property, presumably located on the club farm, such as a meeting room, library, or cafeteria. Other club property would include various kinds of tools, including office, scientific, and farming equipment. Some clubs would require members to contribute a part of their own farms, gardens, and equipment to the club activities.

If the club is large enough, and able to afford it, it might have a professional farm manager, employed either on a consultancy basis, or full-time. A retired professional may be willing to do this work, possibly in exchange for free occupancy of the club farmhouse.

Some clubs may undertake commercial farming activities, particularly organic farming, in order to pay the rent. However, the tail should not be allowed to wag the dog.

Breeding Cycles

A breeding cycle involves all the breeding activities from one cross-pollination to the next. These may include other activities such as a crossing generation, a multiplication generation, several selfing generations, and a screening generation with late selection. Any technique, such as a heated greenhouse in winter, that reduces the length of each breeding cycle, will accelerate the breeding process. For example, a one-year breeding cycle might require 5-10 years to produce new cultivars. If that cycle was reduced to half a year, this period would also be halved.

Breeding clubs should aim at as short a breeding cycle as possible if they want to get results quickly.

Complaints from Neighbours

One of the oldest of agricultural disputes is caused by the farmer who neglects his weeding, and allows weed seeds to blow on to his neighbours land. Similar disputes can arise from breeders clubs which deliberately encourage pests and diseases which can then spread on to their neighbours‘ crops. Very recently, the pollen blowing across farm boundaries from open-pollinated transgenic plants has also become a matter of dispute that can also involve the owner of the plant patent concerned.

These disputes can become acrimonious and they may even lead to legal battles. However, in principle, most farmer neighbours will be pleased to learn of the club's aims and objectives, and will be willing to cooperate.

The best means of avoiding this kind of dispute is for a club officer to make prior visits to the various nearby farmers and explain exactly what the club is doing, and why. The basic explanations are as follows: (i) Soil-borne parasites will not normally spread to the neighbours' land. (ii) Water-borne parasites may spread in surface drainage water, or in a stream or river that is supplying irrigation water, but this is a relatively rare occurrence, and can usually be controlled or avoided. (iii) Minor wind-borne parasites do not matter. (iv) Major wind-borne parasites are around anyway, regardless of anything the club might do and, if the farmer is using pesticide controls, these should not matter. If necessary, the club could accept responsibility for any extra expense or work required for additional pesticide controls. But, in general, if the farmer's spray schedule is not working this is either because he is using inappropriate techniques, or because a new pesticide-resistant strain of the parasite had appeared. In neither event can the club be blamed. (v) If the farmer is using a cultivar with a vertical resistance that breaks down during the club activities, it should be explained that the designated pathotypes (see Chapter 25) used by the club are all common races that have been around for some time. The club cannot be blamed for a normal failure of vertical resistance on someone else's land.

It may also be possible for the club to isolate its work to some extent. For example, the screening plots might be located in the middle of a large field or farm growing a different species of crop. In general, however, the requirements of on-site screening restrict the possibilities of isolation in both time and space.

Illegal Parasites

In most countries, working with some parasites is illegal because they are under legislative control. For example, it is illegal to work with potato wart disease (*Synchytrium endobioticum*) in much of Europe and North America, or with the Colorado potato beetle; (*Leptinotarsa decemlineata*) in Britain, and the golden nematode (*Globodera rostochiensis*) in most of Canada. Active members should never attempt to break the law in this respect, and they must accept that their new cultivars will be susceptible, and possibly vulnerable, to these foreign parasites. The only way they can be tested is by sending them to an area where the parasite occurs. However, this may lead to phytosanitary problems. Should the foreign parasite ever be accidentally introduced, and become established, the breeders can breed for resistance to it, and adequate resistance can probably be accumulated within a few years.

It must be clearly recognised that this limitation can occasionally restrict the geographic range of club cultivars. For example, potatoes that were bred by a club in England would have no resistance to the Colorado beetle, and they might have a reduced value in continental Europe or North America for this reason. Conversely, of course, potatoes that were bred in continental Europe, and were highly resistant to Colorado beetle, could be grown in Britain. Provided that these new cultivars were popular, the crop vulnerability caused by this insect would then decline, and the need for this legislation would also decline.

Genetic Engineering

Genetic engineering produces GMOs (genetically modified organisms). It does this by transferring a single gene from one organism to a totally unrelated organism. At first sight, this appears to make plant breeding quicker and easier. For example, a gene for resistance to blight, as well as another gene for resistance to Colorado beetle, could be transferred into a popular potato variety such as *Russet Burbank* without altering that variety. This would eliminate all that back-crossing. But the process is highly technical.

Genetic engineering apparently makes plant breeding even more technical, expensive, and out of reach to amateur breeders. In practice, however, the scope of genetic engineering in crops appears to be rather limited.

One of the problems of genetic engineering is that it can normally handle single-gene characters only. This surrounds it with limitations comparable to the Mendelian single-gene breeding. As we have seen (Chapter 1), single-gene characters of economic importance are rather rare in plants. Genetic engineering has broadened the scope of single-gene breeding because it permits gene-transfers that would otherwise be impossible. Nevertheless, the range of single-gene characters that are economically important remains very limited.

At the time of writing, the GMOs available to farmers included cultivars of a few crops such as cotton, maize, soya, potatoes, canola (rapeseed oil), and tomatoes. Only two genes have proved economically viable. These are the gene for resistance to the herbicide glyphosate, and the gene for production of the *Bt* (*Bacillus thurengiensis*) toxin that is supposedly harmless to people but lethal to some insects. There is also a lot of talk about the so-called ‘terminator gene’ which would prevent seed propagation, and thereby eliminate the need for both patents (as with hybrid maize) and the farmer’s privilege. In addition, a number of genes for resistance to crop parasites have been identified, but these resistances are likely to be as ephemeral as vertical resistance.

The glyphosate-resistance gene has produced some unexpected problems. In canola, for example, it leads to crops that are spectacularly free of weeds. However, canola is open-pollinated, and its pollen carries the new gene to other farmers’ canola crops. Furthermore, the modified canola is liable to become a weed that may be difficult to control in a rotation. This means that the canola crop must be followed by a monocotyledonous crop (i.e., a cereal or fodder grass) so that the canola weeds can be destroyed by a selective herbicide. There is also a rather remote fear that the gene may get into wild plants by cross-pollination. Finally, many people fear that this herbicide-resistance gene may have undetected side-effects on people. These problems exist with other open-pollinated crops, such as maize, and with many other crops that have a limited cross-pollination, such as tomatoes.

The *Bt* gene is expected to break down to new *Bt*-resistant strains of insect pests. This would be a pity, because it is now used as an insecticidal spray by organic farmers who have few natural insecticides available to them. If the use of the *Bt* toxin were limited to organic farmers, its breakdown would be unlikely.

There are other problems associated with genetic engineering. In theory, the process transfers a single gene. But, in practice, it transfers a group of genes and the receptor plant may be significantly altered as a result. Back-crossing may be necessary after all. The transfer process may also involve allergens that can get into processed foods without anyone being aware of their presence.

In conclusion, genetic engineering does not eliminate the need for traditional plant breeding. In particular, it is no substitute for horizontal resistance. Amateur plant breeders who organise themselves into a club need have no fear of competition from the big chemical corporations. Indeed, if there are enough of them, these clubs will provide very real competition that the corporations cannot defeat. Equally, club members should not feel that they must work with transgenic plants in order to be ‘modern’.

Newsletters

A large club may care to have a newsletter for the dissemination of information among its members. Clubs with similar interests may also care to exchange newsletters. Most clubs are likely to own a computer, and desktop publishing, e-mail, and bulletin boards can be very useful in this respect. The Internet is likely to become the main medium of international communication between clubs all over the world (see Cyber-Clubs below).

Associations of Clubs

If the idea of breeding clubs becomes popular, it may be possible to form national associations of breeding clubs and, eventually, perhaps, an international association.

Professional Societies

It is often possible for private breeding clubs to obtain membership in professional societies or associations, such as national and international plant breeding, plant pathological, entomological, horticultural, agricultural, and forestry societies. Even without membership, these associations will often sell teaching supplies (e.g., photographic slides and posters of parasite symptoms, microscope slides of parasites, leaflets, books), and some offer services, such as providing lecturers, specimen identification, and specialist advice.

Scientific Publication

Individual club members, or teams of club members, may make a discovery that justifies publication in a scientific journal. The rules following such publication should be the same as in a scientific institute. That is, the paper should be published under its author(s)' name(s) but the name of the club, in which the authors did their research, should be acknowledged. This is because the credit for scientific discoveries goes to the individuals who made them, but credit should also be given to the source of their research funds and facilities.

Financial Audits

The club treasurer would be responsible for keeping the club books, which should be audited at regular intervals.

Cyber Clubs

Any plant breeding club is likely to be linked to the Internet. The world needs a number of well-organised home pages to keep plant breeding clubs in touch with each other, and with the latest available information. University clubs are the most suited to providing such a service.

Charitable Clubs

Charitable breeding clubs would be organised with a view to helping non-industrial, tropical countries. They would operate in much the same way that missionary societies operated during the nineteenth century. That is, they would collect funds in the home country, and send plant breeders to one or more of the poorer, non-industrial countries in order to assist in the production of new subsistence cultivars. This kind of activity could also be a distant aim of ordinary breeding clubs, should they ever win big money from breeders' royalties.

There are two special reasons for this charitable activity. First, tropical crops are divided into cash crops, such as tea, coffee, cocoa, sugarcane, and rubber, and subsistence food crops, such as maize, rice, sorghum, millets, sweet potatoes, cassava, taro, beans, and yams. Subsistence crops are grown to feed the farmer and his family and, apart from an occasional sale of surpluses, they earn no money. Traditionally, the cash crops have always earned enough money to finance their own research, usually with a small, nationally imposed export tax. But the subsistence crops earn no money at all, for either the farmer or his government. These crops have suffered from a dearth of research. They are the crops that feed the people who constitute most of the population of a non-industrial country. Recently, the International Research Centres have been doing research on these subsistence food crops but they have been plagued by all the problems associated with Mendelian breeding and scientific monopolies (Chapter 19). These international research centres need competition, because of their scientific monopolies. Science thrives on competition, and suffocates without it. Furthermore, farmers in non-industrial countries need help. Far more help, indeed, than the International Research Centres, and the farmers' own national governments, can be expected to provide.

If it so desires, a wealthy breeding club, or one that is supported by a wealthy foundation, can be charitable in another way. It can refrain from collecting royalties from its new cultivars. However, these cultivars should be registered, and formally put into the public domain (in order to prevent anyone else from patenting them), so that they become available to everyone, free of royalties.

Research Grants

In many countries, clubs will be able to apply for research grants, either from their Government, or from various charitable foundations. Such a grant could be of crucial importance in setting up a new club that is to be well organised with proper facilities and equipment. The winning of grants will be one of the main tasks of the club treasurer, and it will become much easier as the idea of plant breeding clubs becomes better known.

Tropical Farmer Participation Schemes

Some subsistence crops in non-industrial countries are amenable to farmer participation schemes. These schemes would have to be organised by a central breeding station in the country concerned. The setting up and operation of such a station would normally be undertaken by the government, but it could also be undertaken by a charitable breeding club, working with government co-operation.

For these reasons, Chapter 27 concerns tropical farmer participation schemes.

Mexico

The University of Chapingo, in Mexico, has the honour of having established the first plant breeding club for horizontal resistance. This was a bean breeding club established in March 1995. Clubs for several other crops have been formed since then.

Chapter 25

Techniques

Notes for Readers

About 130 different techniques are described in this section. The only reasonable way to list these techniques seemed to be in alphabetical order, even though this can be irritating at times. I have tried to avoid the obsessively strict ordering found in military parlance (e.g., “Soap, toilet, officers, commissioned, for the use of”) and I have felt free to index under adjectives. Equally, I wanted to avoid the more asinine type of cook-book index entry in which beans are listed under ‘H’ (i.e., “How to cook beans”). So it is entirely possible that my listing will please no one. If a half-remembered technique cannot be found, try either the list of contents, or search for the term..

Technical terms are used in these descriptions, but every one of them is explained and defined, either in the text or in the glossary. Some repetition has proved inevitable and readers are asked to be patient with this.

Bees

When a club is working with a bee-pollinated species of crop, the use of beehives in, or near, the population that is to be randomly cross-pollinated, can be very effective. Such a club may choose to have an apiarist member, or it may invite a friendly apiarist to devote one or more hives to the club activities.

Bees will visit any flower that provides nectar, and it is the breeder’s function to ensure that only desirable plants of the crop being improved are available to the bees. This can be achieved in one of two ways. One method is to have a special crossing generation, grown well away from other crops of the same species, in either time or space, and with its own beehive. However, this method is likely to waste every alternate screening season, and thereby double the duration of the breeding program.

The other method is to use the screening generation as the crossing generation also. In this case, there must be a negative screening to remove all the unselected plants, or their inflorescences, before flowering starts. This means that there may be rather few plants left for the bees to visit. Although this is mainly a problem for the bees, it may encourage them to go elsewhere. The problem can be solved by planting a surround of a different species of plant which the bees like just as well. There will then be enough bees to visit every flower in the screening population also.

With crops that are normally self-pollinated, but which can also be cross-pollinated by bees (e.g., beans), a marker gene will be necessary to identify the seeds or plants that are the result of cross-pollination. (See marker genes, below). This is one of the few instances when single-gene Mendelian characters can be really useful when breeding for horizontal resistance.

Bulk Breeding

A method of breeding self-pollinated plants, in which there is late rather than early selection (see below). A large sample of a variable population is self-pollinated for several generations, without any selection, to produce a mixed population that is highly representative of the original, but in which every individual has a fairly high degree of homozygosity. The screening is conducted on this heterogenous population of relatively homozygous individuals. This late selection is more efficient than early selection because it eliminates the unwanted effects of heterosis (i.e., hybrid vigour) and it permits the expression of recessive polygenes for horizontal resistance. An alternative, and generally preferable method of late selection involves single seed descent (see below).

Catalogues

The choosing of equipment can often be difficult, either because there is a plethora of options available in an industrial country, or because there is a dearth of options in a non-industrial country. Breeding clubs should obtain as many manufacturer's catalogues as possible. Catalogues are a rich source of ideas and information about labour-saving devices, and one judicious purchase may easily eliminate hundreds of hours of tedious work. Equipment varies considerably in price and quality, and a specialist should be consulted before expensive purchases are made. Novel uses for equipment, or equipment that proves to be exceptionally useful, should be recommended in the club newsletter, home page, and e-mail. A regular exchange of information between clubs can be very useful in this respect.

Categories of Parasite

Parasites can be classified in a variety of ways, quite apart from their taxonomic classification. They can be grouped according to their method of dispersal. Thus soil-borne, air-borne, seed-borne, water-borne (i.e., with irrigation) parasites. They can be classified according to the number of reproduction cycles they go through in each epidemic cycle, each season. Thus there are monocyclic (one cycle), oligocyclic (few-cycle), and polycyclic (many-cycle) parasites. Another classification concerns the type of damage that they cause. Thus diseases can be grouped into wilts, smuts, rusts, blights, rots, and galls, while insect pests can be grouped into stem borers, leaf miners, sucking bugs, root eaters, leaf eaters, and so on. Parasites also differ widely in the frequency of their parasitism, and the injury of their parasitism.

The techniques of culturing and inoculation differ considerably with these various categories of parasite, and the ease of screening also varies. The details are beyond the scope of this book and, if in doubt, specialists should be consulted before the breeding program is launched.

Cereals, Selection Procedures

M.A. Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, Agric. Univ. Wageningen Papers 88-2; 114pp), working Brazil, tested four different selection procedures for cereals. These were (i) *Single Plant Selection* (SPS), which is here called early selection; (ii) *Bulk Seed Selection* (BS), which is called bulk breeding in this book; (iii) *Line Selection* (LS), which is called family selection here; and (iv) *Natural Selection* (NS) which leaves all selection to nature. The original publication should be consulted for details which are beyond the scope of this book. It will suffice that all procedures produced results, but the family selection was the most effective.

Clonal Multiplication

In a vegetatively propagated crop, the selected clones of each screening season should multiplied vegetatively for test purposes, and as possible parents of the next screening generation. The main tests are designed to reveal a potential new cultivar. They include field trials to determine resistance under field conditions, agronomic suitability, and the yield and quality of crop product that the clone produces when it is propagated vegetatively, and without crop protection chemicals.

Commercial Contracts

A breeding club may choose to take out commercial contracts for such activities as soil preparation, soil inoculation, and seed sowing in pots. Many commercial firms have machines for preparing and treating soil in bulk, and for mechanically sowing large numbers of seeds in banks of pots.

Comprehensive Horizontal Resistance

When breeding for comprehensive horizontal resistance, the club should aim at relatively small, but simultaneous increases in resistance to all the locally important parasites. A cultivar that had very high horizontal resistance to some species of parasite, but was very susceptible to others, would have little value. The best selections in each screening generation should all have approximately the same level of horizontal resistance to all the locally important parasites, but this level would be higher than that of the previous screening season. This is the holistic approach.

It should be remembered also that screening seasons vary. The selections of the current season may even appear to be worse than those of the previous season. This can be alarming unless it is realised that the current season was, perhaps, more humid, and it consequently had far more parasite damage, than the previous season. Equally, an apparently large jump in the level of resistance may be no more than the result of a reduced parasite epidemiological competence in the current season.

Conflicts Between Local and Cosmopolitan Cultivars

When using the qualitative characters of Mendelian genetics, such as vertical resistances, it is possible to produce cultivars that have a very wide geographic range. This has led to the concept of a central breeding station that uses ‘multi-locational testing’ to produce cultivars with a cosmopolitan adaptation. The early miracle wheats and rices of the Green Revolution, for example, consisted of very few cultivars which, however, were cultivated in huge areas, in many different countries, producing an alarming genetic uniformity. There was also an alarming crop vulnerability, because of the potential failure of those vertical resistances. The success of these ‘miracle’ wheats and rices apparently confirmed a widespread Mendelian view that a cultivar that performs well in one region will perform equally well in other regions.

Breeders working with quantitative characters, such as horizontal resistances, have a different view. Here the idea is to produce a balanced system. The many quantitative variables of the cultivar must balance the many quantitative variables of the local agro-ecosystem. In particular, its many horizontal resistances must balance the differing epidemiological competences of the many species of parasite. Move that balanced cultivar to another agro-ecosystem, where the epidemiological competences differ, and the cultivar will be out of balance. It will have too much resistance to some species of parasite, and too little resistance to others. This is the basic reason for on-site selection (see below).

Ambitious club members should accordingly refrain from dreams of a new cosmopolitan cultivar that is going to dominate the world and earn them fame and fortune. This is a case where “small is beautiful”.

In practice, of course, each breeding ‘site’ is usually quite large. A potato cultivar, for example, might be successful in much of

Europe. But it would be unrealistic to expect it to do equally well in, say, Mexico, the Highlands of Ethiopia, or Northern India.

This is one of the advantages of a multiplicity of private plant breeding clubs, employing horizontal resistances, and encouraged by plant breeders' rights. It will allow us to escape from this misleading concept of cosmopolitan 'miracle' cultivars, and the dangerous genetic uniformity that this concept produces. We can then develop both a rich genetic diversity, a wide choice of cultivars for farmers, and a wide selection of products for consumers.

Contamination of Members' Land

Active members must accept that their greenhouses, fields, and gardens will become heavily contaminated with the various parasites used in the screening process. Indeed, effective screening positively requires heavy contamination. Some members may fear that this contamination is permanent, and that their gardens or fields will suffer lasting damage. However, this fear is groundless. Once the screening work is finished, and given a suitable rotation, the contamination will normally disappear in a few years.

Crop Protection Chemicals

In the early stages of a horizontal resistance breeding program, the parasites may threaten total destruction of the screening population. In these circumstances, it is entirely reasonable to use crop protection chemicals towards the end of the screening generation, to ensure that the least susceptible plants survive and produce a few seeds.

However, this can be a problem for clubs that are working on an organic farm, because the use of crop protection chemicals would nullify the organic status of that farm. There is much to be said, therefore, for screening the early generations on land that is not part of a certified organic farm.

Cross-Pollination

Cross-pollination is an essential feature of recurrent mass selection. It ensures that the final selections of each screening generation, which become the parents of the next screening generation, will share their genes to the maximum extent. Each final selection is cross-pollinated with all the others, either randomly, or with controlled crosses, depending on the crop in question.

With out-breeding plants, cross-pollination occurs naturally, and the screening generation is usually the crossing generation also. However, there must be a negative screening to remove all unwanted pollen, by removing entire plants, or flowers, as the case may be. This will ensure that only final selections can become male and female parents.

Some in-breeding plants, such as cereals, can be converted to the out-breeding habit with the use of male gametocides.

Other in-breeding plants must be cross-pollinated by hand, and emasculation is usually necessary. The techniques of hand-pollination vary from species to species, and a specialist should be consulted. Occasionally, it may be possible to use pollinating insects to achieve a random cross-pollination in an in-breeding species.

It must be remembered that a limited amount of self-pollination does not matter when the plants are heterozygous. This is because a heterozygous plant produces considerable variation in its progeny, even with self-pollination.

If the original parents were pure lines, the first generation of seeds will not exhibit any variation, and it cannot be used for screening. The second generation will exhibit considerable variation, and it can be used for screening. However, this second generation is also a multiplication generation, which is often necessary anyway, in order to produce sufficient numbers of seeds for the first screening population.

In the initial cross of designated parents (for inactivation of vertical resistance, see below) the parents are cross-pollinated in all combinations. That is, each designated parent must be crossed with every other designated parent to produce approximately equal numbers of seeds from each cross. It does not matter very much which parent is male, and which female, in any particular cross. The aim is that each designated parent should be represented more or less equally in the breeding population.

(See also: male gametocides, marker genes).

Cross-Pollination, Cereals

Cross-pollination of cereals can be done in the field, during the screening generation, or in the greenhouse during a separate crossing generation.

Field crossing is the easiest. It also produces much larger numbers of crosses, and is recommended. A negative screening must be conducted before anthesis to ensure that no undesirable plants are producing pollen. If the breeding involves an in-breeding cereal, a male gametocide (see below) will have to be used, producing 60-80% of cross-pollination, which is entirely adequate. A male gametocide is not necessary with rice because a single multiplication generation produces so many segregating seeds.

Greenhouse pollination is more effective, but it involves quite a lot of finicky work and, because relatively few crosses are produced, this method will probably necessitates a multiplication generation. Special techniques are available for emasculating the various species of cereals. A specialist should be consulted.

Cross-Pollination, Grain Legumes

No satisfactory male gametocides are known for the *Leguminoseae*. This means that all cross-pollination must be done by hand. This is possibly the most labour-intensive part of the entire breeding cycle, and it is a time when all active members must pull their weight.

The flower petals should be opened the day before opening, and the stamens removed with a pair of fine forceps. When the emasculated flower has opened naturally, the stigma is touched with a mature anther, or with a fine camel hair brush holding pollen. Some breeders like to label the pollinated flowers with a light, tie-on label. However, this is a pedigree breeding habit and, provided all the flowers that have not been emasculated are removed, there is no need for labels. Every pod or fruit will be the result of cross-pollination. Care should be taken to ensure that each parent is represented more or less equally in the crossing, but even this is not too critical. If an occasional self-pollinated flower is accidentally included, this is not very important.

Pollination requires a humid atmosphere. The greenhouse floor should be kept wet during this work, and pollinated plants should be lightly sprayed with a fine water mist. Once the day's task is finished, the entire greenhouse should be well watered. If high rates of pollination failure occur, an inadequate humidity is usually to blame. Some breeders like to bag each pollinated flower with a small plastic bag, but this requires considerable extra work, and should be regarded as a last resort. Greenhouses dry out much less quickly during the night, and there is much to be said for doing this work in the late afternoon and evening, provided that the species concerned is not pollination-sensitive to the time of day.

It is important to be comfortable during this pollination work. Use a comfortable stool or chair of an appropriate height. Plants with a determinate habit should be on benches, or should be carried to a working bench, for pollination. Climbing plants are usually in pots on the ground, and are climbing up a string. Seats of various heights should be available for pollinating flowers at various levels on the vine.

Crossing Generation

Many crops, which cannot easily be cross-pollinated during the screening generation (e.g., beans), will require a crossing generation. Several seeds of each new parent are planted and grown in the club greenhouse for cross-pollination. The total number of parents, and the total number of seeds planted from each parent, are easily calculated from the needs of the club as a whole. If there is a multiplication generation (see below), these numbers can be reduced very considerably.

First, the 10-20 pure line cultivars, the original parents, must be crossed in all combinations, and in roughly equal proportions, to produce the first generation. If these parents were pure lines, these seeds will not exhibit any variation. They must be grown and allowed to self-pollinate to produce the second generation, which will exhibit considerable variation. However, such a multiplication generation is necessary anyway, in order to produce sufficient numbers of seeds for the first screening population. Remember, the more plants that are screened, the greater the rate of progress.

After each screening generation is completed (see below), the seeds of the selected plants must be planted to become the parents of the next generation. These parents must be cross-pollinated in the same was as the original parents were crossed. If required, the resulting seed may then be grown once, and allowed to self-pollinate, as a multiplication generation. If late selection and family selection are being used, the seed should be self-pollinated for 3-4 generations.

The crossing and multiplication generations should be protected with crop protection chemicals, at least in the early breeding cycles, because they are still quite susceptible and should not be exposed to any risk of loss.

These procedures will vary slightly with late selection and family selection.

Cultivar Characteristics

Within a single crop species, there are usually a variety of different types of cultivar. Thus, early, maincrop, and late potatoes; eating and cooking apples; white, brown, red, or black beans; and so on. A breeding club must decide both what crop species it wishes to work with, and what category of cultivar within that species. Some clubs may choose to work with more than one category of one crop species, particularly if they are using interleaved breeding programs (see below).

Cultivar Multiplication

When the club has a potential new cultivar, its propagation material must be regarded as ‘foundation stock‘ that has to be multiplied. This multiplication is required first to produce material that is sent to the plant breeders’ rights registration authority. If the new cultivar is accepted and registered, propagating material may be required for the one or more seed production organisations licensed by the club to produce and sell its cultivars.

This initial multiplication is often a skilled and complicated business, if the foundation stock is not to become contaminated with foreign plant material, or parasites of various kinds. Furthermore, the club's foundation stock will almost certainly be carrying various parasites as a result of its exposure during screening.

Depending on the country, its legislation, and the crop being developed, the club may decide to contract such multiplication work out to a specialised organisation that is skilled in the handling and production of foundation stock seed and propagating material.

(See also: purification of foundation stock).

Cyclone Separation

A cyclone separator is a device for separating particles of dust from the air in which they are suspended. The dusty air is thrown into a swirling, miniature cyclone inside a hollow cone. The dust particles are thrown against the sides of the cone by centrifugal force, and they drop through the bottom of the cone into a collecting container. The device is usually quite large, and is used for extracting dust from the air of factories, mills, etc.

A miniature cyclone separator, only an inch or two in diameter, is an excellent method of collecting both pollen and fungus spores. Its use will require a portable vacuum pump, or a vacuum line in the greenhouse. Only a low vacuum is needed, such as the suction produced by a water suction pump. If this work is being done in the field, a spare wheel from a car is a useful source of air pressure to produce suction with a Venturi tube. Use manufacturer's catalogues, where cyclone separators may be listed under other names, e.g., pollen-collector, spore collector, etc.

Dangers of Foreign Pollen

Plant populations which are to provide parents for the next screening generation must be isolated from foreign pollen of the same species, originating in a nearby crop, or even from rogue plants surviving from an earlier crop. This pollen can be damaging in two ways. It might introduce vertical resistance genes that will not be matched by the designated pathotype. Or it might introduce susceptibility into a screening population that has already accumulated considerable horizontal resistance.

There are three methods of providing this isolation, and the choice of method depends largely on the crop in question, the nature of its flowers, and in which type of population (i.e., screening or crossing) the pollination occurs. The first is by physical protection. The flowers that are to be cross-pollinated are enclosed in paper or plastic bags to keep out wind-borne pollen, or pollinating insects. The second is by distance. The isolated crop is located so far from any other plants of the same species that cross-pollination is virtually impossible. Lastly, there can be isolation in time. The population that is be cross-pollinated is grown at a time of year when no other plants of the same species are producing pollen.

(See also: spreader rows and surrounds).

Designation

Designation is necessary in all crops in which gene-for-gene relationships occur. This is to ensure that no vertical resistances are functioning during the screening process, and it is the basis of the one-pathotype technique (see below). It is a critically important aspect of the horizontal resistance breeding program, and negligence at this step can easily ruin the entire program. This is also the part of the program in which amateur plant breeders will most need to consult specialists. There are six steps in the designation process, as follows:-

1. List all the important parasites that occur in the breeding site, and then identify each one of them that has a gene-for-gene relationship. In most breeding programs, there will be only a few such species. (However, a crop species which is derived from a continuous wild pathosystem will have no gene-for-gene relationships).

2. For each species of parasite with a gene-for-gene relationship, choose a once-popular cultivar in which the vertical resistance has broken down. This may be a cultivar which is still being cultivated, because of its high yield and quality, but in which cultivation is possible only under the protection of fungicides and/or insecticides. A pure line or clone of the cultivar, as the case may be, is chosen as the designated host. This designated host must be continuously maintained in the form of succeeding, over-lapping generations, for the entire duration of the breeding program. This

work will normally require a greenhouse. It may be possible to have a single designated host that will carry all of the designated pathotypes. This is the ideal situation, if it can be achieved. Alternatively, at the other extreme, it may prove necessary to have a separate designated host for each species of parasite.

3. Choose one vertical pathotype of each species of parasite in which a gene-for-gene relationship occurs. Each vertical pathotype must be chosen because it matches the designated host. It then becomes the designated vertical pathotype. It is *essential* that there is only *one* designated pathotype for each species of parasite.

4. Each designated pathotype is cultured on plants of its designated host for the entire duration of the breeding program. Each designated pathotype will be used to inoculate each screening population to ensure that any vertical resistances that may be present will be inoperative during the screening process.

5. Each designated pathotype is inoculated on to each of a range of cultivars, which have been chosen as potential parents in the breeding program. Only those cultivars which are *susceptible* to *every* designated pathotype may be used as parents. Cultivars which are not susceptible to even one designated pathotype have a

functioning vertical resistance and, for this reason, cannot be used as parents.

6. The aim is to identify some 10-20 cultivars each of which is susceptible to every one of the designated pathotypes. These cultivars become the original parents of the screening population. A small seed stock of each one of these parents must be maintained, and replenished if necessary, for the duration of the breeding program. These will be required for testing purposes if a designated pathotype is lost, and must be replaced.

Early Selection

Early selection means that the screening is conducted on a heterozygous population that is the result of cross-pollination. It has the advantage that a complete breeding cycle (i.e., from one cross-pollination to the next) can normally be completed in one year. However, it is normally useful only in open-pollinated crops. (See also: Late selection).

Emasculation

When hand-pollinating the flower of a dicotyledonous inbreeder, it is necessary to remove the immature anthers in order to prevent any possibility of self-pollination. This is usually done one day before the flower is due to open, and the petals of the closed flower must be separated in order to reach the anthers. The anthers, which are still immature and sterile, are then broken off with a needle, or plucked off with forceps, and dropped to the ground. The flower will open the following day, and the stigma will be receptive to pollen.

With obligately out-breeding species, emasculation is unnecessary. This is because the plant's own pollen is incompatible, and self-pollination cannot occur. With optionally out-breeding species, and some in-breeding species, pollen from another plant is more effective than the plant's own pollen. Emasculation is then unnecessary, if there is an early cross-pollination by hand.

When working with in-breeding members of the grass family (*Gramineae*), such as wheat, barley, and oats, the use of a male gametocide (see below) is recommended.

Emergency Reserve

Depending on the nature of the crop being improved, the spare seed from the screening, crossing, or multiplication generation, should be preserved as an emergency reserve. This seed is carefully stored with a dehydrating agent (e.g., silica gel crystals) in air-tight containers in a refrigerator. It will be required if there is a disaster that ruins or destroys the next screening, crossing, or multiplication generation

If the crop in question is an annual that is propagated vegetatively (e.g., potatoes), the emergency reserve will usually have to be maintained as a living population. If it is a perennial (e.g., apples) it can be maintained either as rooted cuttings, or grafts on a mature tree.

If the crop in question is being subjected to late selection, and single seed descent of true seed, emergency reserves can be maintained simply by keeping the surplus seed of each ‘family’, after the single seed has been extracted.

Equipment

See: catalogues, farm machinery, greenhouses, head to row sowing, laboratory, library, office, plant pots, seed cleaning, seed counting, seed sorting, seed sowing (greenhouse/field), soil pasteurisation, soil processing (fertilisers), threshing.

Extension Services

Most governments, through their ministries of agriculture, operate extension services that provide specialised information and advice for farmers. Many of these services also provide beautifully illustrated pamphlets on crop cultivars, and the parasites of crops. Breeding clubs should possess a comprehensive collection of pamphlets on the crop of their choice. They should also establish friendly relations with their nearest extension service centre, which they should regard as their first stepping stone to specialised advice.

Family Selection

When working with pure line crops, there is much to be said for using the ‘head to row’ technique. This term is derived from cereal breeding, and it means that all the seeds derived from one ‘head’ or ‘ear’, or from one plant, constitute a ‘family’. All the members of one family are planted in one row, or in one small plot. The selection involves families first. Only the best families are kept. Then a second selection involves individual plants within those best families. Only the best individuals, from the best families, are kept. This technique leads to a more rapid genetic advance. However, if late selection is also being used, all the members of one family are very similar, and the selection of individuals becomes relatively unimportant.

(See also: field screening, greenhouse screening, grid screening, laboratory screening, late selection, negative screening, on-site screening, popularity screening).

Farm Machinery

The farm machinery required should not normally exceed that of a small and simple farm. That is, there should be a mechanical cultivator, or a small tractor with the appropriate implements for ploughing, sowing, cultivating, and harvesting the crop being improved. For some clubs, a special machine, usually called a ‘precision planter’, for sowing ‘families’ in separate plots for family, or head to row, selection may be worth its purchase price which, however, is usually quite high.

Farmer Selection of Seed

The cost of expensive, certified seed can often be eliminated by a farmer selecting healthy plants for seed within his own crop. This is particularly true of potatoes. The farmer should go through his crop just before harvest, and dig up the best looking plants for seed, until he has enough tubers to plant his next crop. This practice, combined with good levels of resistance, can control tuber-borne parasites if the horizontal resistance is not entirely adequate. Farmer selection of potato seed is at its most valuable in non-industrial countries when certified seed tubers are not be available. It is also a practice that is normal among subsistence farmers, and it can be taken into account by breeding clubs when planning their breeding policy.

Field Screening

Field screening is population screening conducted in the field, as opposed to the laboratory. Field screening involves selecting a small minority of the best plants out of the entire screening population. This selection is normally made by eye, and it involves choosing the least parasitised plants. Practice is necessary because the differences between the least and most parasitised plants may be quite small, because of parasite interference (Chapter 14). As far as possible, the eye-score should include the other main objectives of crop improvement which are yield, quality of crop product, and agronomic suitability. When these characteristics cannot be judged by eye in the field, a correspondingly larger number of the best plants should be selected to allow for further screening in the laboratory.

Sometimes, several screenings may be possible. Thus, with a cereal crop, the best 1% of plants may be labelled. Later, the best 10% of these labelled plants are labelled a second time with a second label. At the time of harvest, the best 10% of the doubly labelled plants are harvested. The selected plants are then taken to the laboratory to be individually assessed.

The first screening usually involves choosing the greenest plants, as this is the best indicator of the level of parasitism. A second screening based on parasitism itself may be desirable as the level of parasitism increases towards the end of the season

It must be remembered that there may be escapes from parasitism. Such plants will have an entirely false appearance of resistance, and they must be avoided. Parasite gradients are avoided by grid screening (see below). If there is a patchy distribution of the parasitism, the patches of escape should be excluded from the screening process. If these patches of escape are too large to exclude, there can be no screening for resistance to that particular parasite in that screening season. If this problem persists, a specialist should be consulted, and it may even be necessary to conduct some inoculation under his direction.

If family selection is being used, the grid is replaced by family plots. The best families are selected first, and only the best plants within those families can become final selections. Some parts of the screening population may escape a major parasite entirely. These areas should be marked off, and they should not be used for screening.

Occasionally, there may be a single, incredible, green, and healthy plant that makes all the other plants in the screening population look dingy in the extreme. It may be a fluke escape, although this is generally unlikely. It is more likely to have an unmatched vertical resistance, resulting from an accidental contamination with foreign pollen. Or it may be the parent of a stunning new cultivar. So do not throw it out, on the grounds that its apparent resistance is either false or vertical. Harvest it separately, for individual study.

If a male gametocide has been used on a cereal crop, the screening is conducted only in the alternate rows that have been treated with the male gametocide (i.e., the female population). A negative screening will have been carried out on the male populations. The best male plants will be self-fertilised and will have contributed their pollen to the next breeding cycle. For these reasons, there is little point in screening them for seed. However, if there is a scarcity of good plants for screening, the male plants may be screened also.

There are various methods of labelling the selected plants. The best is probably to tie a piece of brightly coloured knitting wool round the top of a stem. The wool can be pre-cut by wrapping it round a card and cutting down one edge. In some areas, particularly in Africa, small children find these bits of wool attractive, and they cannot resist removing them. If this is a problem, a non-toxic paint should be used.

It needs a ‘good eye’ to make these eye scores. Most people can develop a good eye quite quickly, usually within a few minutes. Some, however, find this kind of assessment work difficult to learn because, after all, aptitudes vary widely among people. Clubs should be tolerant of these differing aptitudes, and allot work accordingly.

If there are several, consecutive field screenings, and coloured labels are being used, each screening can be labelled differently. If the first selections are labelled, say, red, the next selection involves only red-labelled plants, and the best of these are labelled with another colour, and two or three screenings are usually adequate.

With crops that have an underground harvestable product (e.g., potatoes, garden beet, carrots, parsnips, radishes, turnips, mangolds, sugar beet, Jerusalem artichokes, peanuts, sweet potatoes, cassava, yams) each plant must be individually dug or pulled, and left lying on the soil surface for an assessor to either select or reject. However, the number of plants to be dug or pulled can be drastically reduced by earlier screenings based on eye-scores of the growth and health of the foliage.

(See also: greenhouse screening, grid screening, head to row screening, laboratory screening, negative screening, on-site screening, popularity screening).

Field Trials

Statistically controlled field trials will usually be necessary to compare potential new cultivars with an industry standard, and these will require statistical analysis. In general, this work is not recommended for breeding clubs, although statistical analysis is now very easy with computer software. The field trial comparisons should involve yield, quality of crop product, and agronomic suitability, both with and without pesticide protection. If a club does decide to undertake its own trials, a specialist should be consulted for the details of designing, conducting, and analysing them. The results of these trials will determine which lines will be sent to the authorities for registration as new cultivars which, if approved, will be entitled to plant breeders' royalties. The club target should be new cultivars that equal, or even out-perform the industry standard.

These criteria should apply when the club cultivars are not protected with crop protection chemicals, even though the industry standard is protected in this way.

Grafting

Grafting is the technique of joining a bud, or a shoot, called the scion, to another plant, called the stock. The usual purpose of grafting is to protect very susceptible, high quality clones from root diseases, by grafting them on to resistant rootstocks. Most fruit trees (e.g., grapes, citrus, stone and pome fruits) are grafted on to resistant rootstocks for this reason. Grafting is also a useful technique in potato breeding, used to induce flowering by preventing tuber formation. This is done by grafting potato scions on to tomato stocks. The potato stem then grows continually upward, producing an inflorescence every few inches. (See also: Potato Grafting).

Greenhouse Screening

In view of the importance of on-site screening, screening in the greenhouse would normally be permitted only for greenhouse crops. However, it is permissible to do a preliminary screening of seedlings (e.g., tomatoes, potatoes) in the greenhouse, just as it is permitted to do a final screening of the harvested product in the laboratory. Greenhouse screening would usually involve *extreme* parasite susceptibility to parasites that were used to inoculate the potting soil, or the seedlings themselves (e.g., soil-borne parasites, potato blight). This level of susceptibility normally results in the death of the seedling. It is useful in that it can reduce the work of transplanting, and the size of the screening population, very considerably. However, this type of screening must not be over-done because it might then eliminate useful levels of adult plant resistance. (See also: field screening, grid screening, head to row screening, laboratory screening, negative screening, on-site screening, popularity screening).

Greenhouses

The function of a greenhouse is to provide improved growing conditions for plants. In particular, a greenhouse will keep plants warm in winter, and it will protect them from the extremes of temperature, wind, rain, hail, snow, and sun. Occasionally, a research greenhouse is made insect-proof in order to keep plants free of insects.

In a breeding program, a greenhouse can often double the rate of progress by allowing functions such as crossing and/or multiplication to be carried out during a temperate winter or a tropical dry season. It is then possible to have a screening generation every summer (or rainy season in the tropics) instead of every alternate growing season. A greenhouse is also essential for on-site selection if the crop being improved is a greenhouse crop (e.g., tomatoes, cucumbers).

Depending on the crop being improved, a club greenhouse will usually be necessary for a variety of other functions, such as the cultivation of designated hosts, and the culture of both designated and undesignated parasites. With some crops (e.g., potatoes, tomatoes), each active member may require his or her own private greenhouse also. Possession of a private greenhouse could thus become a prime criterion both of club membership, and of the choice of crop by a club.

A greenhouse keeps warm because glass is transparent to light but opaque to radiant heat. Light is absorbed by objects inside the greenhouse, and it is then radiated as heat which cannot escape. In the tropics, and in a temperate summer, there is often too much heat. And, at night, and in a temperate winter, there is often too little heat. Most of the problems with greenhouses are associated with temperature control.

Cooling of an over-heated greenhouse is very important. Never attempt to cool a greenhouse with a refrigeration unit because, to be effective, refrigeration is prohibitively expensive. The only effective cooling method is to ensure a good flow of air through the greenhouse, and to evaporate large amounts of water inside it. (Ventilation without massive evaporation is inefficient, and it can lead to a catastrophic drying out of the greenhouse, and the plants inside it). Water absorbs a lot of heat when it evaporates, and ventilation is necessary because the saturated air must be removed and replaced with drier air. The natural tendency of hot air to rise provides natural ventilation. The humid, hot air will rise through vents in the roof, and drier, cooler air will enter through vents near the floor. All these vents can be closed at night, or during cold weather, and, in the more efficient greenhouses, they are automatically controlled, being opened and closed by servomechanisms. The rate of air movement can be increased with extraction fans, and these too can be automatically controlled. Equally, many of the inside surfaces of the greenhouse, including the plants themselves, must be kept wet. In a small greenhouse, this is easily achieved by hand, using a fine spray nozzle on a water hose. However, efficiency is increased by the used of a piped system of spray nozzles and automatic controls.

Heating of a greenhouse is not usually necessary in the tropics (except at high altitude, where frosts can occur at night), or during a temperate summer. However, if there is danger of frost damage to the plants, particularly in a temperate winter, heating is essential. The two main problems with heating are the cost of both the fuel, and the heating system, which must ensure a good distribution of heat, and the fact that heated air tends to be too dry. Double glazing will greatly reduce heat loss, and useful insulating sheets of double transparent plastic are now available.

Shading of a greenhouse if often undertaken to reduce the light intensity and, hence, over-heating. In the tropics, a well shaded greenhouse that is properly ventilated and watered, can provide a micro-climate that is a positive pleasure to walk into. However, it should be mentioned also that too much shading can be deleterious because plants like plenty of light. The most common method of shading is to paint the glass. White paint is the best, and it should be applied to the outside. Plastic emulsion paint that has been very considerably diluted with water is suitable, and it can be applied with a plant sprayer equipped with a fine spray nozzle. It is best to dilute the paint too much at first, because a second coat can always be applied if necessary, but the removal of excessive paint is difficult. Some greenhouses are shaded with a variable arrangement of blinds or lattices, which may be automatically controlled, but these are not generally recommended because of their complexity and expense.

Greenhouses may be constructed of glass or plastic. Traditionally, the glass panes were mounted in timber but, these days, steel or extruded aluminium is more common. Timber is out of favour because of its expense, and its relatively short life due to rotting. Steel is the strongest material but requires painting to prevent rust. Overall, aluminium is probably the best material for constructing the frame, as it does not rust or rot, and it does not require painting.

Plastic greenhouses consist of large sheets of poly-ethylene stretched over a light metal frame. Their great advantage is cheapness. However, the plastic has a short life as it tends to polymerise in the sun, and to tear from wind damage. A more expensive plastic film, made specially for greenhouses, has a nylon reinforcement, and it lasts considerably longer. Alternatively, a cheaper film can be sandwiched between two layers of chicken wire to protect it from wind damage.

The floor of a greenhouse is more important than most people realise. A concrete floor may appear cleaner and more efficient but, in fact, an earth or gravel floor provides a far better heat and humidity buffer, particularly if it is kept damp.

Finally, a word should be said about benching. Tall plants, which grow as vines, such as tomatoes, cucumbers, or runner beans, must be planted ground level. If they are planted in the greenhouse floor, this can lead to problems of rotation, soil preparation, and excessive bending for workers. If the plants can be grown in pots, these problems are ameliorated. The easiest work is with plants that are placed on benches at about waist level. Traditionally, greenhouse benches were made of timber supports with timber slats to facilitate draining. Light benching can be constructed out of metal tubing or light girders, with expanded metal sheet on top. More permanent (and expensive) benching can be constructed from concrete. For some crops, special benches that can be flooded may be useful for inoculating large numbers of small pots with a bacterial root pathogen.

Depending on the nature of the crop being improved, a fairly large club greenhouse will usually be required. The main functions of the club greenhouse are likely to be maintenance of designated hosts and parasites, preparation of inoculum, cross-pollination, and seed multiplication. If the breeding process requires the rooting of cuttings, or the grafting of scions, a mist propagator (see below) will be necessary.

If there is a centralised club organisation, a large club greenhouse will be essential. The club greenhouse must be heated if there is a danger of frost, and it must be well ventilated, with plenty of water evaporation, in warm weather, and warm climates. The greenhouse will have four main functions, depending on the crop being improved. These are cross-pollination, multiplication, single seed descent, and maintenance of designated host and pathotypes (see below).

If there is decentralised organisation, and late selection (see below), it may be useful for active members to have their own individual greenhouses in order to assist with the work of single seed descent.

(See also: off-site multiplication, plant pots).

Grid Screening

With grid screening, a screening population is divided into relatively small squares, each of convenient size. For small grain cereals such as wheat, the squares should be about one metre to a side. Larger plants (e.g., potatoes) will require correspondingly larger squares. The final selections must include the best plant (or plants) from each grid square, regardless of the level of parasitism in that square. This method eliminates the effects of parasite gradients.

(See also: field screening, greenhouse screening, head to row screening, laboratory screening, negative screening, on-site screening, popularity screening).

Harvesting

A special aspect of recurrent mass selection is that every plant must be harvested individually. This means that the harvesting must be done by hand. However, when harvest time arrives, there will normally be few plants left, or few plants specially labelled to indicate that they are final selections. Each individual plant, or its harvest, must be put in a separate container, such as an envelope, or a brown paper bag, and taken indoors for the post-harvest screening.

Head to Row Selection

See family selection.

Head to Row Sowing Equipment

Special equipment is available for sowing all the seeds of one ‘head’ or ‘family’ in one row, for purposes of family selection. This equipment is often called a precision planter, and it is particularly useful for crops such as cereals and grain legumes.

(See also: catalogues, family selection).

Horizontal Resistance, Demonstration

Before a potential new cultivar is sent to the licensing authorities, or released to farmers, the horizontal nature of its resistance must be established. However, this is not necessary in crops that were derived from continuous wild pathosystems, and which consequently lack gene-for-gene relationships, or for parasites that are known not to have a gene-for-gene relationship.

The nature of the breeding technique is often a good indication of horizontal resistance. That is, the fact that the cultivar was produced by recurrent mass selection, with quantitative increases in resistance, and under conditions in which all vertical resistances were either matched or absent, may be evidence enough. However, there is always a remote possibility that the resistance in question may be an unmatched vertical resistance that was inadvertently introduced to the screening population in foreign pollen.

Proof of the horizontal nature of the resistance is best obtained by making an experimental cross between the new cultivar and a highly susceptible plant of the same species. There should be about 100 progeny from this experimental cross. If the progeny show a normal distribution of resistance, ranging from the most resistant to the least resistant, the resistance is horizontal. If the progeny segregate into resistant and susceptible individuals, with a three to one ratio, the resistance is vertical.

If the mechanism of vertical resistance is hypersensitivity, and hypersensitive flecks are produced with the designated pathotype, the resistance is vertical.

Horizontal Resistance, Measurement

Horizontal resistance is best measured in terms of other, well known cultivars. That is, the resistance is stated to be greater than ‘Cultivar A’ but less than ‘Cultivar B’. A similar comparison would have to be made for the resistance to every locally important species of parasite. These are relative measurements, made in the field, under conditions free from parasite interference. They also happen to be the easiest measurements to make, and they are the most useful measurements in terms of practical farming. They are recommended for breeding clubs. If there is biological anarchy, all cultivars will be affected equally, and their resistances will remain the same, relative to each other.

Field measurements can also be made relative to an absolute standard of control obtained with crop protection chemicals. These measurements make use of crop loss assessment techniques. They would indicate how much crop loss would occur, if that cultivar were to lack the appropriate pesticide, when grown during a normal season in farmers' fields that are free from parasite interference, and that have fully restored biological controls. Alternatively, they would indicate how much pesticide, applied with what frequency, would be necessary to prevent that damage. However, these crop loss assessment measurements are difficult to make, and are not generally recommended for breeding clubs.

It is also possible to make very accurate laboratory measurements of horizontal resistance but these require complex equipment (e.g., plant growth chambers). These measurements are difficult to make, and they are often difficult to relate to field performance. They are not recommended for breeding clubs.

Hybrid Varieties

The detailed techniques of hybrid variety production are beyond the scope of this book. Any club which embarks on breeding hybrid varieties in maize, or the various crop species of the cucumber and onion families (*Cucurbitaceae* and *Liliaceae*), will have to obtain specialised manuals from experts. All that need be mentioned here is that hybrid variety production requires the in-breeding of selected lines to produce in-breeding depression, followed by the crossing of these depressed lines to produce seed with hybrid vigour. Any breeding for horizontal resistance must be completed *before* the in-breeding is started, and the selection pressures for resistance must continue during the formation of the inbred lines.

Hydroponics

Hydroponics, sometimes called 'water culture', means the cultivation of plants in a nutrient solution instead of soil. The roots can be suspended directly in the solution, or in an inert rooting medium, such as gravel, wetted with the solution, or inside plastic, tubular, film that is lying flattened on the ground. In the last case, the plant grows through a small hole in the film, and nutrient solution is pumped continuously through the tube. The advantages of hydroponics are (i) a high density of plants requiring a reduced greenhouse space, (ii) rapid growth and maturation leading to a shorted breeding cycle, (iii) general freedom from pests and diseases, and (iv) labour-saving. Equipment of various kinds is commercially available and catalogues should be consulted. A hydroponic system is recommended particularly for single seed descent, used for both late selection and the formation of pure lines.

Working in Brazil, M.A. Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, Agric. Univ. Wageningen Papers 88-2; 114pp) used hydroponics for multiplying his wheat in the off-season, and for single seed descent. Beek discovered that wheat grown in the off-season in the field would have a multiplication factor of 10-20. The same wheat grown in hydroponics in the greenhouse had a multiplication factor of 1200-4000. Beek found that 15,000 wheat plants could easily be grown in a greenhouse measuring 8 x 12m.

This high multiplication rate has four advantages. First, when using early selection, it provides a very large population of F_2 seed for the screening population. Second, it provides a safe and rapid means of multiplying potential new cultivars. Third, it permits hand crossing which provides a 100% crossing rate, compared with a 60-80% crossing rate with male gametocides. Lastly, it is very useful for single seed descent. Another advantage of hydroponics is the general freedom from adverse factors, such as bad weather, and soil-borne parasites.

In-breeding Cereals

Our experience with in-breeding cereals is based mainly on the work of M.A. Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, *Agric. Univ. Wageningen Papers* 88-2; 114pp), who worked with horizontal resistance to wheat parasites at Passo Fundo, in Brazil. His project was a component of the Food & Agriculture Organisation's International Program on Horizontal Resistance (Chapter 7).

Inoculation

The screening population will usually have to be inoculated with various species of parasite to ensure:

That the species of parasite in question is present and exerting selection pressure for horizontal resistance.

That the parasite in question is present with as uniform a distribution as possible.

That the designated pathotype is present, if a gene-for-gene relationship occurs.

Depending on the nature of both the crop, and the parasite, there are three methods of inoculating:

1. It may be possible to inoculate the seed, before it is sown. This is particularly true of bacterial diseases, and some fungal diseases.

Alternatively, it may be feasible to inoculate young seedlings which are produced in the club greenhouse for transplanting. Soil-borne parasites, such as nematodes, some insects, and various fungal and bacterial diseases, can be added to the potting soil, or to the potted seedlings. Seedlings can also be inoculated by flooding with a suspension of a water-borne parasite, particularly bacterial parasites. This requires special benches or trays that can be flooded and that will hold a parasite suspension in water for a short period prior to transplanting. The pots absorb the parasite suspension, and the parasite is then evenly distributed in the field.

Lastly, the screening population itself can be inoculated. This can be done by spraying with a water suspension of various fungal and bacterial parasites, or by releasing large numbers of airborne insects or spores from laboratory cultures. Airborne insect infestations are usually initiated by taking insect cages to the field and lifting off the cover, thus releasing the insects allowing them to migrate to plants in the screening population. The cages should be evenly distributed within the screening population to reduce parasite density gradients as much as possible. Redistribution of some species (e.g., leaf hoppers, white flies) is possibly by mechanical agitation. Alternatively, it may be preferable to infest spreader rows or surrounds. Another method involves carrying heavily diseased, potted plants from the greenhouse to the field, and relying on natural dispersal. The inoculator plants should be placed downwind if wind-borne parasites are involved. This method is used mainly with parasites that are difficult to handle (e.g., aphids). Virus parasites are transmitted either mechanically or by insects. Mechanical transmission usually involves grinding some diseased tissue in a pestle and mortar with fine carborundum powder and water. Some of this mixture is then rubbed with the fingers on to each plant in the screening population. This procedure is acceptable with seedlings in a greenhouse, prior to transplanting, but it is very laborious with plants in the field. Field inoculation may be possible with spraying but a specialist should be consulted. Insect transmitted viruses must be inoculated by means of insects that have been feeding on virus infected plants, using the methods for insect inoculation described above.

Inoculation is usually best carried out at sunset, and immediately after the plants have been thoroughly wetted with overhead irrigation. Some insects, however, may do better if released in the early morning. A specialist should be consulted.

In the early stages of the program, there is a very real danger of killing off the entire screening population, if it is inoculated with too many species of parasite. Apart from the designated pathotypes, it may be a good idea to add only one more species of parasite to the inoculation list, after each breeding cycle.

(See also: patchy distribution, spreader rows and surrounds).

Insect Culture

There are two reasons for culturing insect parasites. The first is to provide cultures of a designated strain in order to match vertical resistances in the screening population. The second is to increase an infestation of a parasite species in which vertical resistances do not occur.

The use of designated strains to match vertical resistances will not occur often because gene-for-gene relationships are rare with the insect parasites of plants. They are known to occur with Hessian fly (*Mayetiola destructor*) of wheat, some plant hoppers of rice, particularly the brown plant hopper (*Niloparvata lugens*), and certain aphids.

The culturing of insect parasites for general inoculation purposes will be much more common. The usual procedure will be to maintain stocks of insects on living plant hosts growing inside insect-proof cages in a greenhouse. Insects which have an obligate dormancy will have to be appropriately stored during the winter or tropical dry season. These stocks must be multiplied into suitably large populations for infesting the screening population. This is done on potted host plants growing inside insect cages which will eventually be carried to the screening population where the cages will be lifted off the plants, allowing the insects to escape. The escaping insects can be induced either to infest susceptible spreader rows or surrounds, before the screening population is available, or to invade the screening population directly.

The techniques of culturing insects vary considerably and specialist advice should be obtained. Insect cages usually consist of a wire frame covered with mosquito netting or window screen. The wire frame can either be pushed into the soil of the pot, or it can cover the entire pot. In either case, the netting must be tightly closed at the base to prevent insect escape. With some insect parasites it may be preferable to work inside an insect-proof greenhouse, and to infest the screening population directly, while it still consists of young seedlings, prior to transplanting into the field.

Inter-Leaved Breeding Programs

When practicing late selection (see below), each breeding cycle is likely to require one and a half or two years. This means that one screening season in temperate regions (three screening seasons in the tropics with bimodal rainfall) is wasted in each breeding cycle. These wasted seasons can be utilised with an entirely separate, second (or third) breeding program that is run in parallel, but out of phase, with the first. Such ‘inter-leaved’ breeding programs double or treble the scope of the breeding club by permitting entirely different populations (e.g., white beans and red beans), or similar populations with entirely different parents, to be bred more or less concurrently.

International Agricultural Bureaux

The International Agricultural Bureaux are located in the United Kingdom, and they provide various services to national governments, research institutes, and *bona fide* research workers throughout the world. Their main function is to produce abstracts of all the papers published in the various agricultural disciplines. These are now available on CD-ROM disks for computers, and they are a magnificent new tool for information retrieval, and library research. However these disks are expensive and clubs are advised to consult specialised libraries rather than purchasing their own systems. For a fee, the following institutes, which are part of CABI, will identify crop pathogens, insects, and nematodes, respectively: (1)

International Mycological Institute, Bakeham Lane, Egham, Surrey, TW20 9TY, England; (2) International Institute of Entomology, 56 Queen’s Gate, London, SW& 5JR, England; (3) International Institute of Parasitology, 395A, Hatfield Road, St. Albans, Herts, AL4 0XU, England.

Jury

The club jury is a panel elected by a club with a decentralised organisation to make the final selections from among the many individual plants submitted by the active members. The jury selects the best 10-20 plants as (i) parents of the next screening generation, and (ii) potential new cultivars. These selections are usually made on the basis of yield and quality, it being assumed that they have the best levels of horizontal resistance currently available. It must be remembered that these plants were not protected with crop protection chemicals, and they will have suffered severe parasite interference. All measurements must accordingly be relative measurements. The best are selected, regardless of how poor they may look.

Each jury selection becomes a club line. It should be labelled with a code name that need never be changed unless the line becomes a registered and named cultivar. Each label should indicate the name of the club, the year of selection, and the number of the line. In addition, the club jury should announce and record the name of the active member who produced each jury selection, for purposes of recognition, and the allocation of possible royalties (see below).

Laboratory

Most clubs will need a laboratory of some sort. In general, a club laboratory serves three functions. The first is essential, and is laboratory screening (see below). The second is optional, and is parasite identification. The third depends on the species of crop, and the nature of the parasite, and is parasite multiplication.

A club laboratory should consist of two entirely separate rooms, called the clean and the field labs, respectively. Depending on the crop, the clean lab should might contain both a dissecting and a compound microscope, and simple equipment for fungal and/or bacterial culture. The field lab would be used for post-harvest screening and would contain equipment for individual plant assessment, seed storage, etc. The field lab is likely to produce quite a lot of dust, and care should be taken to keep this out of the clean lab.

Laboratory Equipment

Most clubs will want to have a small laboratory which may be no more than a room where post-harvest screening activities are carried out. As the club increases in size and wealth, the laboratory can become increasingly sophisticated. However, the rule that small is beautiful should usually apply. It is very easy to spend large sums on expensive equipment that turns out to be a white elephant. Laboratory equipment should be purchased only if there are one or more club members both able and willing to use it.

Screening equipment

This is usually the cheapest equipment, but its cost varies with the nature of the crop being screened. It is required for the laboratory screening of individual plants selected in the field. Machines for threshing individual plants, and equipment for weighing and counting seeds, are the most important items for cereals and grain legumes. With other crops (e.g., fruit, tubers) hand counting is easy, and weighing is not difficult. Simple cooking and tasting equipment may be desirable. More complex tests can usually be contracted out to government or commercial laboratories.

Parasite identification equipment

Insects. It is a good idea (but not essential) to keep specimens of the insects actually parasitising each screening generation. An insect cabinet, and the usual killing jar and mounting pins will be necessary. Small insects, such as aphids and white flies, can be stored in preservative fluid in specimen tubes, or mounted on microscope slides. A collection of the club's important insect parasites, with confirmed identity, will be useful for the information of club members. Both a dissecting and a compound microscope will be useful, but see plant disease equipment, below.

Nematodes. A collection of microscope slides of identified nematodes will be useful to assist in identification work. Simple washing equipment for separating nematodes from soil or vegetation may also be needed. A nematode counting system may also be necessary. Both a dissecting and a compound microscope are essential for nematode work, but see plant disease equipment below.

Plant diseases. The most expensive items are a dissecting microscope, and a compound microscope. These are essential if plant disease laboratory work is to be undertaken at all. However, these microscopes can also be used for the entomological and nematological work. Apart from the microscopes, cheap domestic equipment will often substitute for expensive laboratory equipment. I have run a perfectly adequate plant pathological laboratory in the remote African bush, equipped almost entirely with household equipment and ingredients. A domestic pressure cooker makes an inexpensive but effective substitute for an autoclave for sterilising culture media. A cooking stove run on bottled gas provides an entirely effective sterilising oven. Domestic glassware, such as medicine and milk bottles, will substitute for much expensive laboratory glassware. Many cooking ingredients, such as gelatine, prunes, fruit juices, potatoes, and vegetables, as well as household chemicals, such as detergents and bleach, substitute for culture media and laboratory chemicals. Otherwise, a minimum of dissecting tools, microscope slides, cover slips, stains, Petri dishes, mounting and culture media, etc., are relatively inexpensive, and can be ordered from most pharmacies.

Parasite multiplication

The screening population must normally be inoculated with various species of parasite to ensure that infestations and epidemics occur, that they are as uniform as possible throughout the screening population, and that they involve the designated pathotypes, if these are required. This is work for a technician member of the club.

Many of the fungal pathogens of plants are obligate parasites (e.g., rusts, mildews), and must be cultured on living hosts in the greenhouse. Other fungi are facultative parasites (e.g., wilts, anthracnoses, bacteria), and may be cultured in glass vessels in the laboratory. Depending on the pathogen, they can be cultured on the surface of agar or gelatine jelly in a Petri dish or flask. Others can be cultured in cotton wool plugged bottles of damp, sterilised bran or sawdust, which may or may not have had nutrients added to it. Liquid cultures in large conical flasks are also possible with some pathogens, provided they are kept aerated with a magnetic stirrer. Some insect cages are also easier to culture in the laboratory than the greenhouse (see: Insect culture).

Equipment for working with mechanically transmitted viruses need be no more than a an electric blender and some carborundum powder for rubbing a virus extract onto leaves. However, sophisticated virus equipment, such as an ultra-centrifuge or an electron microscope, is far too expensive and complicated to be considered by a breeding club.

(See also: catalogues, inoculation, laboratory screening).

Laboratory Screening

With many crops, it is possible to conduct a final screening in the laboratory, employing tests that cannot easily be conducted in the field. These tests may involve the yield and quality of the seeds of cereals and grain legumes, taste and cooking tests of various fruit and vegetables, analyses of the content of sugar, fibre, starch, and other food components, measurements of colour, size, and shape, and so on. As a general rule, the least complex, cheapest, and easiest tests are conducted first, while the most complex, expensive, and difficult tests are conducted last. The reason for this is obvious. There are many selected plants to be tested at the start of the laboratory screening, but only a few plants at the end.

Many of these laboratory tests are destructive and, when the harvestable product is a seed (e.g., cereals, grain legumes), they must involve negative screening, in the sense that only the unwanted seeds are destroyed. This will ensure that the surviving seeds can become the parents of the next screening generation. For example, wheat seeds can be squeezed between pressure controlled rollers. Soft seeds, which make poor quality bread, will be crushed and destroyed, while hard seeds, which make good quality bread, will survive.

Other tests are non-destructive. For example, a wide range of laboratory machines will count seeds, and sort them on the basis of size, weight, shape, specific gravity, colour, skin texture, etc. If destructive tests on seeds are essential (e.g., bread making of wheat, malting quality of barley), they must be postponed until a small bulk of a pure line or hybrid variety is available.

It is often possible to conduct destructive tests on fruits (e.g., tomatoes) after the seeds have been extracted. Destructive tests on vegetatively propagated crops (e.g., sugarcane) are usually possible immediately after selection, provided that they involve only small amounts of tissue. But comprehensive tests on a clone of potatoes, for example, require the destruction of several pounds of tubers for quality assessments in the various cooking methods, such as boiling, salads, deep frying, roasting, baking, mashing, and dehydrating, as well as chemical tests for the content of starch, vitamin C, protein, etc. Potato tubers must also be tested for their poisonous glyco-alkaloids, and this will usually require technical assistance from commercial or government laboratories. All such tests can be conducted only after some multiplication of the clone has occurred.

The details of most laboratory tests are too complex for the present book, and each club should obtain specialist assistance and technical manuals on the crop of its choice. Many countries have government and/or commercial laboratories that will undertake tests for a fee. However, it should be remembered also that these tests are called laboratory tests mainly to distinguish them from field tests. The laboratory itself, and the equipment in it, is usually quite simple and cheap, and is generally within the financial and technical capacities of a breeding club.

(See also: catalogues, field screening, greenhouse screening, grid screening, head to row screening, negative screening, on-site screening, popularity screening, threshing).

Late Selection and Early Selection

Traditionally, recurrent mass selection of in-breeding crops is conducted by selection within the variable progeny of cross-pollinated parents. The selection work is thus conducted on highly heterozygous individuals which then become the parents of the next screening generation. This procedure is now called ‘early selection’.

Late selection involves self-pollinating the variable progeny for 3-4 generations, using either the bulk breeding method (see above) or single seed descent, and producing a mixed population of relatively homozygous individuals. The late selection is made among these relatively homozygous individuals.

Although, at first sight, it appears to be much more work, late selection is likely to produce better results, more reliably, and more quickly, than early selection. The several hundred best plants are selected from the screening population, and are subjected to 3-4 generations of single seed descent (see below). The seed of the final generation of single seed descent is used for field screening, using family selection (see above) if desired. This will eliminate the misleading, non-inherited effects of heterosis (hybrid vigour), and it will lead to a greater frequency of recessive alleles for horizontal resistance, which are revealed only in the homozygous state. A further advantage of late selection is that potential new cultivars are very close to being homozygous and, consequently, they can be utilised quite quickly.

With late selection, there are a total of four or five plant generations in each breeding cycle. Each on-site field screening must be conducted in the time of year of future cultivation. In practice, this usually means a summer crop. If each generation can be completed in 60 days (by harvesting immature plants, etc.), it may be possible to complete each breeding cycle in one year, using only three generations of single seed descent. If this schedule is too crowded, a two-year cycle may be preferred, particularly as this would permit four generations of single seed descent, and the harvesting of mature plants. With some species of crop (e.g., various cereals), either the crossing generation, or the bulking generation, or both, may be unnecessary. A one-year cycle would then be much less crowded.

If it transpires that one breeding cycle requires two years, the club could conduct two parallel breeding programs. ‘Program A’ might then be screened in odd-numbered years, while ‘Program B’ would be screened in even-numbered years. A similar scheme could operate for a three-year cycle. (See: inter-leaved breeding programs).

The advantage of this strategy is that two or three entirely different genetic populations could be screened in parallel. If one proved disappointing, the other(s) would compensate. If none disappointed, as the inter-leaved programs matured, the total number of new cultivars would be two or three time as large. A further advantage of parallel (inter-leaved) programs is that they could differ, with one program, say, aimed at early-maturing varieties, and another at late-maturing varieties, or large and small bean varieties. There are usually many such varietal differences within a single crop species.

It should be added that a breeding strategy that employs late selection in a breeding cycle of two years, is likely to produce better results, in a shorter total time, than a strategy that uses early selection in a one-year cycle. However, a specialist should be consulted before any final decisions are made.

Library

Most clubs will want to start a small club library and, perhaps, to elect a club librarian responsible for the choice, purchase, and care of books and periodicals. The librarian might also organise the club home page and e-mail exchange with other clubs.

(See also: newsletters and publications).

Lupins

Of special interest is the lupin breeding program of Wallace Cowling working in Perth, in the Department of Agriculture of Western Australia. He started this program in 1982, and based it on the new theories of horizontal resistance. Cowling deliberately set out to breed white lupins (*Lupinus augustifolius*) for horizontal resistance. This crop was a wild plant until the 1960s, when it was first domesticated in Western Australia. After ten years of population breeding in this self-pollinated crop, Cowling has obtained increased disease resistance and yield, and reduced seed alkaloids, and he has a new lines approaching variety release.

Male Gametocides

A male gametocide is a substance that is sprayed on to inbreeding plants in order to make them male sterile and, thus, to convert them into outbreeders. With some crops, the use of male gametocides can save an enormous amount of work by eliminating labour-intensive hand-pollination. In crops such as wheat, barley, and oats, male gametocides can easily induce millions of cross-pollinations by the simple expedient of spraying about half of a small breeding population. However, in many other crops, particularly the dicotyledons, male gametocides are less effective, or even entirely ineffectual.

A decision on the use of male gametocides is one of the first that a new club will have to make. The use of a male gametocide will not be necessary if hand-pollination is easy, and if one hand-pollination produces many seeds. Alternatively, a male gametocide may be desirable but impractical because no suitable gametocide is known. If the use of a male gametocide is feasible, the club will still have to obtain specialist information on the best substance to use, and its rates and time of application. Research on male gametocides is relatively easy, and a club may decide to conduct its own investigations, taking advice from specialists. Even when a satisfactory male gametocide is in routine use, the club may still wish to investigate alternative substances and techniques with a view to finding improvements.

Working with wheat, Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, *Agric. Univ. Wageningen Papers* 88-2; 114pp) used Ethrel (2-chloro ethyl phosphoric acid) at a concentration of 2000 parts per million (ppm) in water, sprayed at a rate of 1000 litres per hectare, followed by a spray with gibberellic acid-3 at a concentration of 150 ppm at early to mid-boot stage (i.e., when the ear fills about one third of the sheath). This produced 60-80% cross pollination which is entirely adequate because any self-pollination that may occur involves heterozygous plants that will still produce a variable progeny. This treatment had some side-effects, such as an increased susceptibility to some diseases, and altered growth habits.

The male gametocide is applied to the plants that are to become the female parents, usually in strips that are two metres wide. The male parents are left untreated, and need be in strips of only one metre wide. The sprayer consists of several nozzles mounted on a harness that straddles the female strip. This harness is carried by two people who walk down the strip spraying the plants to run-off. A plastic sheet is dragged behind the sprayer to prevent drift on to the male strips. The spray harness is connected with a pressure hose to a pressurised tank on a tractor which is on the edge of the experimental plot. The tractor should keep pace with the people carrying the spray harness, and it may be necessary to have one or two people holding up the pressure hose to prevent it damaging the intervening wheat.

A negative screening must be conducted before anthesis in order to eliminate undesirable pollen. This can be quite a lot of work but it is very important. The best technique is to cut off every stem that has not been labelled during field screening. A large, comfortable pair of scissors, or a pair of secateurs, should be used. Both the male and the female strips should be screened in this way as even plants that have been treated with a male gametocide will produce some pollen.

Marker Genes

A single Mendelian gene which controls a simple character such as colour or hairiness, can be a useful proof of cross-pollination. This proof of natural cross-pollination can be used as a breeding technique in an in-breeding species which has a low percentage of cross-pollination. For example, all the plants used as female parents would lack this gene, while all plants used as male parents would possess it. Only the female parents are kept. Their progeny segregate into those with the gene, and those without it. Only those that possess the marker gene are kept for screening because they are the result of cross-pollination. The marker gene can be eliminated in the last screening, if it is undesirable.

Mechanical Planters

Sowing seed by hand in a field can be a laborious business. On the other hand, ‘family’ selection prohibits the bulking of seed for sowing in a commercial planter. Several companies manufacture special seed planters for plant breeders. These precision planters keep the seed of each ‘family’ separate, and plant it in a separate row, with appropriate distances between the rows, and between the plants within each row. These machines are rather expensive, but their cost has two very real justifications. They save a lot of back-breaking labour. And they increase the accuracy of the planting by eliminating human error. Consult agricultural research catalogues.

A second class of machines sow seeds into trays, or banks of small pots, for germination in a greenhouse. Similar machines will fill the pots with special potting soil that can be inoculated with various parasites. Consult commercial greenhouse equipment suppliers.

Mist Propagators

In the old days, horticulturists would induce cuttings to root by removing most of the leaf to reduce water loss, lowering the light intensity with heavy shade to reduce transpiration, and using a rooting medium that was rich in both micro-organisms and plant nutrients. Under these conditions, the cuttings would produce roots so slowly that the stems often rotted before roots could develop.

These problems can be avoided with a mist propagator. The cuttings are given the maximum leaf area, and the maximum light, to permit rapid photosynthesis and growth. Water loss is prevented by a frequent, automatic wetting with water mist (hence the name). The mist can be controlled either with a humidity switch, or with a timer. If too much heat develops from the maximum light, cooling can be induced by ventilation and water evaporation, with an increased rate of misting, if necessary. The rooting medium should also be biologically and nutritionally inert to reduce the risks of rotting. Vermiculite, or a mixture of sand and expanded polystyrene granules, is suitable. A rooting hormone may assist with species that are particularly difficult to root.

With a mist propagator, green potato cuttings will produce roots in 5-10 days. Species that had previously proved impossible to root, such as tea and coffee, will usually produce roots in less than ten weeks. Once roots have formed, the cuttings should be potted and given a few days of intensive care before being taken outside the greenhouse.

Multiplication

If early selection is practiced, with a screening generation each year, it may be necessary to have a multiplication generation after the cross-pollination is completed, in order to produce enough seed for the next screening generation.

The multiplication generation may be protected with crop protection chemicals, fertilised, irrigated, and otherwise pampered to ensure the maximum yield of seed. It is also allowed to self-pollinate, as an alternation between self- and cross-pollination has genetic advantages. There are three ways to handle the multiplication generation. These are in a greenhouse during winter, in the field during summer, or in the opposite hemisphere during the club's winter.

The greenhouse during winter is probably the most satisfactory, if not the cheapest method. It is fast, permitting a screening generation every summer, and the plants remain under the total control of the club members. Hydroponics may be useful here.

The field multiplication during summer is the cheapest method, and it retains total control of the plants. However, it wastes a screening season, and the duration of the breeding program will be doubled, because every alternate summer is used for multiplication rather than for screening.

Using the opposite hemisphere means sending the multiplication seed to that hemisphere for field multiplication during their summer. If a cooperating breeders' club can be found, this method is cheap and efficient. It costs no more than the air freight, and the reciprocal multiplication of their seed during our summer. However, this approach has three problems, which can be formidable. The first concerns international phytosanitary regulations, and the possible need for plant quarantine. Depending on which two countries are involved, these restrictions may entirely prevent seed exchange. Secondly, there are likely to be many more breeders' clubs in the northern hemisphere than in the southern hemisphere. The shortage in the southern hemisphere could be overcome by using financial reimbursement as an alternative to reciprocal multiplication of their seed. It may also be possible to find a competent farmer who would undertake the multiplication for a suitable fee. Finally, there is the problem of reliability. Club members may not relish the thought of their precious seed being trusted to strangers half a world away.

Note that there must be no screening whatever during the process of multiplication, as this would seriously interfere with the fundamental concept of on-site screening.

Natural Cross-Pollination

Most self-pollinating plants exhibit a small amount of natural cross-pollination. The rate of natural cross-pollination is usually greater in warm climates. In haricot beans, for example, it can reach 3-5% in the tropics. By making use of a marker gene (e.g., black seed, when breeding white seeded beans), this natural cross-pollination can be exploited, with very considerable savings in hand labour. With species that are pollinated by bees, the rate of cross-pollination can often be increased by placing a beehive in the middle of the crossing population.

Negative Screening

Negative screening can often be used profitably with recurrent mass selection. Instead of selecting and keeping the best plants, the majority of the less desirable plants are weeded out, and the survivors are left to cross-pollinate and reproduce.

In some crops (e.g., wheat), the screening generation can also be the crossing generation, if early selection is being used. This is because a male gametocide has been used to make the female sub-population male-sterile. Under these circumstances, there must be a negative screening to ensure that all the undesirable plants in the male sub-population are destroyed before anthesis. The destruction may involve complete removal of the unwanted plants by pulling, or decapitation of the immature inflorescences by cutting. Only the least parasitised males are allowed to produce pollen and to become parents of the next screening generation. It may be necessary to conduct a negative screening in the female sub-population also, if the male gametocide is not fully effective. This is because undesirable plants in the female sub-population may produce small quantities of unwanted pollen.

(See also: field screening, greenhouse screening, grid screening, laboratory screening, on-site screening, popularity screening; and Chapter 26, Cocoa).

Newsletters

Some clubs may choose to produce their own newsletter. The primary function of the newsletter is to keep members informed about developments within the club. A secondary function is to exchange newsletters with other clubs, so that they can both give and receive useful tips and hints. Occasionally, a simple tip can be incredibly helpful, and it may save many hundreds of hours of work. Some club members may feel that they are giving away trade secrets by broadcasting them to other clubs in a newsletter. But this is not generally so. Most clubs will not be competing with each other because they are breeding different species of crop, and they are doing on-site breeding. This means that the cultivars of one club may not be ideal in the area of another club. And, even if they are, competition is healthy. More important, however, is the fact that everyone gains from sharing information, and that this more than makes up for any loss of 'trade secrets'. In practice, most newsletters will take the form of computer home pages, bulletin boards, and e-mail.

Nitrogen-Fixation

Crops which belong to the botanical family *Leguminoseae*, and are called legumes, are rich in protein. The main chemical constituent of protein is nitrogen, and legumes are unique in the plant world in that they have nitrogen-fixing root nodules. These nodules are formed by bacteria called *Rhizobium* which are able to extract nitrogen from the air and convert it into protein. A true cooperation (or symbiosis) takes place. The plant provides the bacterium with carbohydrates, and the bacterium provides the plant with protein. Such a subsystem of an ecosystem is sometimes known as a symbiosystem.

A club that is breeding either a grain or a fodder legume should include symbiosystem efficiency in its selection criteria. Both the legume and the bacterium vary in their symbiosystem effectiveness, and the agricultural yield varies accordingly. If there is to be selection for highly effective nitrogen fixation, there must be simultaneous selection of both the legume plant and the *Rhizobium* strain. By screening a wide genetic range of the legume against a wide genetic range of the bacterium, it should be possible to find very effective combinations of the two. Some clubs may prefer to ignore this criterion, and concentrate more simply and easily on yield, quality, and resistance. Alternatively, a club may choose to embrace this aspect of screening, and the following points should then be noted.

Effective nitrogen fixation is indicated by two criteria. First, the legume growth must be vigorous and dark green in the *absence* of any recent use of nitrogenous fertiliser or manure. So absolutely no use of manure, green manure, or nitrogenous fertilisers is permitted in the fields or gardens used for screening. Second, the roots must carry large numbers of well-developed root nodules that are red inside. If either one of these indications is lacking, the nitrogen fixation is poor. However, if there is exceptionally fine fixation, both the bacteria and the legume host should be preserved.

The *Rhizobium* bacteria can be preserved by drying the nodules in a dessicator, and they can then be kept for several weeks. To be used, they should be wetted and crushed. This paste can then be mixed in an electric blender with a small amount of skim milk, and the seeds to be inoculated are wetted with it, and then dried in a shady place, just prior to planting.

If the club has a technician capable of handling bacterial cultures, the *Rhizobium* bacteria can be isolated, cultured and purified. It is not difficult to test *Rhizobium* cultures for efficacy, but the details are beyond the scope of this book. A specialist should be consulted. The main point is that a club with an unusually good combination of *Rhizobium* and legume pure line, may care to market both the legume and its inoculant together.

Cultures of *Rhizobium* are produced commercially for inoculating legume seed. In some countries, it may be possible for a club to patent, and collect breeders' royalties, on its *Rhizobium* strains as well as its legume cultivars.

Numbers of Seedlings

Within limits, each breeding cycle should have as many seedlings as possible in the screening generation. The upper limit is usually set by the size of the individual plants of the crop being improved, the club facilities, and the number of its active members.

Office Equipment

Small clubs can usually rely on their individual members to contribute their own time, and the services of their own computer, photocopier, telephone, fax, etc., to club administrative activities, and to paper work such as newsletters, minutes, and notices. Larger and richer clubs, which have their own premises, may prefer to purchase their own office equipment. However, there is often a tendency for the tail to wag the dog, and administrators often seem to think that their work is more important than the activities that their office was created to support.

On-site Screening

All screening must be done ‘on-site‘. This means three things. It means that the screening generation must be grown in the *area* of future cultivation, in the *time of year* of future cultivation, and according to the *farming methods* of future cultivation. It is pointless, for example, to screen inside a greenhouse during winter, if the crop is to be cultivated in the field during summer, because the resulting cultivars would be entirely unsuitable.

There is some latitude in these requirements. Thus, the active members of a decentralised club do not all have to plant their screening populations on the same day, but they should plant within a week of two of each other. Equally, they do not all have to be in the same locality, but they should all be within the overall area of future cultivation. And there should be a degree of conformity concerning the husbandry techniques of future cultivation. For example, if the new cultivars are intended for subsistence farmers who never use fertilisers, the screening generations should also be grown without fertilisers.

On-site screening imposes certain limits on a breeding club. It normally confines a decentralised club to active members who live in the area of future cultivation. It also limits the club to crops that are cultivated in its own area. However, on-site screening does ensure that a new cultivar will be in a good state of balance with its own, local agro-ecosystem.

(See also: field screening, greenhouse screening, grid screening, laboratory screening, negative screening, popularity screening).

One-Pathotype Technique

It is impossible to see, measure, or screen for horizontal resistance if vertical resistances are present and operating. For this reason, all vertical resistances must be matched, and thus inactivated, during the screening work. The one-pathotype technique is the only really effective method of ensuring this. This is the most technical aspect of the breeding process and it will normally be tackled by a biologist, or a technician experienced in the culturing of plant parasites.

For each species of parasite in which a gene-for-gene relationship occurs, a single vertical pathotype (i.e., biotype, race, or strain defined by characteristics of vertical resistance) is chosen. This becomes the designated pathotype, and it must be cultured on its matching, designated host for the entire duration of the breeding program. It is used to inoculate every screening population. It is absolutely *essential* that only *one* pathotype is designated for each species of parasite.

The identification, isolation, and culture of designated pathotypes is the part of the program in which the amateur breeder is most likely to require help from specialists. Help may be needed as follows:

1. Obtaining samples of the parasites concerned.

Confirming their identification.

Matching and inoculating the designated host.

Maintaining the cultures.

Inoculating the screening population with the designated pathotypes.

The one-pathotype technique *must* be used with every species of parasite in which a gene-for-gene relationship (vertical resistance) occurs. Failure to do this may prevent the breeding program from accumulating horizontal resistance to the parasite in question.

Occasionally, the parasite produces new vertical pathotypes so rapidly that the one-pathotype technique is unnecessary. This happened with the maize in tropical Africa (Chapter 20), and with potatoes in Mexico (Chapter 18). When breeding potatoes in areas where the A2 mating type of blight (*Phytophthora infestans*) has been introduced, the one-pathotype technique is probably not necessary for this disease. Usually, the one-pathotype technique is also unnecessary when breeding a crop in its centre of origin because all vertical resistances will be matched quite quickly.

(See also: designation)

Original Parents

At the start of the breeding program, each of the original parents of the breeding population must be selected with special care. The original parents should be cultivars with good yields, high quality of crop product, and good agronomic suitability. Depending on the crop being developed, there should be some 10-20 different parents. The remainder of this section concerns crops in which vertical resistances occur.

Each cultivar that is chosen as a parent must be susceptible to the designated pathotype of every species of parasite in which a gene-for-gene relationship occurs. There is no harm in repeating this comment, which is the crux of the one-pathotype technique. It ensures that all vertical resistances are matched during screening, throughout the entire breeding program. All resistances which function during the screening will then be horizontal resistance, at however low a level they may occur initially.

If the crop in question has, say, five species of parasite with gene-for-gene relationships, there will be five designated pathotypes. It may be difficult to find enough designated parents that are susceptible to all of those pathotypes. This may be a task for a specialist. It should be remembered that the first research should be library research. There is an enormous amount of published information on the vertical resistances of many species of crop. The parents may well be tentatively designated on the basis of published data only. The only experimental data that will then be needed is a practical confirmation of each parent’s susceptibilities.

A technical point must be mentioned. A few vertical resistances are quantitative in their effects. These occur mainly in the small grain cereals, such as wheat and barley. Quantitative (or incomplete) vertical resistance is easily mistaken for horizontal resistance, and it must be avoided at all costs. The best way to avoid it is to designate as parents only those cultivars that have a complete vertical resistance that is matched by the designated pathotype. This, again, is a task for a specialist, and it will involve mainly library research.

Each of the original parents must be crossed with every other parent. If these cultivars are pure lines, there will be no segregation in the first progeny (F_1) which should accordingly be multiplied by selfing to produce the second generation (F_2) which will be segregating freely. If there are enough seeds, this can be used as the first screening generation. Otherwise, a further multiplication may be necessary.

Out-breeding Cereals

As a general rule, out-breeding cereals are not recommended for breeding clubs for one of two reasons. Either they are rather unimportant (e.g., rye) or they have already had so much work done on them that further improvement will be difficult. Hybrid maize falls into this second category. However, many organic farmers wish to work with open-pollinated (i.e., non-hybrid) maize in order to obtain their own seed each season. Some of the tropical, out-breeding cereals (e.g., sorghum, millets) are locally important but are generally beyond the reach of breeding clubs. Nevertheless, a brief outline of the methods will not be out of place.

When working with an unimproved, local landrace, it is often quite easy to produce an improved population by selecting the best plants for seed, particularly if the local farmers can be persuaded to use a modicum of fertiliser. After a few generations of selection, an improved landrace will be obtained that yields significantly better than its progenitor. Such an improved landrace is sometimes called a synthetic variety. Ideally, farmers who use such improved landraces should maintain selection pressures for high yield, quality, and resistance by continuing to select the best individuals for seed. (See also Rimpau, Chapter 26).

A more complicated alternative is to produce inbred lines with a view to breeding hybrid varieties. The methods can become quite technical and they are beyond the scope of this book. However, should a breeding club wish to undertake the production of hybrid varieties, there are some excellent technical manuals. Highly successful hybrid varieties of sorghum have been produced in the U.S.A., and hybrid maize varieties exist worldwide. The only important point to note here is that all the screening for horizontal resistance must be conducted on the inbred lines, *before* any attempt is made to produce hybrid seed.

A cautionary tale comes from India. A very successful new hybrid variety of pearl millet (*Pennisetum typhoides*) yielded so well that the total production was more than doubled without any increase in the area under cultivation. The Indian plant breeders were elated, and they congratulated themselves that they too could produce a spectacular green revolution. Tragically, their elation was premature. They had used a Mendelian source of resistance to a disease called downy mildew (*Sclerospora graminicola*) and this vertical resistance failed. Within a single season, this wonderful new hybrid variety was ruined and abandoned.

Ownership of Breeders' Rights

The club should be the sole owner of any cultivars that it may produce, and of any breeders' royalties that it might earn. However, these royalties would have to allocated to club expenses and to club members according to the club's constitution.

Parasite Gradients

A parasite gradient means that, from one part of a screening population to another, there is a gradual increase or decrease in the population density of the parasite. If the parasite gradient is not understood, there may be a tendency to select plants in the area of low population density of the parasite, on the grounds that these are the least parasitised and, hence, the most resistant. This error can be avoided by using grid screening.

(See also: family screening, field screening, greenhouse screening, laboratory screening, negative screening, on-site screening, popularity screening).

Parasite Identification

There are usually some 10-20 diseases of a single species of crop and, perhaps, twice as many insect pests. A club technician or professional member should have little difficulty in learning how to identify them all with confidence. If in doubt, an outside specialist should be consulted

Most countries have a government crop advisory service which includes a pest and disease identification service, and the publication of advisory leaflets. One of the most authoritative parasite identification services is offered by the Commonwealth

Agricultural Bureaux International, located in England, and this may be the only service available to clubs in non-industrial countries.

Parasite Infested Soil

Many plant parasites are soil-borne. These include root-feeding insects, such as wireworms, as well as nematode worms, wilt diseases, and root rots. The problem with screening for resistance to these parasites is that they normally have a very uneven distribution in the soil. Effective screening requires that every plant in the screening population must be equally exposed to these parasites, but this will obviously not happen when there is a patchy distribution (see below) of the pests. There are various techniques for handling a patchy distribution of soil-borne parasites, but a specialist should usually be consulted.

If the parasite is microscopic (e.g., a bacterium or fungus), it is often possible to inoculate the seed of the screening population prior to sowing. This provides a very uniform distribution of the parasite.

Small parasites, which are sub-microscopic (e.g., nematodes) can often be cultured in the laboratory or greenhouse to produce pots of heavily contaminated soil. Some of this soil can then be included in the sowing operation in the same way as both seed and artificial fertiliser are applied to the field with one machine, in one operation. Alternatively, if transplants are being used, the infested soil can be mixed with the potting soil at the time of sowing the seed, or it can be added to each pot later.

Large parasites, such as wire worms, are often the most difficult to handle because it may be difficult to breed them up in sufficient numbers. If all else fails, the screening can be restricted to areas of obvious infestation. However, if the frequency of a parasite is too low even for this, do not worry about it. Go ahead and screen for other parasites anyway, assuming that a solution to this problem will be found in the future. There are plenty of other parasites to worry about in the meanwhile, and no one expects the earlier club cultivars to be perfect.

Patchy Distribution

During the screening process it is most desirable that every host individual is parasitised and, secondly, that every host individual is equally parasitised. Many parasites have what ecologists call a ‘patchy distribution’. That is, their population density varies greatly from one part of the host population to another. This means that some host individuals are heavily parasitised, while others are parasite-free. This makes screening for resistance rather difficult.

There are various reasons for a patchy distribution. In general, the soil-borne parasites exhibit the most marked patchy distributions. This is usually because they are immobile, and they just remain dormant in the soil until a host plant starts growing right on top of them. These include the various root-eating insects, nematode worms, and both fungi and bacteria that cause wilts and root rots.

Some insect-transmitted viruses spread only slowly, because the insects which are actually carrying the virus are rather rare. This can mean that only a few plants in the screening population become infected with these viruses.

Some insect parasites are gregarious. They either like to be in a crowd, or their mother laid all her eggs in one place, and there they stayed. Other parasites of the aerial parts of plants are unable to allo-infect other plants. These include scale insects and wingless aphids.

A uniform distribution of soil-borne parasites is best achieved by inoculating every seed or seedling that is put into the screening population. For example, a small amount of parasite culture can be added to each pot just before the soil is put in. This is usually a task for the club greenhouse technician. Equally, every seedling can be inoculated with a virus before being transplanted. And gregarious insects can often be disturbed, and induced to go to another part of the screening population.

(See also: grid screening, parasite gradients, spreader rows and surrounds).

Pedigree Breeding

Pedigree breeding is the traditional breeding method of the Mendelians. The method typically involves single-gene characters in a wild plant that are transferred to a good cultivar by back-crossing. The method is of limited interest to clubs working with horizontal resistance.

Plant Pots

If the breeding involves a crop that has to be transplanted, there is much to be said for using peat pots. The whole pot, with its seedling, can be planted out, and the peat pot decays in the soil, allowing the roots to grow through it. Alternatively, planting blocks made of fibrous, bio-degradable plastic behave in the same way. Both the peat pots and the blocks are available in sheets which can be cut up into individual pots or blocks in the field. Trays of plastic pots are also available for small seedlings, but the seedlings must be removed from the pot before planting out.

One advantage of these trays of small pots is that they can be fed into an automatic seed sowing machine. One of these machines can save hundreds of hours of work if seeds are being sown in individual pots by the tens of thousands.

For larger plants, such as young trees, clear, transparent plastic bags makes excellent pots. Holes must be punched in the bottom to allow drainage. If the sides of the bag are exposed to light, green algae will grow on the inside of the plastic, and their photosynthesis will add to the oxygen supply in the soil.

Many horticulturists prefer the old-fashioned terracotta pots because these are porous and permit considerable aeration of the roots. They can also be re-used many times. However, they are expensive and they break easily. Plastic pots are not normally re-usable and they require a much lighter soil mixture so that air can reach the roots. But they are cheap, particularly if small pots are needed by the tens of thousands. In general, the peat pots, and bio-degradable plastic blocks, are the best.

Popularity Screening

There are many screening tests which involve value judgements. These include characteristics such as colour, flavour, and scent, which are not easily assessed by chemical analyses or physical measurements. This is one of the advantages of belonging to a large club with many members. It is then possible to conduct popularity polls among many members. By keeping accurate records, it is also possible to assess individual member skills, identifying those members who have the most reliable sense of smell, colour, or taste. (See also: field screening, greenhouse screening, grid screening, head to row screening, laboratory screening, negative screening).

Potato Blight

Potato blight (*Phytophthora infestans*) has two mating types which are both hermaphrodite but self-sterile. This means that oospores and sexual recombination can occur only if both mating types are present. For about a century and a half, following the great Irish famine, and the ‘Hungry Forties’ (Chapter 18), only one mating type (A1) was present in the potato areas outside of Mexico (which is the centre of origin of this disease). The second mating type (A2) has been very carelessly allowed to spread all over the Northern Hemisphere, and oospore formation is now common. This has made the disease considerably more damaging, but it has the advantage for breeders that the ‘one-pathotype technique’ is not longer necessary. Sexual recombination produces new blight races so rapidly that all vertical resistances will be matched quite soon. If in doubt, the presence of a functioning vertical resistance will be revealed by hypersensitive flecks.

Potato Grafting

A vegetative shoot of potato can be grafted on to a tomato rootstock. The advantage of this technique is that the potato shoot will grow up to the greenhouse roof, if supported by a string, with an inflorescence of flowers every few inches. This is very useful for purposes of hand pollination and true seed production.

Using a new razor blade, a tomato seedling stem is cut across, just above the first two leaves. A vertical cut is made down the centre of the stem. The potato shoot, about 1-2 inches long, has its base trimmed to a wedge shape, and the wedge is pushed into the cut of the tomato stem. The graft is wrapped in grafting tape (e.g., cling wrap or thin plastic film) and the grafted plant is kept for a few days in a mist propagator. Once the potato scion begins to grow, the last two tomato leaves, and their axillary buds, can be cut off, and the grafting tape removed.

Potato Pollination

The objective of pollination in potatoes is to produce true seed by cross-pollinating the best selections of the previous summer’s screening. Each seed parent can serve as both a male and a female parent because potato flowers are hermaphrodite. That is, each flower has both male and female organs.

Flowers that are to produce fruits must be emasculated to prevent any risk of self-pollination. The flower is emasculated the day before it is due to open, when the petals are fully formed, but not yet separated. A biologist's dissecting needle is used to separate the petals, and to expose the style and stamens. The stamens are broken off by bending them away from the stigma. They can be allowed fall to the ground. The emasculated flower will be clearly recognisable the next day by the absence of anthers. The petals will be wide open, and the stigma will be fertile, and ready to receive pollen.

Flowers which are to produce pollen must be left to open naturally. These flowers are easily recognised by the presence of the yellow anthers. The entire flower should be picked off and carried to the emasculated flowers that are to be pollinated. One anther should be picked off with a pair of forceps, and its pollen surface should be touched to the stigma. A small speck of yellow pollen should be visible on the stigma. The pollen cells are microscopic, and such a speck will contain thousands of cells. One anther provides enough pollen to pollinate several emasculated flowers.

There is no need to label the pollinated flowers, or to record the identity of the male parent. However, every open flower that has stamens in it should be removed at the end of the day. This will ensure that every surviving berry is the result of cross-pollination. It is also a good idea to note which clones were used as pollen donors each day, so that every clone can be represented more or less equally in the overall process of cross-pollination. All the clones should also be represented more or less equally among the female parents. This will ensure that the genetic base does not become too narrow.

Potato Rapid Multiplication

Potatoes are usually multiplied by planting ‘seed’ tubers. However, when only a few tubers of a promising new clone are available, this can be an agonisingly slow process. A very rapid multiplication can be achieved with stem cuttings. The top one or two inches of actively growing stems are cut off with a very sharp knife and put into a mist propagator. These cuttings form roots in about ten days. They are then planted out in pots, and they too will soon provide new cuttings. In the meanwhile, the original plants have produced a new harvest of cuttings. The number of cuttings taken from each plant doubles with each harvest, because the two axillary buds immediately below each growing point are stimulated to grow when that growing point is removed. Once there are more rooted cuttings than can be conveniently handled, the older cuttings are transplanted into the field where they can produce tubers.

Potato True Seed

In a temperate country, the entire winter is available for the production of true seed of potato. Potato fruits look like small tomatoes, and they usually contain 100-300 seeds. They remain green when ripe, or they may develop a reddish or bronze tinge. Ripeness is determined by a slight softening of the fruit and, possibly, a slight shrinking with a corresponding wrinkling of the skin. If in doubt, leave the fruits on the plant for another week or two.

The ripe fruits should be lightly macerated in water in an electric blender. Do not over-do this as the seeds may be broken.

The macerated mixture should be left to ferment in a clean plastic bucket for twenty four hours. The whole lot should then be poured, with plenty of clean water, through a set of soil sieves. This is a special set of sieves in which each sieve has a finer mesh than the one above it. In this way, the largest particles remain in the top sieve, and the smallest penetrate the bottom sieve. The seeds will be found in one of the middle sieves. They can be spread on absorbent paper to dry. The fermentation will have broken their dormancy and, if necessary, they can be germinated immediately. If they are to be kept for future use, they should be stored with silica gel in an airtight container in a refrigerator at about 4ºC.

Potential New Cultivars

A club can begin producing potential new cultivars at quite an early stage of the breeding program, so long as it is realised that many potential new cultivars will not survive the final field trials, in which they are compared with the best available commercial cultivars. Individual club members should not allow themselves to become emotionally involved with their own selections, because the chances are they will be disappointed. This precaution apart, it is better to have too many potential new cultivars than too few. And don't forget those questions of population immunity, parasite interference, and biological control (Chapter 14), which all suggest that we may need much less horizontal resistance than we think.

Program Expansion

It may occasionally be necessary to expand the breeding program in one of three ways.

First, the original genetic base (i.e., the original parents of the screening population) may prove to be too narrow to accumulate the required level of horizontal resistance. The genetic base must then be broadened by introducing new genetic material to the screening population. Any good modern cultivars may be used provided they are susceptible to all the designated pathotypes.

Second, it may decided that the original agro-ecosystem (for on-site selection) is too large. It may then be desirable to split the screening population into two or more sub-populations, each with a somewhat different agro-ecosystem, and a somewhat different patterns of pathosystems.

Third, a previously absent, foreign species of parasite may be inadvertently introduced to the area concerned. For example, the Colorado beetle of potatoes might become established in the United Kingdom. The breeding program would then have to take this new species of parasite into account. If vertical resistances occur, it will also be necessary to designate a pathotype that matches all the original, designated hosts.

Pure Line Formation

There are three methods of forming pure lines from a genetically diverse screening population of heterozygous plants.

First, is the traditional method used by pedigree breeders. The best plants in a genetically diverse, heterozygous population are allowed to self-pollinate, and their seeds are kept for planting in the next screening season. This progeny is still variable, but less so. The best plants within this progeny (family selection is recommended) are again allowed to self-pollinate, and their seeds are kept for planting in the next screening generation. This process is repeated for some 4-6 generations. The best plants are then sufficiently homozygous to form pure lines. The disadvantage of this method is that it requires one screening season for each generation of selfing (i.e., 4-6 screening seasons).

Second is the bulk breeding method, in which a genetically mixed population is allowed to self-pollinate for 4-6 generations, while retaining the original degree of genetic diversity. At the end of this process, all the plants are homozygous, and the best of them are selected to produced new pure lines. This method avoids selection in each generation, and it is quicker for this reason (i.e., the population can also be grown during an off-season or in a greenhouse).

Third is single seed descent (see below). The advantage of this method is that it saves much time, and it can produce new pure lines in as little as two years. This is the generally recommended procedure.

Purification of Foundation Stock

The first available propagating material of a new cultivar is called foundation stock. This material must be very pure it two respects.

It must be genetically pure in the sense that it 'breeds true to type'. If it is an inbreeder, this means that it must be a pure line, and that there must have been no accidental cross-pollination with foreign pollen. If it is a clone, it must be free of mutants and accidental contamination with material from another clone.

Secondly, it must be hygienically pure in the sense that it is free of all parasites that can be transmitted in the propagating material. This is a problem that is more acute with horizontal resistance breeding than with vertical resistance breeding. The reason is that vertical resistance confers complete protection, while horizontal resistance usually confers incomplete protection. It follows that plants that have been screened for horizontal resistance will have been exposed to all the relevant parasites, and will be carrying those that are transmitted in the propagating material. Because vertical resistance breeding has dominated crop science so completely, this is a relatively new problem.

Foundation stock produced by a breeders' club will need to be purified. There are various techniques for doing this, depending on the parasite in question. For example, stem cuttings of potatoes rooted in a sterile medium will leave most soil-borne parasites behind. Foundation stock can be purified of viruses by long-term heat treatment and/or meristem culture, but these are techniques for specialists. True seeds of, say, cereals, may be either contaminated or infected. Contaminated seed has fungal spores, or bacteria, on the outside of the seed. These can be destroyed by chemical seed dressings. Infected seed has fungi or bacteria inside the seed. These can be destroyed by heat treatment or by various specialised chemicals, such as systemic fungicides, or antibiotics. But these too are techniques for specialists. Much the same is true of the propagating material of vegetatively propagated clones.

As a general rule, these hygiene treatments are too complicated for most clubs, and will have to be contracted out to specialists. However, this requirement will vary considerably with different species of crop, and consultant advice should be sought.

It can be argued that these new cultivars will have so much horizontal resistance that the fact they are carrying parasites does not matter. This is true enough so far as the new cultivars themselves are concerned. But, if they act as sources of infection for neighbours' crops, there might be a fuss. And the authorities who accept new cultivars for breeders' rights registration are steeped in the 'certified seed mentality' and they may hesitate to register a new cultivar that is a symptomless carrier of various parasites, particularly if it is actually carrying those parasites when submitted for registration.

It is to be hoped that the use of horizontally resistant cultivars will eventually be so common that the thought of these cultivars being symptomless carriers will worry no one.

Quality of Crop Product

Measuring the quality of crop product can be a complicated procedure. For example, bread wheats that have a low protein content have a low bread making quality, and their flour must be blended with that of high protein wheats to make decent bread. High protein generally means a strong grain and a high gluten, suitable for bread, while low protein means a weak grain and low gluten, producing flour suitable for crumbling biscuits. Similarly, with barley, the malting quality depends on uniform, well-filled grains with a high germination rate and a high enzyme content to convert the starch to sugars. The highest yielding barleys may be unsuitable for malting, and can be used only for animal feed.

There have been some dramatic improvements in measurement techniques in recent years, particularly with respect to obtaining accurate measurements of complex variables in very large numbers of very small samples. However, most of these measurements require complex laboratories an are beyond the capacity of most breeding clubs.

Breeding clubs should generally assume that their primary concern is breeding for *resistance*, and that the other qualities of the original parents will be largely preserved during this breeding. To some extent, their breeding work will be a gamble, producing cultivars with excellent resistance but which may, or may not, be suitable for this, that, or the other purpose. In other words, the tests for quality will be conducted by professional laboratories only after the breeding work is completed and pure lines have been produced. If a club becomes very wealthy from breeders' royalties, it may consider having its own laboratory and employing its own technicians, with a view to producing specific qualities.

Quantitative Vertical Resistance

Quantitative vertical resistance must be avoided because it provides incomplete protection before it is matched, and no protection after it is matched. It is easily confused with horizontal resistance, and it can be a frightful nuisance in a breeding program. Fortunately, it is a problem only occasionally, mainly in small grain cereals. If in doubt, a specialist should be consulted.

The best way to avoid quantitative vertical resistance is to use only parents that exhibit *qualitative* vertical resistance, or parents with no vertical resistance at all, if any are available. Probably the best way to resolve this point is by literature research, as quantitative vertical resistance is rare, and its occurrence is usually noted in the scientific literature.

Recurrent Mass Selection

The breeding method used for accumulating horizontal resistance is recurrent mass selection. This is the breeding method of the biometricians (Chapter 2). It is also a very easy method to use. Some 10-20 good cultivars are selected as the original parents of the breeding population. These are cross-pollinated in all combinations. Depending on the reproductive rate of the crop in question, a multiplication generation may be necessary to obtain enough seed for the screening generation. The best plants of the screening generation then become the parents of the next generation. This process can be repeated for as long as progress is being made.

The method as described above involves early selection, in which the parents of the next screening generation are highly heterozygous. Late selection (see above), after about four generations of selfing, using the bulk breeding method (see above) or, preferably, single seed descent (see below), produces parents that have considerable homozygosity. Late selection, using single seed descent, has various genetic advantages and is recommended. The clones of vegetatively propagated crops can, of course, be utilised immediately.

See also: family selection.

Relative Measurements

When screening for horizontal resistance, the entire screening population is likely to look terrible, particularly in the earlier screening generations. Only the least terrible plants should be selected, however awful they may appear. The current appearance of these plants bears little relation to future generations that will have higher levels of horizontal resistance, or to future crops in farmers' fields that are free from parasite interference and biological anarchy (Chapter 14). When screening, therefore, all assessments must be made relative to the screening population as a whole, rather than to absolute standards of freedom from parasites.

Research

During the nineteenth century, people spoke of the 'gifted amateur' who was not a professional scientist but who nevertheless managed to make important scientific discoveries. With an increasing bureaucratisation of science in the twentieth century, gifted amateurs have been squeezed out of active research. Breeding clubs offer them a chance to return, and club newsletters offer them a chance to publish. Indeed, the very notion of a breeding club is a clarion call to gifted amateurs.

When vanilla (*Vanilla fragrans*) was first taken from its centre of origin in Central America, to the Old World tropics, it grew well but it yielded nothing, because the flowers would never produce pods. We now know that this was because of the absence of its natural pollinating insects. In 1841, a gifted amateur in Réunion, called Edmond Albius, who had been a slave, discovered how to pollinate vanilla flowers with a toothpick, and his method is still used to this day. Any member of any breeding club has the potential to make a discovery of comparable importance.

The best research comes from first identifying a problem, then having an idea of how to solve it, and then testing the idea. Identifying a problem correctly is really a matter of asking the right questions, because the cause of a problem is often misunderstood. Amateurs often have an advantage over professional scientists when it comes to having new ideas, because they are free of much routine thinking, and many preconceived ideas. Intelligence, after all, is only the ability to solve new problems, and one does not have to be a trained scientist to be intelligent. The testing of an idea can be at least as exciting as solving a difficult puzzle or game, and it will provide a far greater sense of achievement. Finally, because the entire area of horizontal resistance and recurrent mass selection has been so disgracefully neglected during the twentieth century, there are many discoveries waiting to be made.

It is impossible to predict successful research, and the most that can be suggested here is to point out areas that are likely to be fruitful.

One of the more promising areas concerns new methods of overcoming a patchy distribution of parasites in the screening population. My friend Ivan Buddenhagen found a simple solution to the patchy distribution of the maize leaf hopper (*Cicadulina* spp.) that carries streak virus in Africa (Chapter 20). He had two men drag a pole horizontally through the tops of the young maize plants. This made all the hoppers jump, and they usually came down on a different plant. By doing this every day, all the maize plants were soon infected with the virus.

Another area requiring investigation concerns random cross-pollination, with in-breeding species of crop. The use of male gametocides, particularly with in-breeding dicotyledons is of special importance. This involves both the testing of new substances, and identifying the best rates and times of application. The use of bees and, possibly, other insects, for random cross-pollination also merits investigation.

It is in the general area of parasite distribution problems that purely pragmatic research will most likely be required. Amateur scientists often come up with ingenious solutions that might never occur to a professional. Don't be modest about proposing a possible answer to a problem. Equally, don’t hesitate to consult a professional. Discuss your problem with him. Most governments employ professionals whose sole function is to advise growers. So don’t feel guilty about making demands on their time. That is what professionals are for.

Rice, Special Aspects

One of the main differences between rice and the other in-breeding cereals is that the pollen is very short-lived, and it is highly sensitive to desiccation. This means that cross-pollination with male gametocides is much less effective with rice than with the other in-breeding cereals. However, rice has a far greater reproduction rate, and the single plant grown from one seed will produce several hundred seeds. Hand-crossing followed by a multiplication generation is thus very effective.

Rotation

When breeding for horizontal resistance to soil-borne parasites, it is necessary to *avoid* rotation between screening generations. In other words, the screening population should be grown on the same plot of land, and in the same soil, year after year. This is done in order to build up a high density of soil-borne parasites. Club members may be distressed at the thought of damaging their field or garden soil in this way. However, most soil-borne parasites disappear quite quickly in the absence of their host plants, and the soils will recover with normal rotation at the conclusion of the breeding work. In any event, a successful breeding program is far more valuable than the build up of parasites in the soil of some fields or gardens, or a small club farm, and this temporary inconvenience should be regarded as a small but very worthwhile price to pay.

Screening

Screening is the process, in recurrent mass selection, in which a plant population is examined with a view to identifying the best plants. Screening is normally done by eye, and all measurements should be relative. That is, only the least parasitised plants, or the greenest plants, are selected, regardless of how poor they may seem in absolute terms.

It should be remembered that the first screening population is going to look terrible. In fact, it may even be necessary to apply crop protection chemicals to it, if there is a danger of the entire population being killed off by parasites. Three comments are important. First, as far as possible, let the parasites do all the screening work for you. We may as well get some good out of these pesky creatures. Second, various factors such as parasite interference, and biological anarchy (Chapter 14), will make the most resistant plants appear much more susceptible than they really are. Finally, the screening population may look so appalling that some club members will despair, and want to abandon the entire breeding program, then and there. Don't. The next screening generation will look better. And the next will be better still. Remember those maize landraces in tropical Africa (Chapter 18), and the people who owned, and had faith, in them.

After a few generations of screening, so much horizontal resistance will have accumulated that the parasites are no longer doing all the screening work for you. What is more, the selection pressures for resistance will be reduced accordingly, and the rate of accumulation of horizontal resistance will decline considerably. One solution is to use spreader rows and surrounds.

There are four simple rules when screening for horizontal resistance. First, use on-site screening. Second, screen for yield, on the grounds that only resistant plants will yield well. Third, inoculate the screening population to ensure that the high yields are due to resistance and not to chance escape from infestation or infection. Fourth, use the one-pathotype technique to ensure that the resistance is horizontal and not vertical.

(See also: field screening, greenhouse screening, grid screening, laboratory screening, negative screening, on-site screening, parasite gradients, popularity screening).

Screening for Rooting Quality

When Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, *Agric. Univ. Wageningen Papers* 88-2; 114pp) was screening wheat at Passo Fundo, he had to confront the serious problem of acid tropical soils, and the attendant problems of aluminium and manganese toxicities. Plants that were susceptible to these toxicities had very weak rooting systems. There were also serious problems with various species of root parasite which also weakened the rooting system. One of his screening criteria was consequently the strength of the rooting system of each plant. At the time of harvest, each selected plant was pulled from the ground. Plants which came up easily had weak rooting systems and were rejected. Those which required a powerful pull to get them out of the ground had a strong rooting system and were retained.

Some clubs may choose to use this selection criterion, if only to eliminate weak rooting systems resulting from soil-borne parasites. However, pulling up many wheat plants that have strong rooting systems is back-breaking work. Plants that do not come easily with a good tug should accordingly be harvested by cutting off all the heads, which must then be separately stored in their own paper bag for individual laboratory assessment.

Screening Overkill

There is a considerable danger that the screening population will be so damaged by parasites during the early screening generations that it will be destroyed entirely. Consequently, it may be a good idea to inoculate the screening population with only one or two species of major parasite in the first screening generation, and then to add one additional species of major parasite to the inoculation process with each succeeding generation of screening. Equally, it may be necessary to protect the screening population with crop protection chemicals to prevent its total destruction. For this reason, the early screening generations should not be conducted on a certified organic farm.

Seed Cleaning

Newly harvested seed is usually mixed up with a fair amount of plant debris, soil, and other rubbish. Seed cleaning is necessary before the seed is to counted, weighed, screened, etc. Seed testing laboratories have all sorts of equipment for this purpose, and catalogues are available. If there is a seed testing laboratory near you, the staff, who probably take great pride in their laboratory, will be only too pleased to show you round, advise you of their practical experience with various kinds of equipment, let you consult their catalogues, and so on.

Seed Counting

When assessing yields of seed-producing crops, it is usually necessary to know both the weight and the number of seeds produced by each plant. With white haricot beans, for example, it may be necessary to have a low ‘hundred seed weight’, because small seeds are preferred. With wheat, on the other hand, the ‘thousand seed weight’ should be high, because large seeds are preferred. These comments are important in relation to total yield which must be high, regardless of the average seed weight.

Various laboratory machines are available for seed counting, and comments given under ‘seed cleaning’, above, apply.

Seed Germination

Some seeds (e.g., some legumes, cassava) have tough seed coats, or a stubborn dormancy, and are difficult to germinate. Such seeds often have to be treated with hot water, sulphuric acid, sand-paper, etc. Other seeds need to be vernalised (i.e., given a spell of cold) before they will germinate. Yet other seeds will begin to germinate immediately they are wetted, and without any further difficulties. Normally, a club should not have any problem in learning about the germination of the seeds of the crop of its choice.

Depending on the crop being bred, seed can be germinated either before or after being planted. Pre-germinated seed requires more work, but it saves the wastage of empty pots and flats that result from a low rate of germination. On the other hand, modern, commercial, horticultural equipment can sow thousands of seeds individually into small pots, and save hundreds of hours of tedious work.

Modern commercial horticulturists have sophisticated machines for sowing seeds in special ‘flats’ that can later be broken up into individual pots. These pots are usually made of plastic, but the most suitable pots are made of peat, so that the entire pot can be transplanted when the seedling is ready. The peat disintegrates in the soil, and the seedling can easily thrust its roots through the disintegrating peat, and into the surrounding soil. Special rooting ‘blocks‘ made of a biodegradable foam plastic can achieve the same thing. The machines for doing this work are expensive and, if it owned one, the club would use its machine only once a year. The club should accordingly consider the possibility of a commercial grower willing to sow its seeds on contract. A minor problem with this method is that the seeds never have a 100% germination rate, and both pots and bench space are wasted when seeds fail to germinate. However, the saving in the many, somewhat tedious, hours of work more than compensates for this.

The alternative is to sow the seeds by hand. This is labour-intensive but may be preferred if the club is short of cash. The best method is to pre-germinate the seeds on a moist paper towel. When the young root is showing, the seedling is transplanted with a biologist's needle into the moist soil of its pot. With practice, it is possible to sow several hundred, pre-germinated seeds per hour. In this kind of work, it is always important to be comfortable, with a decent bench and chair, and proper tools. Discomfort can reduce speed and efficiency to a remarkable extent.

Selection Coefficient

In a screening population, the selection coefficient is the difference between the number of the plants retained, and the number of plants discarded.

Single Seed Descent

Single seed descent (SSD) is probably the best, and certainly the quickest, method of producing pure lines from a genetically diverse, and heterozygous, breeding population of an in-breeding crop (e.g., wheat, rice, beans). This technique is designed to produce many homozygous lines within a breeding population of, perhaps, several hundred heterozygous individuals. Only one self-pollinated seed is kept from each individual within that population, and each of these seeds is grown to produce the next generation. This process is repeated 4-6 times. The final population will have the same total variation as the original, but each individual will be homozygous. Because there is no screening for yield, quality, resistance, or any other character, in each generation, the process is rapid. In a greenhouse, it is usually possible to grow three generations each year of annual species of crop, and hydroponics will accelerate the process. With many species, the generation time can be reduced by an early harvest of the first seeds, even when these are immature. This rapid propagation means that an adequate homozygosity can be achieved in two years or less. When all the individuals in the population are homozygous, the entire population is screened under ‘on-site’ field conditions, and the best individuals are then multiplied as new pure lines.

Soil Inoculation

When transplanted seedlings are used as a screening population, inoculation of the soil in each seedling pot is the best way to avoid a patchy distribution of soil-borne parasites, and to ensure that there are no chance escapes from infection. But seedlings are delicate things, and horizontal resistance often develops only as the seedling matures. It would be counter-productive to kill off too many of the seedlings prematurely.

To avoid this danger, it is probably a good idea to inoculate with only one species of parasite each season, but to use a different species of parasite in each succeeding season. In this way, each species of parasite will become even distributed in the screening plots, and the even distribution will be maintained by repeated cultivation in the same plot every season. Equally, the screening population will be exposed to an increasing range of parasites as it slowly develops comprehensive resistance. If the seedlings were exposed to all these parasites at the beginning, there would probably be a total mortality.

A second way to avoid the risk of an excessive mortality is to inoculate the pots at the time of transplanting, rather than at the time of sowing. Alternatively, the inoculation can be made directly into the hole in the ground, just before the seedling is transplanted. This can lead to a considerable saving of both inoculum and person-hours, because many seedlings are likely to be eliminated by other parasites during the seedling screening.

The actual method of inoculation will depend on the parasite concerned. Many fungal and bacterial parasites can be inoculated as a water suspension, either with a watering can, or by flooding a tray holding the pots. Other parasites are better diluted in a solid medium, such as sawdust, bran, or soil. The preparation of the inoculum itself should be a club responsibility, undertaken by a technician member, and the club, in its turn, will require the assistance of specialists, at least initially.

Soil Pasteurisation

Soil used for germinating and growing seedlings must usually be treated to eliminate undesirable plant parasites, most notably, the ‘damping-off‘ fungi, and root chewing insects. These parasites can destroy very young, and delicate seedlings long before any possible resistance can be manifested.

Moist soil is pasteurised when it is heated to about 80°C. This kills most plant parasites but enables many other, beneficial, soil micro-organisms to survive. The advantage of pasteurised soil is that it can be used as soon as it is cool. Sterilised soil, on the other hand, has been heated to the point of killing everything within it, usually at temperatures of about 120°C., or it has been sterilised with chemicals. Sterilised soil must be kept for at least three weeks before being used, to allow beneficial micro-organisms to colonise it.

Soil Processing

When seed is sown into pots in the greenhouse, a good quality potting mixture should be used. There are many different recipes for potting mixtures which usually contain sand, soil, and humus (i.e., rotting vegetable remains such as peat moss or leaf mould) in roughly equal proportions. Plant nutrients can be added as artificial fertilisers at the time of mixing, or later, as liquid nutrients in the irrigation water.

Many amateur gardeners have their own special recipe for potting soil, that they swear by, and these people may well prove adamant in insisting that their own favourite is adopted by the club. In fact, the exact composition of the potting mixture is not critical, and most plants are tolerant of quite wide variations in this matter.

Sorting

When the harvestable product is a seed (e.g., cereals, grain legumes), the seed can be sorted on the basis of size, colour, specific gravity, hardness, etc. This sorting is often part of the post-harvest screening process, and various laboratory machines are available which can do this work very quickly and efficiently. (See ‘seed cleaning’, above, for comments on equipment). Alternatively, if only a few seeds need to be sorted, the club members may prefer to do this work by hand.

Specialised Help

Every club is going to need help from specialists in matters that are beyond the expertise of its own members. Each club should try to establish friendly relations with a nearby agricultural advisory centre whose mandate is to assist farmers. The specialists in such a centre are unlikely to have all the answers that a breeding club may require, but they will at least know where to go, and who to consult, in order to get those answers.

A few specialists are likely to disapprove of this book because it openly invites competition from amateurs and, furthermore, it claims that this competition is needed, and that it will be effective. Specialists are people too, and the vast majority of them will be open-minded, friendly, and cooperative. But you may come across some who are difficult. Do not be put off by any who put apparently insuperable difficulties in your way, or who claim that 'it cannot be done'. Just ignore them, and look for others. The Internet can be very useful in this respect.

Spreader Rows and Surrounds

Spreader rows and surrounds are lines of very susceptible plants that either intersect the screening population, or surround it. Their function is to produce large numbers of parasites which then spread into the screening population. If designated parasites are involved, the spreader rows or surrounds must contain the designated hosts. Spreaders of undesignated parasites are not normally necessary in the early screening generations when the screening population itself is highly susceptible. However, they become increasingly valuable in the later screening generations, as the screening population accumulates more and more resistance. Usually, the spreaders themselves will have to be inoculated and, if designated hosts are being used, the designated pathotypes will have to be used also.

The use of spreaders is a deliberate exploitation of parasite interference, and it will lead to an entirely false impression of susceptibility in the screening population. Club members should not be deceived by this phenomenon, which can be very demoralising if it is not understood. Equally, spreaders can produce marked parasite gradients, and grid screening is then highly desirable. If many different species of parasite are involved, it may be necessary to use a mixture of spreader plants with a variety of susceptibilities to different parasites.

A special danger of susceptible spreader plants is that they can introduce thoroughly undesirable pollen into the screening population. This is usually avoided by asynchronous flowering. That is, the spreader plants are sown early, or late, so that their pollen production is finished, or not yet started, when the screening population comes into flower. Alternatively, and depending on the species involved, the spreader plants can be decapitated to destroy their flowers, or they can be weeded out entirely shortly before the screening population comes into flower.

(See also: grid screening, parasite gradients).

Threshing

The threshing of the selected plants of grain crops (cereals, grain legumes) should normally be done in the club laboratory, and each plant should be threshed individually so that various components of yield and quality can be determined. This process constitutes a laboratory screening which will eliminate perhaps 90% of the plants selected in the final field screening.

Trouble-Shooting

Occasionally, things can go badly wrong in a breeding program, and it is then very easy to give way to despair. In fact, virtually all errors and accidents are repairable, and the worst that can happen is a loss of time. Some of the more alarming mishaps are as follows.

1. Appearance of a new species of parasite. Sometimes a new species of parasite can appear, and the screening population is susceptible to it. There are several possible explanations for this. It may have been a freak season, and a parasite which is normally harmless, and unrecognised, became temporarily serious. Or, the screening population may be abnormally susceptible to an otherwise obscure and unimportant parasite. Or there may have been a genuine manifestation of crop vulnerability, in the sense that a foreign species of parasite has been accidentally introduced into the local agro-ecosystem. This sort of thing can be a setback, but it is not a

disaster. If the new parasite continues to be serious, just screen for resistance to it.

2. Loss of designated pathotype. Sometimes a living culture of a designated pathotype can die out, and then there is no inoculant for the screening population. The first thing to remember is that a designated pathotype can be recovered. Just grow some of the designated host in the field and it should soon pick up the designated pathotype. Alternatively, it is permissible to use any pathotype that matches every one of the original parents of the screening population. The second thing to remember is that it does not matter too much if you miss one season of screening for one species of parasite. Possible insurance against this kind of loss is to have an agreement with a neighbouring club to use the same designated pathotypes. It is most unlikely that two clubs will both lose the same designated pathotype at the same time. Alternatively, you can designate a pathotype that is maintained routinely in a research station, so that the friendly scientists at that station can always help out.

3. Loss of designated host. Provided you have used a well-known cultivar as your designated host, seed stocks should be

available, even if only in a gene bank in a research station. However, a club should have no difficulty in maintaining its own stock of propagating material of designated hosts. If a very obscure host was used, and it got lost, a new host can be designated. The only criterion is that its matching pathotype must match all the original parents of the screening population.

4. Suspected vertical resistance operating in the screening population. This can be very alarming but do not panic. Take one or two of the suspected plants and experimentally cross them with a susceptible plant to see how the progeny segregate. If there is continuous variation, the resistance was horizontal. If there is a Mendelian ratio, you have one or more functioning vertical resistances in the screening population. Provided that it is not quantitative vertical resistance (see below), the best method of getting rid of it is to simply weed out any plant that shows evidence of it. This evidence is (i) a complete absence of parasitism, and (ii) the presence of hypersensitive flecks, if a hypersensitivity mechanism is involved. This weeding out must be done before any cross-pollination can occur, and the elimination should be repeated

every screening season until there is no more evidence of a functioning vertical resistance.

5. Suspected quantitative vertical resistance. This kind of resistance is rare, and it is usually found only in the small-grain cereals. The best way to avoid it is to use original parents that have qualitative vertical resistances, and that are very susceptible to the designated pathotypes of parasite species in which quantitative vertical resistances occur. This is, without question, the most difficult aspect of breeding for horizontal resistance. If in doubt, consult a specialist. But try to do this before the breeding is started.

6. The genetic base of the screening population proves to be too narrow. New host material can be added to the screening population at any time. The essential precaution is that each new host must be susceptible to every one of the designated pathotypes, to ensure that its vertical resistances, if any occur, are matched during screening.

Vertical Resistance, Avoidance During Breeding

In order to assess the level of horizontal resistance, all vertical resistances must be either eliminated or inactivated during the screening process. The most effective way of inactivating vertical resistance is the one pathotype technique, using a designated host and pathotype. The genetic elimination of vertical resistance is much easier because it eliminates the need for a designated pathotype, but it is not often practical. It consists of using only original parents that possess no vertical resistance genes. Unfortunately, this is rarely possible because, in most crops, such parents do not exist. Potato blight (Chapter 18) is one of the few examples in which a genetic elimination of vertical resistance is feasible. Another method involves the swamping technique, as happens with potato blight when both mating types are present. So many vertical pathotypes are around that all vertical resistances fail quite quickly. This approach is usually successful when breeding a crop in its centre of origin, but it is not generally recommended. However, it can be used with some heteroecious parasites, such as the rust fungi or various aphids, by growing the winter host close to the screening population.

Vertical Resistance, What Happens to It?

A vertical resistance that was matched during the screening process is still present in the new cultivars that emerge from the breeding program. It may even be unmatched and functioning when these cultivars are first grown by farmers. It may even break down during commercial cultivation of those cultivars. But when it does break down, no one is likely to notice, because there should be so much horizontal resistance that the breakdown will not be obvious.

Weed Suppression

Farmers in temperate countries usually regard potatoes as a ‘cleaning’ crop in the sense that a field is cleaned of weeds when it is under potatoes. This is because the potato plant has such a dense foliage that weeds growing under it are deprived of light, and cannot flourish. With close planting, both between rows, and within rows, the potato foliage shades the entire field and this has a powerful suppressive effect on the weeds. The relatively few weeds that survive the potato shading are easily destroyed by cultivation.

It may be possible to breed other crops for this ‘cleaning’ effect. For example, beans with a lush foliage will make weeding much easier, and more effective. The lush foliage will probably contribute to yield also, and such a character could be a useful selection criterion.

Wheat

Any club planning to breed wheat for horizontal resistance should consult Beek (*Selection Procedures for Durable Resistance in Wheat*, 1988, Agric. Univ. Wageningen Papers 88-2; 114pp). His use of a male gametocide and single seed descent with hydroponics for late selection permitted massive cross-pollination and a one-year breeding cycle. This is a major departure from the classic breeding techniques of the Mendelian school. These various techniques are described under their own headings. It is likely that the same techniques can be used with other self-pollinating, small grain cereals.

Widening the Genetic Base

(See: program expansion, trouble-shooting).

Chapter 26

Screening Existing Populations

It is often possible, and highly profitable, to exploit an existing plant population that has genetic diversity. Most modern crops are unsuitable for this purpose because they have genetic uniformity, being pure lines, clones, or hybrid varieties. But there are still many plant populations which do exhibit genetic diversity. In commercial agriculture, these are mainly the fodder plants, such as grasses, and various fodder legumes, including clovers, alfalfa, etc. Many subsistence crops in the tropics are landraces, and can also be exploited in this way, while subsistence clonal crops often contain a wide variety of different clones. There are also various tropical tree crops that can be used for both positive and negative screening. Positive screening identifies the best individuals for propagation elsewhere. Negative screening protects an existing population because it identifies the most susceptible individuals with a view to taking them out, ending parasite interference, and allowing population immunity to operate (Chapter 14).

There are various precautions to be observed when screening existing populations. The first, and most obvious, is that it is pointless to select individual plants that look good only because they have a functioning vertical resistance. If there are gene-for-gene relationships, it is best to select plants with slight parasitism, rather than plants with no parasitism. This is usually a reliable indication of the horizontal nature of the resistance.

A second point is that parasite interference will be operating in a mixed population. Consequently, any selected individual can be expected to perform rather better when grown as a uniform population well away from susceptible individuals, and free from parasite interference. The real danger of this situation is that the original population may appear to be so parasitised that any thought of selecting within it is dismissed as unrealistic.

A third and obvious precaution is that the population being screened must be entirely free of crop protection chemicals.

It should perhaps be mentioned that selection within existing populations has been the standard method of crop improvement since the dawn of agriculture. And this improvement was almost invariably the work of farmers. The following examples consequently represent only the very small tip of a very large iceberg.

Cocoa

Negative screening can be used only occasionally for parasite control but, when it is feasible, it is likely to be very useful indeed. There are two requirements. First, the technique will function only with a tree crop and, second, the crop must be genetically diverse. A cocoa crop that is severely diseased with witch's broom disease (*Crinipellis perniciosa*) provides an example. This disease produces a proliferation of the twig growing points, resulting in an unsightly bunch of twigs like the sweeping end of a witch's broom.

This control technique relies on a normal distribution of resistance within the genetically diverse crop. That is, there is a minority of highly resistant trees, and another minority of highly susceptible trees. The majority, or mode, are halfway between these two extremes. The more commonly used screening technique involves a positive selection by the identification and propagation of the most resistant trees. However, this results in destruction of the old crop, and the planting of a new crop. Negative selection involves the identification and destruction of the most susceptible trees. The control method works because parasite interference is eliminated, and population immunity then operates (Chapter 14).

Think of each tree as a plot in a field trial. A highly susceptible tree is surrounded by more resistant trees. Because of parasite interference, each of those surrounding trees has many times more disease than if there were no interference. The trees beyond them have less disease, but they still have more disease than they would if there were no interference. If the susceptible tree is taken out and burnt, and the witch's brooms on the surrounding trees are pruned out and also burnt, the interference will stop. On average, the surrounding trees will have a medium level of horizontal resistance. This level is probably enough to provide population immunity (Chapter 14), and to control the disease, when there is no parasite interference.

By identifying and eradicating a minority (perhaps 1-3%) of the most susceptible trees in the crop as a whole, and pruning out all diseased branches, parasite interference is eliminated, and the disease will be permanently controlled. In practice, an experimental approach will probably be necessary. The first eradication may not achieve a complete control, and a second eradication may be required in order to remove the minority of the next most susceptible trees.

Most tree crops are propagated in genetically uniform populations, either as clones (e.g., stone and pome fruits, citrus, olives, figs, dates, grapes) or pure lines (e.g., arabica coffee). Other perennial crops (e.g., currants, hops, banana, sugarcane, pineapples, black pepper, yams) are also cultivated as clones. This is why the technique of negative screening is of limited application. However, it is likely to be useful in open-pollinated, seed-propagated, tropical tree crops, such as cocoa, cashews, mangoes, and tea. The technique may also prove useful in young plantation forests.

Coconut

There is a disease of coconuts (*Cocos nucifera*) in the Philippines called *cadang-cadang*, which means "death-death". This disease was first observed in 1926 on San Miguel Island, off the east coast of southern Luzon, near the town of Legaspi. This small island had a single, commercial coconut plantation of 200,000 coconut palms. Within twenty years, all but eighty of them had been killed by *cadang-cadang*. The total number of palms killed on Luzon is difficult to estimate but, by now, is probably approaching twenty million.

In 1945, A.E. Bigornia, a Philippine scientist, and a little known but wise plant pathologist, visited San Miguel Island, and decided that the eighty remaining palms must be resistant as, indeed, they undoubtedly are. Because coconuts have a continuous pathosystem, this must be horizontal resistance. Bigornia collected nuts from the best of these palms and planted them on mainland Luzon where they now form a new, resistant landrace.

The Philippines has an excellent hybrid coconut scheme, in which tall palms are crossed with dwarf palms to produce high-yielding hybrids, in a manner similar to hybrid maize. Bigornia's new landrace is an obvious tall parent in this hybrid scheme.

Coffee

The identification of coffee trees resistant to coffee berry disease in the genetically diverse populations of Ethiopia has already been described (Chapter 21), and only a brief reiteration is necessary here. About one tree in a thousand was resistant, and rather more than five hundred resistant trees were identified. In other words, about half a million trees had to be examined in order to find the perfect tree called ‘741’. This may sound like a lot of work but, in fact, it is only a small fraction of the work involved in a formal tree breeding program. Even more important, it produced spectacular results in only a small fraction of the *time* required for a formal breeding program, in a tree crop with a generation time of three years.

It is also worth reiterating that the work of Doughty (Chapter 21) in re-synthesising *Coffea arabica* should be repeated. Because new allotetraploids are genetically stable, they can be used immediately as new cultivars, provided that their other attributes are satisfactory. If many new allotetraploids can be produced, this approach is the one most likely to produce new cultivars with comprehensive and complete horizontal resistance in a very short time.

Pasture Species

Many species of pasture grasses and legumes are open-pollinated. In the industrial countries, most of them have already been improved and breeding clubs should do fairly careful investigations before launching an improvement program.

Landraces

Most subsistence agriculture in the tropics involves landraces of the various seed-propagated food crops. Both the yield and the quality of these crops can usually be improved selecting within those landraces. This is often a method of obtaining useful results well in advance of the more fundamental improvements that emerge from a more formal breeding program. It should perhaps be added that most tropical landraces have excellent levels of horizontal resistance to all the locally important parasites. The breeding objective must consequently be to increase the yield and, possibly, the quality and agronomic suitability, without any loss of this resistance. This is the exact converse of breeding modern industrial crops for horizontal resistance, where the objective is to increase the resistance without any loss of yield, quality, or agronomic suitability.

Rice

One of the most spectacular rice cultures in the world belongs to the Igorot people, who live in the northern mountains of Luzon, in the Philippines, where the sides of entire mountains have been terraced to make rice paddies. These stone-faced terraces are ancient, and many generations of farmers have contributed to the enormous task of their construction, during the course of some fifteen centuries. These terraces are justly famous, and most people will have seen pictures of them, soaring up the sides of high mountains, with the highest terraces often lost in the clouds.

This is an area of high rainfall, and the paddies are filled by rain, with any surplus water being allowed to drain from terrace to terrace down the mountain. The people live in villages, and each village has its own temple, and its own priests. One of the duties of the priests is to go into the rice fields each season, just before the rice is harvested. They select the best individual plants, and take them to the temple, where they are carefully preserved, because they are the seed of the next crop.

This process of selecting the best plants for seed has continued for centuries. It is, of course, an excellent method of crop improvement, and it is no less than recurrent mass selection. These rice varieties are landraces, and they are made up of many, closely similar, but nonetheless different genetic lines. Each landrace is perfectly balanced with its own agro-ecosystem. It has adequate resistance to all the locally important pests and diseases, and it has the maximum yield that is possible with this traditional farming method. Each landrace also has exactly the cooking and eating qualities that the people like most.

Now let us suppose that the plant breeders want to make changes. This can be illustrated by a story, no doubt apocryphal, that foreign scientists visited these mountain villages and advised the people that, if they applied nitrogenous fertilizer to their rice crops, they would double their yields. So some of the people broke with their ancient traditions, and used this fertilizer. The rice yields were indeed doubled but, unfortunately, the plants were so luxuriant, and their maturation was so delayed, that they were totally destroyed by a disease called blast, and the doubled yields were reduced to nothing.

Landraces that are in balance with the local agro-ecosystem will lose that balance if the farming system is changed in any important way, such as the addition of nitrogenous fertilizer. If these villagers want to change their farming system to one of high nitrogen applications, they must make the change very slowly. Each season they must apply only a little more nitrogen than in the previous season. And, before each harvest, the priests must select the best plants as seed for the next season. Provided that this process is given enough time, there will be no disruption, and no loss of agro-ecosystem balance. This illustrates how very profoundly recurrent mass selection can change plant populations.

Rice is a self-pollinating cereal and this means that it cross-pollinates only rarely. Recurrent mass selection is consequently slow in a self-pollinating crop. But, if the breeders artificially cross-pollinate the selected plants each generation, the whole process is quick, and it can be completed in a few years.

There is another story, no doubt apocryphal also, that scientists advised these mountain people that, if they grew the new miracle rices of the green revolution, and used nitrogenous fertilizer as well, they would double their yields. A few farmers tried these new varieties and, with fertilizer, the yields were indeed doubled. But, unfortunately, the cooking qualities of the new varieties were so different from the traditional rice, that no one would eat them.

The moral of this story is that subsistence farmers are wise and cautious people, who are usually less likely to make mistakes over their food supply than are visiting scientists, who are often a little brash and, perhaps, a bit too confident. And the local priests who select the next season's seed are also wise and cautious people. They may not know any science, but their ancient traditions are more reliable, and often more appropriate, than the ideas of a foreign scientist, probably trained in the Mendelian school of genetics, and in the spirit of an industrialised, mechanised agriculture.

Rubber

Rubber (*Hevea brasiliensis*) is a tree that is native to the Amazon basin, in an area where, it is said, they have only two seasons each year. In one season, it rains every day. In the other season, it rains *all* day. The Amazon, which is reputed to hold one fifth of all the world’s fresh water, runs roughly along the line of the equator. Rubber thus grows in an area that is constantly warm and wet.

In spite of this constant, warm, tropical humidity, the rubber tree is deciduous (Chapter 6), and each tree is leafless for about one month each year. The leaf pathosystems of rubber are thus discontinuous, and rubber has vertical resistance to a disease called South American Leaf Blight (SALB) caused by the microscopic fungus *Microcyclus ulei*. This disease caused one of the very few defeats of Henry Ford, of ‘Model T’ fame.

Ford decided to produce his own rubber, in order to manufacture his own tyres, for his motor cars. To this end, the Ford Motor Company established a rubber plantation in Brazil, near Boim, on the Tapajoz River, in 1928, and they called it Fordlandia. But the plantation failed because so many of the trees died of leaf blight. In 1934, Ford established a second plantation at Belterra, also on the Rio Tapajoz, but this too failed. So did smaller plantations in other parts of the Amazon basin.

There is a gene-for-gene relationship, and a system of locking, that obviously functions in the wild pathosystem of SALB.

And, because every tree is apparently matched sooner or later in each leaf cycle, each tree obviously has horizontal resistance to SALB. However, both kinds of resistance evolved to function in a dense, tropical, rain forest in which rubber trees occur with a maximum population density of only eight per acre. This means that the SALB spores have great difficulty in finding a host, let alone a matching host.

The effectiveness of both kinds of resistance was lost in the rubber plantations of Fordlandia and Belterra. The trees were so close together, and the spore density was so high, that every biochemical lock was matched early in the season and, and every tree was bombarded with spores. After a few years, the most susceptible trees died from an excessive loss of leaf.

However, many trees survived in both Belterra and Fordlandia, and these now constitute a wonderful screening population for scientists who are looking for both high yields, and high levels of horizontal resistance to SALB, as well as resistance to other pests and diseases.

Rye

To the best of our knowledge, a European farmer, called Rimpau, who lived in Schlanstedt, was the first scientifically recorded person to employ recurrent mass selection for the purposes of crop improvement. He worked with rye, which is open-pollinated, and he started in 1866. At each harvest, he would collect the best looking heads and keep them for seed and, after twenty years, his rye was famous as the ‘Schlanstedt Rye‘, with long heads and kernels that were nearly double the size of the unimproved, local, rye landraces.

There are several points of interest in Rimpau’s work. First, because rye is open-pollinated, it is genetically flexible and genetically diverse. Consequently, it can respond to selection pressures during cultivation. In this regard, it is similar to the subsistence maize crops of tropical Africa (Chapter 20).

Second, Rimpau apparently made no effort to select his male parents. Had he conducted a negative screening, to eliminate all the worst plants that would later produce undesirable pollen, he would have had a more rapid genetic advance. As it was, his screening work took him twenty years.

Third, Rimpau's work was typical of plant breeding before the recognition of Mendel's laws of inheritance in 1900. Had Rimpau selected any single-gene characters, such as vertical resistances, he would not have recognised the fact. His Schlanstedt rye probably possessed a number of different vertical resistances, and it almost certainly had systems of locking against several different parasites. These systems of locking were probably not as effective as those in a well balanced, wild pathosystem, but they were undoubtedly superior to the monolock (Chapter 7) of modern agriculture.

It is also interesting that Rimpau was doing on-site selection. Had the Schlanstedt rye been grown in a markedly different agro-ecosystem, it would have performed less well.

Lastly, Rimpau's work, and his example, were largely forgotten when Mendel's laws of inheritance were finally recognised. He was quite definitely on the side of the biometricians. As a result, most modern crop scientists do not even know his name.

Tea

The tea crop is a vast hybrid swarm between the two species *Thea sinensis* and *Thea assamensis*. The variation in this hybrid swarm is so great that it is believed that no two tea bushes, grown from true seed, are identical. This means that tea crops grown from true seed are very variable, and that about 60% of the yield comes from perhaps 30% of the bushes. Furthermore, the plucked leaf has to be fermented in order to make black tea, and the fermentation times vary considerably between different tea bushes. With variable tea, it is inevitable that some of the leaf is over-fermented, and some is under-fermented. This uneven fermentation reduces the cup quality of the tea.

Tea is consequently a crop that cries out for the vegetative propagation of selected clones. However, vegetative propagation from cuttings became possible only with the relatively recent development of mist propagators (Chapter 25).

Tea clones are produced by selecting promising bushes within a variable tea crop grown from true seed. As with all plant selection work, the easiest tests are conducted first, when there are many plants to test, and the most difficult, laborious, and expensive tests are conducted last, when there are only a few remaining plants to test. It is estimated that about one million seedling tea bushes must be screened in order to obtain one really good clone.

The first test is a simple visual assessment, made by skilled people walking through the crop, and about one bush in a thousand is marked as being promising. More detailed, and more difficult, subsequent tests are for yield, cup quality, rooting ability, and resistance to pests and diseases.

For example, a major disease of tea in S.E. Asia is blister blight, caused by the microscopic fungus *Exobasidium vexans*. This disease is normally controlled by spraying with a fungicide, and some ingenious disease forecasting schemes have been worked out to let the tea growers know when to spray. It seems that no one has attempted to breed resistant tea, for the simple reason that no genetic source of resistance could be found. However, tea is derived from a continuous wild pathosystem (Chapter 6), and no gene-for-gene relationships occur. But there is wide variation in the susceptibility to blister blight, and the identification of resistant trees for the production of new clones would appear to be a logical development. However, such screening would have to conducted in unsprayed crops, and the misleading effects of parasite interference (Chapter 14) would have to be taken into account.

After many years of standard breeding work, designed to produce improved seedlings by the crossing of selected clones, the best seedling progenies were found to produce fifty percent more than unimproved seedling tea. But the best clones yield twice as much again, and their cup quality is greatly superior. This point is well illustrated by tea growing in East Africa.

Tea growing was started in Kenya in the 1920s. In those days, it was believed that tea could be grown only on a plantation scale, and the local small farmers were accordingly forbidden by law to grow tea. It was argued that their product would inevitably be inferior, and that this would damage the good name of Kenya tea. The big plantations, of course, were owned by British companies, and the fact that tea grown by native Kenyans would constitute competition was never mentioned. It was also argued that each plantation must have its own tea factory and that, for this reason alone, African small-holders could not grow tea.

In the 1960s, the Tea Research Institute in Kenya produced a remarkable new tea clone called ‘6/8’. Clone 6/8 was not much use to the big companies because all their land was already planted with seedling tea. Once planted, a tea crop is good for a hundred years or more, and replanting is very expensive. But this was the time of Kenya's independence, and the law forbidding native farmers from growing tea was repealed. African small-holders were then positively encouraged to grow tea, and many cooperatively owned tea factories were built to process their crops.

These small-holder tea crops consist mainly of clone 6/8, and today it is the small-holders who are producing the best yields of the best quality tea. Tea produced from clone 6/8 regularly wins top prices in the London market, and it is in great demand for blending with inferior teas.

Today, it is the big commercial plantations in Kenya, with their seedling tea, that are producing the inferior product, which is damaging the good name of Kenya tea. And it is the small-holders, the "peasants" who are producing some of the best tea in the world. This must surely rate as poetic justice of a rare and transparent quality.

Chapter 27

Farmer Participation Schemes

Introduction

The idea behind farmer participation schemes is that a central breeding station does the technical work, and then hands out promising seeds or clones to farmers for evaluation and selection. This concept started in the tropics, with subsistence farmers, but there is no apparent reason why it could not also be attempted with commercial farmers in the rich industrial countries.

Cassava

The concept of farmer participation schemes for plant breeding apparently started with cassava breeding in West Africa, and it was initiated by the International Institute for Tropical Agriculture (IITA) in Nigeria.

Cassava (*Manihot esculenta*) is a tall shrub that produces underground tubers. The leaves of many varieties also make an excellent pot herb. The crop is derived from a continuous wild plant pathosystem and, consequently, no vertical resistances occur

(Chapter 6). Cassava is normally propagated from stem cuttings, and this is probably the origin of the idea that, in the tropics, you have only to push a stick into the ground and it grows. Every cassava cultivar is thus a clone.

The scientists at IITA enlisted the help of small country schools in many agricultural areas of West Africa. They sent true seed, produced by crossing promising clones, to these schools. Cassava is highly heterozygous (Chapter 1), and every seedling is different from every other seedling. It was the school children who were taught how to break the seed dormancy by filing a nick in the tough seed coat. They then germinated the seeds and grew the seedlings, all as part of a school project. They transplanted the seedlings into the school garden and soon started doing various tests on each plant. The first tests involved cooking some leaves from each plant and deciding which tasted best. Each child could choose his own favourite, and take home a cutting to plant in his parents' farm or garden. Eventually, when the crop was mature, each plant was individually harvested and its tubers were weighed, and judged for quality. The children chose the best clones, and there were plenty of cuttings of these clones for them to take home.

This scheme had several obvious advantages. First, it was an excellent education. When these children grew up to have farms of their own, they would be very receptive to the idea of testing new cultivars, and to the idea of selecting the best plants within their own crops.

Second, the farmers got the cultivars that *they* liked best, rather than the cultivars that the scientists at a central breeding station liked best. Plant breeders should behave like sales clerks who believe that "the customer is always right". Their customers are the farmers, and it is logical to let farmers make the final decisions. Equally, farmers who sell their produce to the public will grow only those cultivars that *their* customers like best. This is an example of adaptation in a complex, self-organising system (Chapter 29).

Third, a huge number of seedlings can be screened with a level of care, and attention to detail, that the scientists could never manage on their own. The total number of seedlings screened is then greatly increased, and the accuracy of the screening is also increased. This means that the chances of obtaining really excellent cultivars are increased as well.

Fourth, the scheme can continue indefinitely, with each farm trying out several new clones each season. This means that the screening process can be extended indefinitely, with the better clones being retained the longest, and the less good clones being discarded. The clones which the farmers like best can also be used by the central breeding station for further breeding. The entire scheme will then be cumulative and progressive, in the sense that a good clone need never be replaced, except with a better clone. And the better clone would be better in all respects, including its resistance to all locally important parasites, its yield, the quality of its crop product, and its agronomic suitability.

Fifth, farmers are only people. They are likely to love and cherish their own selections far more than they would value a new cultivar given to them by a government agent, and selected by an anonymous scientist in a remote breeding station.

Sixth, cassava in West Africa suffers from two damaging diseases called mosaic and bacterial blight. Both the school children, and their parents, were warned that there would be great variation in the susceptibility of their new clones to these two diseases. They did not need to be told that the susceptible clones were not worth keeping. But they did need a warning that the susceptibility might not be revealed for a year or two. But they could grow badly diseased cassava close to their screening populations. In the long run, only those clones that were resistant to both diseases would be kept, and the diseases would no longer be important.

Finally, when each farmer selects his own clones, there will be very useful bio-diversity throughout the country, and probably within each farm as well. Besides being valuable in its own right, genetic diversity is a form of insurance. If a disaster were to strike, such as the accidental introduction of a new pest or disease, a widespread genetic uniformity can be very dangerous. Genetic diversity reduces these risks considerably. Ecologists are well aware that diversity is the basis of ecological stability and, apart from anything else, we do not have to be ecologists to know that variety is the spice of life.

Sweet Potato

The sweet potato (*Ipomea batatas*) must not be confused with the so-called Irish potato (*Solanum tuberosum*) described in Chapter 18. Sweet potatoes originated in South America, and they were spread throughout the tropics by three different routes. Polynesian sailors took sweet potatoes from the west coast of South America to Easter Island, Fiji, Hawaii, and New Zealand. They made this incredible journey long before the Europeans had developed ocean-going ships, and long before the discovery of the New World by the Spanish. In these Polynesian islands, the crop is known by its South American name ‘kumara’.

The Spanish took the crop from Mexico to the Philippines, some 350 years ago. In both countries, the crop is known by its Mexican name ‘camote’. At about the same time, the Portuguese took sweet potatoes from the West Indies to Africa, and to the countries of the Indian Ocean, including Indonesia and Papua New Guinea. In these areas this crop is known by its Caribbean name of ‘batatas’. The English word ‘potato’ is a corruption of this Caribbean name.

Sweet potato is a botanical relative of the popular ornamental ‘morning glory’, and both species belong to the family *Convolvulaceae*. Its harvestable product is a tuber which, as its name implies, contains appreciable quantities of sugar, as well as starch. Although the crop is propagated vegetatively, the plant readily forms true seeds which germinate freely. As a consequence, the total number of clones of sweet potato in the world is beyond counting, and the variation is enormous.

The Solomon Islands, in the Western Pacific, provide a useful illustration because it was here that I once proposed a farmer participation breeding scheme for sweet potatoes. To the best of my knowledge, my proposal was never implemented, but that is by the way.

Farmers in the Solomons have many different clones of sweet potato to choose from and, obviously, they tend to cultivate the ones they like best. All their clones are highly resistant to all the locally important parasites because, obviously, any clone that was susceptible would not be kept. Unfortunately, there is a group of obscure parasites that collectively cause a condition known as ‘decline’. Sweet potato clones, like their Irish potato counterparts, tend to accumulate virus diseases and other vegetatively transmitted parasites. As a result, their yields tend to decline and, eventually, they yield so poorly that they are abandoned. As fast as clones are abandoned, new ones appear that are generated from true seeds which were self-sown in farmers’ fields.

The average life of a sweet potato clone in the Solomons is some 10-15 years. But most farmers either have, or know of, one or two *old* clones. They are described as being old because they are at least as old as living memory. Their longevity is at least five times the longevity of the average clone, and they may well survive indefinitely. This can only mean that they are resistant to every one of the viruses and other tuber-borne parasites that cause the decline of the short-lived clones. The purpose of a farmer participation scheme, therefore, would be to produce many more clones with the capability of becoming ‘old clones’.

The proposed farmer participation scheme involved collecting famous old clones from all the islands in the Solomon group, and taking them to a central breeding station, probably in Guadalcanal. Here they would be crossed in all combinations, and large numbers of seedlings would be grown, and tested for resistance to the various, vegetatively transmitted parasites. This resistance might be determined by grafting with clones that had suffered a very severe decline. There would be a very high selection coefficient. That is, only a small proportion of the seedlings would be kept as potential new clones. These selections would be crudely tested for yield and quality, and the best of them would be handed out to participating farmers, at a rate of about new ten clones per farmer. Each farmer would be told that the clones were his property, and that he could do whatever he pleased with them. If he did not like them, he could destroy them. If there were a clone that he did like, it would be his to keep, propagate, and either give or sell it to his neighbours.

After an appropriate interval, of perhaps one or two years, a scientist would visit each participating farmer, and take a cutting from each of the clones that he had decided to keep. These cuttings would then be taken back to the central breeding station where they would be identified and further tested for resistance to various parasites that cause 'decline'. The most popular and the most resistant would then become the parents of the next generation of recurrent mass selection.

Any clone that proved to be inferior to existing clones would be discarded, with no harm done. Any new clone that was superior would be kept. This process would be repeated until a plateau was reached, and little further progress was possible.

Although the scheme is called a ‘farmer participation’ scheme, it does not necessarily involve the farmer himself. It would more likely involve members of his family. Farmers’ wives can be reached through women’s institutes, and farmers’ children can be reached through their schools.

The scheme has a number of advantages, and it could become a model for university clubs, or charitable clubs, operating in non-industrial, tropical countries. First, it is the subsistence farmers themselves, or their families, who do the actual selecting. They know what they like far better than any scientist. Second, the scheme is cheap, requiring a minimum of scientific activity and support. The scheme is also effective in the sense that it provides a very wide range of opportunities for success. It is also enduring, because it involves horizontal resistance, and it is comprehensive because it involves resistance to all the locally important parasites, including the problem of decline. The scheme is also cooperative, educational, progressive, and constructive.

Finally, in this discussion of sweet potatoes, mention should be made of Al Jones, of the United States Department of Agriculture, in Charleston, South Carolina, who is one of the pioneers of horizontal resistance breeding. In 1976, he published, with colleagues, a paper on breeding sweet potatoes, using recurrent mass selection. As we know now, the sweet potato is derived from a continuous wild pathosystem (Chapter 6) and, consequently, it does not possess any vertical resistances. Al Jones was dealing with quantitatively variable, polygenic, horizontal resistances. After about six generations of recurrent mass selection, he obtained good levels of resistance to several species of insect and fungal parasites, as well as considerable improvement in horticultural characteristics.

Al Jones was years ahead of his time and, to this day, only a few scientists have recognised, and appreciated, his originality. He is now retired but, sadly, he never did receive the recognition and rewards that his scientific creativity deserved. It seems that all his peers and superiors were strong partisans of the Mendelian school.

Chapter 28

Crops Best Avoided by Breeding Clubs

At this point, it should perhaps be mentioned that it is usually impossible to breed for resistance in senescent tissues to rotting organisms. These tissues include ripe fruit, and any other seasonal tissue that is approaching the end of its allotted span. In addition, there are a number of crop species in which breeding is extremely difficult for a variety of reasons.

Perhaps difficulties are relative. Until the late eighteenth century, all cloth was produced vary laboriously on hand looms. Although the work of spinning had been mechanised, it was believed that the work of weaving was far too complex to be done by machine. However, there was a clergyman, one Edmund Cartwright, who was rector of Goodby Marwood, near Melton Mowbray, in Leicestershire, England. He was one of those delightfully perverse characters who knew nothing of machinery, but who set out to build a power loom for the simple reason that he had been told it could not be done. He patented his immensely successful machine in 1786.

It is entirely possible that there are groups of equally perverse (and equally delightful) people who would like to form breeding clubs to breed one of the crops mentioned in this chapter. They would do this for the simple reason that they had been told it could not be done. I advise them not to. I *beg* them not to. But, if they go ahead anyway, nothing would give me greater pleasure than to be proved wrong. The least I can do is to point out the difficulties.

It is worth commenting also that there are only eight of these difficult crops listed below, and there are a few other obscure ones that I have not bothered to mention. By way of contrast, there are several hundred species of cultivated plants, and the great majority of them, including all the major food crops, are quite easy to breed for horizontal resistance.

Banana

The edible banana differs from its wild relatives in three important fundamentals. First, it is parthenocarpic. That it, it produces fruits without pollination, without sexual fertilisation. Second, it is sterile. It has both female and male sterility, in the sense that both ovules and pollen may be present but they are nonfunctional. However, a gametic sterility often occurs as well. This means that the ovules and pollen are never formed at all. Third, most banana cultivars are triploids. That is, they have three sets of chromosomes, rather than the usual two. This alone would make the breeding very difficult, even if bananas did set fertile seed.

Incredible though it may seem, banana breeding *is* possible, and the experts think that there is room for cautious optimism. But this is definitely a task for specialists.

Citrus

Citrus is unusual in that it produces nucellar seeds. An ordinary seed is produced by the fusion of a pollen cell with an ovule, and each of these sex cells contains a single set of chromosomes. The resulting seed thus has two sets of chromosomes, with one from each parent. These sexually produced seeds differ genetically among themselves.

A nucellar seed is produced asexually, from maternal tissue only, and it has two sets of chromosomes, both coming from the mother. Nucellar seeds are valuable because they do not differ genetically, either among themselves, or from their maternal parent.

This means, in effect, that a citrus clone can be produced with nucellar seedlings, but without all the diseases, particularly virus diseases, that are transmitted by grafts and cuttings, but which are not seed-transmitted.

Nucellar seeds can cause confusion because they can give an entirely false indication that a citrus cultivar is breeding true to type. They can also be a nuisance in a breeding progeny, because they have to be detected (they are all identical) and removed. In some citrus species, such as oranges, grapefruit, and mandarins, nucellar seedlings often dominate the breeding progeny almost entirely.

Otherwise, citrus breeding is rather like grape breeding (see below). There are usually plenty of fertile seeds, but the variation among true seeds is enormous, and it is difficult to find a new seedling that equals a modern cultivar, let alone surpasses it. Improvements in quality are thus likely to be difficult. However, like grapes, citrus has been plagued by new encounter parasites. A breeding program might be justified on the grounds of attempting to accumulate horizontal resistance in order to reduce or eliminate spraying with crop protection chemicals. But such a program will be difficult, and it is a task for specialists.

Garlic

How do you breed a crop whose wild progenitors are extinct, and which *never* sets seeds? The only possibilities are by mutations induced with mutagenic chemicals or radioactivity, or by genetic engineering. Definitely a task for specialists.

Ginger

Ginger rarely sets seed, and its wild progenitors are extinct. It thus resembles garlic in the difficulties it presents to the breeder.

Grapes

Most grape varieties set seed profusely, and breeding grapes is theoretically a straightforward process. Nevertheless, to produce a wine grape superior to the *Cabernet Sauvignon* of Bordeaux, or the *Pinot Noir* of Burgundy, is possibly the most difficult plant breeding task in the whole world. Undoubtedly, much of the quality of wine depends on post-harvest processes such as fermenting, bottling, and storage. But it is impossible to produce a good wine from bad grapes. And it is equally impossible to envisage wines superior to the best clarets and burgundies. The only remotely realistic possibility would be to replace *Cabernet Sauvignon* or *Pinot Noir* with new varieties of *equal* quality, but with high levels of horizontal resistance to the various new encounter parasites so that the need for chemical pesticides is reduced or eliminated. But the difficulties are enormous.

The chances of breeding a new white wine grape may be slightly better, but only slightly. The chances of breeding a new table grape are better yet, but are still remote. There are, after all, many excellent varieties of table grapes, and it will be difficult to compete with existing varieties. Once again, the most realistic objective would be to produce new varieties with equal fruit quality but superior horizontal resistance.

Another possibility in grape breeding is to produce a wine grape rootstock that is highly resistant to *Phylloxera* but which does not depress the yield of grapes (Chapter 13).

Olives

Every olive contains a seed and, in theory, there are no inherent difficulties in olive breeding. In modern research, trees grown from true seed have never equalled existing cultivars. It must be admitted that this possibility has not been adequately tested, however. But there are difficult logistic problems associated with the screening of *trees* by the tens or hundreds of thousands. If breeding were to be attempted, the most important selection criteria, other than horizontal resistance, would be new characters that would permit mechanical harvesting, involving dehiscing fruits that are easily shaken off by a shaking machine, and fruits that all ripen at the same time.

Pineapple

The two most important crops in Hawaii are sugarcane and pineapple. The breeders in Hawaii have been breeding these two crops for decades, the sugarcane with immense success, and the pineapples with little or no success at all. This is partly because pineapples require four years from seed to fruiting, and the vegetative propagation of a successful new seedling is slow. Furthermore, unlike the cane breeders in Hawaii (Chapter 22), the pineapple breeders have been using Mendelian breeding methods. Wild pineapples have continuous pathosystems and, consequently, no single-gene resistances can be expected (Chapter 6). To be fair to the Mendelians, recurrent mass selection is unlikely to be any faster, but it may be more successful.

Turmeric

Turmeric is a triploid (see banana, above) which is sterile, and it does not set fruit. Its wild progenitors are extinct. It compares with garlic in that its breeding verges on the impossible.

Chapter 29

The Future

If our grandfathers had attempted to foretell the future, when they were young men, they could not have anticipated computers, space travel, antibiotics, quartz watches, television, ball-point pens, or atomic energy. Equally, when we ourselves attempt to discuss future events, we cannot take into account all those things that will be new several decades after we are dead. The most we can do is to acknowledge this impotence, and to recognise that our predictions must be seriously flawed because of it. However, this said, it is still useful to examine current trends, and envisage their further development.

There seems to be little doubt that the most important problem facing the world is the question of human population growth. Even now, our population is too large. Currently, we can feed it only at the expense of environmental pollution with crop protection chemicals. There are other, even more important kinds of pollution that are now excessive, and that threaten our over-crowded environment. The public is well aware of them, and they include greenhouse gasses, sewage, garbage, smog, acid rain, CFC's, agricultural nitrates, and the industrial pollution of the atmosphere, lakes and rivers.

Although humankind is a K-strategist species, we are now undergoing a population explosion. This positive population growth (Chapter 14) must stop. Indeed, we could do with some negative population growth, with one-child families, until such time as our environment is comfortable again. Let us make no mistake about it. Over-crowding kills. And if we do not control our population growth, our descendants will eventually die of starvation, if they do not die of environmental poisoning.

So, birth control is the most important problem facing our species. Our vastly improved medical services, and our greatly enhanced life expectancy, must be balanced by a reduced birth rate. The so-called pro-life, anti-abortionists must appreciate that the loss of an insensate foetus, although deplorable, is greatly preferable to the loss of a highly sensate child, or adult, possibly by starvation. Death by starvation, following, perhaps, a short lifetime of total poverty, misery, and malnutrition, is a horrible way to die. It might be added that it is also a horrible way to live.

Even abortion should become unnecessary. Methods of contraception have been improving very rapidly during the past century, and one of the safer prognoses is that they will continue to improve. We can predict fairly confidently that our positive population growth will stop, and may even become negative, until such time as every human individual can live in peace, safety, and prosperity.

A second prediction that is probably quite dependable, is that food production will increase very considerably. However, the main increases will not come from agriculture. There have been some impressive improvements in agricultural productivity during the past century and a half, but we are now probably reaching the limits of this improvement. We must recognise that, in total, agriculture has increased the human carrying capacity of the environment by several hundred-fold. We must recognise also that this system of planting seeds over vast acreages of soil is a ludicrously inefficient method of producing food. Of all the solar energy that falls on to agricultural land, only about 0.1% is actually ingested by people as dietary calories.

A plausible prediction is that our food production efficiency will be increased by a form of microbiological farming in fermentation tanks in factories. There are two kinds of fermentation by micro-organisms. Destructive fermentation occurs when micro-organisms break down chemical compounds into less complex compounds. Thus yeast will break down sugars, to produce alcohol and carbon dioxide, in wine and beer. Constructive fermentation occurs when micro-organisms build simple compounds into more complex compounds. Thus, the fungus *Penicillium* can be cultured in fermentation tanks to produce the antibiotic penicillin from simple nutrients.

With the very new techniques of genetic engineering, it will become possible to produce modified micro-organisms that make entirely new kinds of constructive fermentation possible. The first of these are already being utilised , and they produce complex pharmaceuticals, because these are the only products that will bear the very high costs of this kind of research.

However, as research proceeds, and costs come down, it will become feasible to manufacture more mundane substances economically. For example, simple petrochemicals and water can be built up into carbohydrates such as sugars. These carbohydrates can then be further built up into starch and vegetable oils. Such foods would be very pure, and indistinguishable from the more traditional plant products. There is no apparent reason why genetically engineered micro-organisms should not produce proteins also, replacing the products of the many species of peas and beans.

Consider a factory occupying one acre of land, and producing two thousand tons of starch each year. This factory would replace about one thousand acres of North American wheat cultivation, or about five hundred acres of maize cultivation. If the factory was producing two thousands tons of sucrose, it would replace about two hundred acres of sugarcane cultivation, or about four hundred acres of sugar beet cultivation. These figures are inevitably vague because crop yields vary widely in different parts of the world. But they indicate some very real possibilities. Food production could increase by 100-1000 times. This is an increase comparable to the total change that occurred as the human species slowly changed from hunter-gathering to modern agriculture.

Large factories built on otherwise unusable land, such as deserts or tundra, would release huge areas of farm land for other purposes. For example, if much of this liberated land were planted to forests, the problem of the greenhouse effect from carbon dioxide would be ameliorated, because trees remove large quantities of this gas from the atmosphere. The problem of the world shortage of timber would also be solved. It need hardly be added that many species of food crop would no longer be cultivated. The need to *breed* such crops would cease, and much of this book would become redundant.

So, how realistic are these ideas, and how do they affect plans that people may have to form plant breeding clubs? The widespread replacement of farming with fermentation factories may never happen. If it does happen, it is unlikely to happen in less than thirty years, maybe even fifty years. During this time, pesticide pollution would continue, and probably increase. There will also be a critical few decades in which world food supplies are likely to be dangerously limiting. On these grounds alone, breeding clubs would be more than justified. However, there are other reasons. We saw in Chapter 10 that modern plant breeding is stuck in a blind alley, apparently unable to back out. But it must back out. Soon. And breeding clubs are the most important single stimulus that will invigorate the somewhat conservative and, indeed, apathetic science of plant breeding that is now stuck in the *cul-de-sac* of Mendelian breeding methods and vertical resistances.

The genetic engineering that transfers foreign genes into crop plants is already happening, and it is a shorter-term, but less realistic threat to the integrity of this book. It is less realistic because this approach has some severe limitations. In particular, it is only feasible to transfer one gene or, at most, a few genes at a time. This means two things. First, most species of crop have many parasites, and different species of parasite will probably require different genes. Transferring a number of genes, for resistance against many parasites, into one cultivar could be a lengthy procedure. Furthermore, if too many genes are transferred, there is a very real risk of changing the crop plant to the point that its usefulness is gravely impaired.

Much more serious, however, is the possibility that these genetically engineered resistances will be *within* the capacity for micro-evolutionary change of the parasites. Such changes would mean that the parasites could produce new strains that were unaffected by the gene in question. This would correspond to the breakdown of vertical resistance, or the loss of the effectiveness of DDT against houseflies and malarial mosquitoes.

The difference between micro-evolution and macro-evolution should perhaps be explained. Macro-evolution (or Darwinian evolution) operates over periods of geological time (i.e., millions of years), and it involves genetic changes that are both new, and irreversible. Micro-evolution differs in that it operates over periods of historical time, and it involves genetic changes that are not new, and that are reversible. In other words, macro-evolution produces new species, while micro-evolution produces new ecotypes.

There are very strict limits to the capacity for micro-evolutionary change of plant parasites. Some factors are *within* that capacity for change, while others are *beyond* it.

Factors that are within the capacity for micro-evolutionary change of a species are those that require relatively simple changes. Let us consider one of the ways in which malarial mosquitoes became resistant to DDT. After a mosquito has bitten someone, it flies to the nearest vertical surface, usually a wall or a window, and it then rests while it starts to digest its meal of blood. Malaria was dramatically controlled, throughout the tropics and subtropics, by spraying the vertical surfaces inside houses with DDT. While resting, a mosquito would absorb a lethal dose of this insecticide, and it would die before it had a chance of biting someone else, and transferring malaria to that second person.

There is now a new strain of mosquitoes, produced by micro-evolution, that do not rest after biting. They fly right out of the house and keep going a fair distance before resting. The chances are that their distant resting surface has no DDT, and they then survive. So, DDT on house walls is an insecticide that is *within* the capacity for micro-evolutionary change of these pests.

There are many other ways in which the parasite can change in order to defeat a pesticide. Very often, the parasite develops a simple enzyme that de-activates the active ingredient in the pesticide. These changes are all within the capacity for micro-evolution of the parasite.

Many other protection mechanisms are within the capacity for micro-evolutionary change of parasites. It is well known, for example, that bacteria which are pathogenic in people can develop resistance to antibiotics. Equally, vertical resistance mechanisms in plants are within the capacity for micro-evolutionary change of plant parasites.

Other protection mechanisms, however, are *beyond* the capacity for micro-evolutionary change of the parasite. Bordeaux mixture is beyond the capacity for micro-evolutionary change of the fungi that cause potato blight and grape downy mildew. There has not been the slightest suggestion of its effectiveness breaking down during more than a century of use since its discovery. Rotenone, which is extracted from derris roots, is beyond the capacity for micro-evolutionary change of insects. This has been demonstrated by centuries, perhaps millennia, of use against human lice in S.E. Asia. And natural pyrethrins, extracted from pyrethrum flowers, are also beyond the capacity for micro-evolutionary change of insects. People in Dalmatia have apparently used wild pyrethrum flowers in their bedding, to control fleas and bed bugs, for the whole of recorded history. (In Britain, dried and ground up pyrethrum flowers used to be sold under the name of Keating's Powder. But this was before the days of DDT.)

A single vertical resistance, used on a basis of genetic uniformity, is *within* the capacity for micro-evolutionary change of parasites, while horizontal resistance is *beyond* the capacity for micro-evolutionary change of parasites. This is why vertical resistances fail, but horizontal resistances do not. In the most simple terms, the difference seems to be a question of complexity. Simple changes are easy, while complex changes are difficult, even impossible. For this reason, simple protection mechanisms, whether resulting from natural resistances, or artificially manufactured crop protection chemicals, are likely to be within the capacity for change of parasites, while complex ones are likely to be beyond that capacity.

Horizontal resistance is complex. It involves many polygenes, controlling many different resistance mechanisms. It is consequently durable. But the protection mechanisms that are put into cultivars by genetic engineering are simple. They cannot be anything else when their inheritance is controlled by only one, or a very few, genes. It is entirely possible and, indeed, likely, that they will be within the capacity for micro-evolutionary change of the parasites, and that they will fail.

Perhaps plant breeders' clubs working with horizontal resistance may not be such a bad idea after all.

Reader's Note

The original edition of this book ended with a glossary of 250 definitions. This glossary has now been expanded to 1750 terms and Latin names, and all cross-references are linked by hypertext. It is called *The Amateur Plant Breeder's Handbook* and it is available for download as shareware at www.sharebooks.ca.

The original edition also had an index. However, a manual index is considered superfluous in an e-book because of the 'search' function available in all word processors.