The Amateur Potato Breeder's Manual

Raoul A. Robinson

Reader's note

When finalised, this manual will be profusely illustrated with colour photographs. One of the advantages of e-books is that colour illustration is not prohibitively expensive, as it would be with printed books. However, much of the biological material required for these photographs was unavailable at the time of this first publication. It was thought preferable to publish the text as it is, adding the photographs later, than to delay publication until all the pictures were ready.

Introduction

In France, in 1882, there was a discovery so dramatic that crop scientists have been looking for comparable successes ever since. This discovery was the first fungicide, called Bordeaux mixture, which saved the French wine industry from absolute ruin, and also provided a complete protection of the potato crop from blight. Twelve years later, Mendel's laws of inheritance were recognised, and they were a major scientific breakthrough. They converted plant breeders from many-gene to single-gene breeding techniques. Forty years later still, DDT was discovered, and this discovery was as dramatic as that of Bordeaux mixture. This insecticide provided a complete control of the Colorado potato beetle, as well as many other insect pests.

These discoveries were collectively responsible for an inappropriate approach to potato breeding during the past 120 years, and this has led to a severe vertifolia effect. As a consequence, most modern cultivars of potato are very susceptible to many species of parasite. (Insect parasites are usually called *pests*, and most other parasites are called *pathogens*, which cause *diseases*). This is why potato cultivation is now so expensive, requiring costly seed tubers certified free from tuber-borne diseases, and repeated, expensive, and dangerous spraying with insecticides and fungicides. This situation can be remedied, and this remedy is most likely to be achieved by amateur breeders who are unaffected by a mindset that developed within crop science, following the discoveries of Bordeaux mixture, Mendel's laws of inheritance, and DDT.

Farmers have been breeding crops for some 9,000 years using mainly *quantitative* assessments (i.e., differences in degree) of yield, quality, and pest and disease resistance. The effect of the new scientific discoveries was to convert many crop scientists to *qualitative* (i.e., differences in kind) assessments of these parameters. This has proved a tragic mistake. Readers wanting to know more about this topic should see *Return to Resistance* (available as a free download at www.sharebooks.ca).

Why Amateurs?

One hundred years of advertising by the seed potato industry have convinced farmers that they should buy new seed tubers for every potato crop. This is in order to control tuber-borne diseases, and particularly virus diseases. And a comparable period of advertising by the chemical industry has convinced farmers, to say nothing of crop scientists, that the best way to control potato pests and diseases is to spray every potato crop, repeatedly, with various crop protection chemicals.

It is in the interests of both these industries that modern potato cultivars should be susceptible, so that farmers *need* certified seed, and they *need* crop protection chemicals. I do not suggest a conspiracy. Things just happened to develop this way. But, neither of these industries is keen to change. With sufficiently resistant cultivars, however, farmers should need neither certified seed, nor crop protection chemicals, and this level of resistance should be the broad objective of amateur potato breeders.

Many of the big chemical corporations have been buying up seed companies. They have also been buying up plant breeding institutes. These take-overs, which have nothing to do with chemical manufacture, will give them an almost monopolistic control of the cultivars available to farmers. And the best way to guarantee their market for crop protection chemicals is to ensure that these cultivars are susceptible, and that they can be cultivated only under the shield of both certified seed and crop protection chemicals.

The best way for crop scientists to combat these commercial trends is to breed crops for horizontal resistance. By and large, they have not done so, and they show few signs of doing so. There is a sad mindset within crop science that rejects the use of horizontal resistance. And, if the scientists refuse to investigate horizontal resistance, and they are backed up by chemical corporations who oppose its use, the only remaining possibility is for the public at large to undertake this task by forming plant breeding clubs. And, once started, and successful, there will be no stopping this trend.

The people most likely to be interested in potato breeding clubs are the organic farmers, as well as anyone who is worried about the high cost of potatoes, and their contamination with both pesticides and genetic engineering.

Anyone who thinks that amateur breeders cannot achieve these objectives should consider the success that amateurs have had in breeding marijuana. Motivation is the prime incentive.

Plant Breeding Clubs

An individual can easily go it alone, particularly if he (or she) is a small farmer or market gardener. And the rewards for a successful cultivar can be huge (see royalties). However, a group of like-minded individuals who organise themselves into a plant breeding club will have many benefits, because they can share their enthusiasm, their knowledge, their work, their costs, their sense of achievement, and their royalties. Possibly the most effective club is the university breeding club, operated by students under the supervision of a professor. An amateur breeding club may wish to associate itself with a university breeding club, for their mutual cooperation and benefit. More information on plant breeding clubs is provided in *Return to Resistance* (available as a free download at www.sharebooks.ca).

If there were 100 potato breeding clubs in the world, each screening 100,000 true seedlings a year, there would be a total of 10 million seedlings being screened annually. After one or two decades of cumulative breeding, there would be:

- A virtual elimination of potato parasites, worldwide,
- A virtual elimination of the need for crop protection chemicals in potato crops, worldwide,
- An elimination of the recurrent need for expensive certified seed, and
- Several near-perfect, but different, potato cultivars for each agro-ecosystem.

There seems to be little doubt that these targets can be achieved with horizontal resistance, and this is a possibility that clearly merits investigation.

University Breeding Clubs

Most universities have photography clubs, chess clubs, and many others. So there is no reason why they should not have plant breeding clubs also. Some agricultural universities may care to convert their breeding clubs into official teaching courses. The students would do all the work of plant breeding, for a full breeding cycle, and this would earn them course credits. The professor in charge would earn teaching credits. Graduates would be given life membership in their clubs and they could both benefit from new club cultivars, and they might contribute breeding material of their own. Graduates would also be encouraged to start amateur breeding clubs in their place of work. University clubs might also link to amateur clubs, or even secondary school clubs, to their mutual benefit.

The Need for Diversity

It is a fundamental principle of ecology that diversity leads to stability. Conversely, uniformity leads to instability. Consider the uniformity of a huge area of wheat, all with the same vertical resistance. The failure of that resistance to a new race of a parasite represents a major instability.

One of the advantages of having many plant breeding clubs, each producing new cultivars for its own agro-ecosystem, is that there would also be a great diversity of cultivars, and a great stability of agricultural production.

The Potato Plant

The modern, cultivated potato (*Solanum tuberosum*) is a tetraploid. That is, it has four sets of chromosomes, instead of the usual two sets that occur in the more normal diploid plants. This means that the cultivated potato cannot easily be crossed with many wild potatoes, which are mostly diploids. Consequently, amateur breeders should not attempt inter-specific crosses. All their potato breeding should be conducted within the cultivated species, but this is not a serious limitation because this species exhibits immense genetic variation.

The potato tuber is the swollen end of an underground stem called a stolon. The number, shape, and size of the tubers of one plant are variable, but the variation between cultivars is even greater.

Potatoes are propagated vegetatively, as clones, using ‘seed’ tubers. Except for an occasional mutation, or ‘sport’, clones do not exhibit genetic variation. This is a considerable advantage for both breeders and farmers, as a true seedling can be immediately stabilised genetically, simply by producing a clone.

Potatoes produce flowers that can be either self-pollinated, or cross-pollinated, to produce fruits and true seed. This true seed exhibits great variation, and it is the basis of potato breeding.

Stable and Unstable Protection

Any mechanism that protects a plant from its parasites is either stable or unstable. A stable mechanism is unaffected by genetic changes in the parasite. An unstable mechanism is liable to stop functioning when the parasite produces a new strain that is immune to that mechanism. DDT-resistant houseflies and mosquitoes are a classic example of an unstable protection.

Stable insecticides include natural pyrethrins and rotenones, soft soap, and oil films on water that kill mosquito larvae. These insecticides never break down to new strains of the parasite. Stable fungicides include those made from copper and the dithiocarbamates. Most modern synthetic crop protection chemicals are unstable, and they stop functioning when new strains of the parasite appear.

This distinction between stable and unstable also applies to host resistance to parasites. Stable resistance, which is *beyond* the capacity for genetic change of the parasite, is called horizontal resistance. And unstable resistance, which is *within* the capacity for genetic change of the parasite, is called vertical resistance.

Horizontal Resistance

Horizontal resistance is stable resistance. It is durable resistance. It will never break down to new strains of the parasite. Justification for this contention will be found in *Return to Resistance* (available as a free download at www.sharebooks.ca).

The inheritance of horizontal resistance is controlled by many genes of small effect. These genes are called polygenes. The inheritance of horizontal resistance is thus quantitative. That is, it can be inherited with any degree of difference between a maximum and a minimum.

The effects of horizontal resistance are also quantitative. That is, the resistance may be exhibited at any level between a maximum and a minimum. In the absence of crop protection chemicals, the minimum level of horizontal resistance normally results in a total loss of crop, while the maximum level results in a negligible loss of crop.

Horizontal resistance to one species of parasite does not normally confer resistance to other species of parasite. When breeding for horizontal resistance, it is necessary to accumulate high levels of resistance to each locally important species of parasite. The accumulation of all these resistances must be done more or less simultaneously. This is quite easy to do, and the way to do it is explained under recurrent mass selection.

The mechanisms of horizontal resistance are many, and they are mostly obscure. (For example, horizontal resistance to potato blight leads to a reduced rate of infection, a reduced rate of colonisation, a reduced sporulating zone, with fewer sporophores per unit area of sporulating zone, and fewer spores per sporophore). For the amateur breeder, these mechanisms are unimportant. All that matters is that the level of resistance is increased, and the level of parasitism is reduced.

Because horizontal resistance is quantitative and durable, breeding for this kind of resistance is cumulative and progressive.

That is, a good horizontally resistant cultivar need never be replaced, except with a better cultivar. This progression of better and better cultivars can continue, with diminishing returns, until a final limit to improvement is reached.

Vertical Resistance

Vertical resistance is single-gene resistance, and it was the resistance of choice among professional plant breeders for most of the twentieth century. It has the advantages of conferring a complete protection, and of functioning over a wide geographic area. It has two grave disadvantages, however. It is liable to break down to new strains of the parasite, and it is thus unstable, or temporary, resistance. And it does not occur against many species of potato parasite.

Vertical resistance can be a nuisance when breeding for horizontal resistance, because the vertical resistance masks the effects of the horizontal resistance entirely. If this problem is serious, the one-pathotype technique should be used. Alternatively, only parents known to lack these vertical resistances should be used in the breeding program.

In general, this is not a difficult problem in potato breeding because vertical resistances are relatively rare. They occur against blight, but the A2 mating type effectively eliminates this problem.

Vertical resistances also occur against wart disease (*Synchytrium endobioticum*) and golden nematode (*Globodera rostochiensis*), which are absent from most potato-growing areas. They also occur against some of the temperate viruses.

These vertical resistances function by means of a mechanism called hypersensitivity. When the microscopic pathogen penetrates a cell, all the surrounding cells react with extreme sensitivity, and they die. The pathogen cannot survive in dead cells and it dies with them. This hypersensitive reaction produces a brown, necrotic 'fleck' that is just visible to the naked eye.

No Good Source of Resistance

When breeding for vertical resistance, you must first find a good source of resistance. This has become a shibboleth among plant breeders, to the point that they generally believe also that you cannot breed for horizontal resistance without first finding a good source of resistance. This misconception is very important. Breeding for a single-gene resistance must start with that single gene (the 'good source') and, without it, the breeding cannot even begin.

But this is *not* true of horizontal resistance, which is polygenically controlled. Start your horizontal resistance breeding with a group of parents that are susceptible, modern cultivars. All that matters is that a reasonably wide genetic base is used. All the polygenes will be present in the breeding population as a whole, even if they occur at too low a frequency in each individual. The breeding technique will increase the polygene frequency using recurrent mass selection and transgressive segregation.

In general terms, it is much easier to increase the levels of horizontal resistance to various locally important parasites, than it is increase other variables, such as the yield and the quality of crop product. For this reason, it is better to start with modern cultivars that have high yields and quality, but low resistance, than it is to start with primitive cultivars, or even wild progenitors, that have high resistances but low yields and quality.

The Vertifolia Effect

The 'vertifolia effect' is a loss of horizontal resistance that occurs when the plant breeding is conducted either in the presence of a functioning vertical resistance, or under the protection of a fungicide or insecticide. It happens because the level of horizontal resistance can be assessed only by the level of parasitism, and this is possible only if the parasitism is present and active. Individual plants with a relatively high level of horizontal resistance are in a minority. If the level of resistance is invisible because there is no parasitism at all, susceptible individuals, which are in the majority, stand a better chance of being selected on the basis of their other attributes.

This loss of horizontal resistance to potato blight began soon after the discovery of the first fungicide, called Bordeaux mixture, in 1882. This fungicide made the breeding much easier because so many seedlings were no longer being killed by blight. The gradual loss of resistance was not recognised at the time and, even if it had been, no one would have cared, because it was believed that resistance was not necessary, as the crops could now be sprayed with Bordeaux mixture. All potato cultivars bred after about 1885 were increasingly susceptible. At about this time, in North America, farmers began to spray against Colorado beetle. The only insecticides they had were very nasty compounds of lead, arsenic, cyanide, and mercury. Later, with the use of vertical resistance, the vertifolia effect continued. And then DDT was discovered, as well as many other synthetic insecticides and fungicides. Because of the vertifolia effect, which has now been operating for a century or more, modern cultivars of potato have less horizontal resistance than the cultivars of 1880. Our task is to ensure that they have much more horizontal resistance than those old varieties.

The Breeding Cycle

A plant breeding cycle would be called a ‘generation’ in people or animals. A plant breeding cycle begins with pollination, and the subsequent production of true seed. It ends when the next pollination occurs among selected plants that become the parents of the next breeding cycle. Most breeding programs require some 10-15 breeding cycles. In the temperate regions, there will normally be one breeding cycle each year but, with potatoes, it may be possible to complete two breeding cycles each year (see 180-day breeding cycle).

Transgressive Segregation

This term means that progeny may have a higher level of an inherited, quantitative variable than either of their parents. Breeding for horizontal resistance depends very heavily on this phenomenon.

Suppose there is a population of wild potatoes in which every individual plant possesses only 10% of the polygenes contributing to horizontal resistance. The population as a whole will be highly susceptible, and so will every individual within that population. But suppose also the every individual possesses a different combination polygenes in its 10% share. This means that all the polygenes are present in the population, but no individual possesses enough of them to be resistant. With random cross-pollination, some of the progeny will have more than 10% of those polygenes (and others will have less). And, given adequate selection pressures, this percentage will increase with each successive generation. After enough generations of cross-pollination, there will be progenies that have most, possibly all, of the polygenes. These individuals will be highly resistant. And their resistance will be durable.

This breeding process of artificially increasing a variable character by transgressive segregation is called recurrent mass selection.

Recurrent Mass Selection

The main feature of recurrent mass selection is that it deals with *quantitative* variables, such as horizontal resistances. And it raises the level of many desired variables simultaneously, including all the horizontal resistances to all the locally important parasites.

The method of recurrent mass selection is to grow a large screening population of seedlings which all genetically different. The best 10-20 individuals in that population are selected, and they become the parents of the next screening generation. Each generation (or breeding cycle) exhibits transgressive segregation, and the desired variables increase accordingly. This increase is usually 10-20% in the early breeding cycles, and the rate of increase gradually declines until no further progress is possible. This ‘ceiling’ is normally reached after 10-15 breeding cycles and, with horizontal resistances, it should provide a complete control of all locally important parasites without any use of crop protection chemicals.

Selection Pressures

The term ‘selection pressure’ is used in the sense of bringing pressure to bear, and it applies to variable populations. For example, if a heterogeneous population of potato seedlings is exposed to a parasite such as blight, the most susceptible individuals will be killed, and the least susceptible individuals will survive, and they will reproduce the most. As a consequence, the next generation will be more resistant.

The selection pressure is exerted by the blight fungus, and this can happen in both a wild population, and the screening population of a breeding program.

Screening in the Tropics

There are no winters in the tropics and breeding can continue throughout the year, particularly if irrigation is available during the dry season. When I was breeding potatoes in Nairobi, Kenya, in the 1960s, I sowed 1000 pre-germinated seeds every working day. At about six weeks of age, these were exposed to blight and bacterial wilt (a tuber-borne disease), and the few survivors were transplanted in the field. The selected parents of the next breeding cycle were grafted on to tomatoes. There were two breeding cycles of recurrent mass selection each year, with some 150,000 seedlings per cycle. This work produced two new cultivars called *Kenya Akiba* and *Kenya Baraka,* which have now been cultivated for about 65 vegetative generations without any renewal of seed stocks, and without any spraying against blight (there are two crops each year in Kenya, and Colorado beetle is absent from this part of the world). According to the Food & Agricultural Organisation of the United Nations, potato production in Kenya has increased 35 times since these cultivars were released to farmers in 1972. Two older cultivars, *Rosslyn Eburu* and *Dutch Robijn*, also have fairly good horizontal resistance to blight and they are still being cultivated.

These Kenya cultivars are short-day plants which cannot be cultivated in the temperate regions, and which should not be used a parents in a temperate region breeding program. However, they would be useful in a tropical breeding program. At present, tropical potato cultivation is confined to the cool, relatively dry, high altitude areas. But there is no reason why attempts should not be made to breed cultivars for the warmer and wetter areas. Note that day-neutral cultivars from temperate countries can be grown in the tropics, and they can be used as parents in a breeding program. Unless stated otherwise, all further discussion concerns potatoes in the temperate regions, but it is generally relevant to the tropics also.

After blight, the most important tropical disease of potatoes is bacterial wilt caused by *Pseudomonas solanacearum*. This is a tuber-borne disease and horizontal resistance to it is important if potatoes are to become an important crop in the country concerned. Colorado beetle has not reached the tropics, and the most serious tropical insect pest is the potato tuber moth.

Choosing the Parents

The breeding should begin with 10-20 parents, and each parent should be a popular modern cultivar. In choosing the parents, the aim is to have as wide a genetic base as possible, while maintaining high standards of yield and quality. There is no need to choose parents on the basis of their resistance to parasites, because a reasonably wide genetic base will accumulate all the horizontal resistance we need by transgressive segregation. If it does not, the genetic base can always be widened later.

Because of possible problems in flower production, or with pollen sterility, it is advisable to use a few more parents than are needed, so that some can be discarded if they prove difficult to cross. Alternatively, new parents can be added to the breeding population at a later date.

Neo-tuberosum

N.W. Simmonds (see Recommended Reading) did an interesting experiment in Scotland. He wanted to prove that *Solanum tuberosum* was derived from the South American species *Solanum andigena*. He also wanted to show that horizontal resistance to blight could be accumulated in the very susceptible *S. andigena*. He proved both these points by recurrent mass selection, and he produced a new kind of potato which he called *neo-tuberosum*. This new potato is closely similar to cultivated potatoes, and it has a useful level of horizontal resistance to blight. It has been used in commercial potato breeding, and these new clones would be useful parents for amateur breeders, particularly if they were trying to widen the genetic base.

Grafting

Recurrent mass selection requires very large numbers of seedlings, almost without limit. Grafting potato scions on to tomato rootstocks is a technique for producing very large numbers of true seeds of potato.

Selected potato scions can be grafted on to tomato rootstocks to induce flowering. Being unable to form tubers, the potato scion grows upwards as a vine, with a bunch of flowers every few inches. These flowers can be used for controlled cross-pollination. One good graft can produce up to fifty fruits, with up to 300 seeds per fruit, totalling some 15,000 true seeds.

There are several steps in this grafting.

Grow one tomato plant in each pot so that it is about six weeks old when the grafting is to take place. Each pot should be fairly large (about 12 inch diameter) to avoid any need for re-potting later.

With a new razor blade, cut off the tomato stem with a horizontal cut, about 1½ inches above the first two leaves (photo in preparation). Then make a vertical cut down the centre of the stem to a depth of about one inch (photo in preparation).

Cut a vegetative shoot off the potato parent, several inches long (photo in preparation). Place it in water and take it immediately to the grafting house. Cut off a terminal shoot about one inch long (photo in preparation) for use as a potato scion. Slice the sides of the scion to make a wedge (photo in preparation).

Insert the wedge into the vertical cut in the tomato stem (photo in preparation).

Wrap the graft union in a ribbon of very thin, transparent, plastic film (photo in preparation). This ribbon serves two purposes. It binds the graft-union surfaces together, and it prevents the union from drying out. It should be fairly tight, but not too tight.

Place the entire pot inside a mist propagator for about five days, or until the potato scion shows signs of active growth (photo in preparation). Alternatively, put three sticks in the pot, and cover the entire pot with a plastic bag that is tied to the top of the pot, in order to maintain a high humidity (photo in preparation).

The two tomato axillary buds may start growing. If they do, cut them off. The tomato leaves should be removed later, when they show signs of senescence. The ribbon of plastic film may be removed soon after the scion starts growing and the graft union is well calloused over.

Place the pot in a greenhouse with a supporting string hanging from the roof. The potato vine may grow to a height of several feet. A few, small aerial tubers may form, and they should be removed.

There should be two grafts of each potato parent, mainly as an insurance in case one graft is lost for any reason. With 10-20 parents, there will be 20-40 grafts. With practice, cross-pollination among this many plants should not require more than 1-2 person-hours of work each day.

Tomato rootstocks are useful because we know that they graft easily and well. However, they have the disadvantage that they can get blight (*Phytophthora infestans*) and, if they do, the entire graft is in grave danger of being lost. There is also a risk of blight attacking the potato scion, particularly in the early breeding cycles. There are two ways of avoiding blight on both the stock and the scion. One is to spray them with a copper or dithiocarbamate fungicide. An alternative is to water the plants from the base of the pots, and to keep both the scion and the above-ground stock dry at all times. This is easily achieved in a greenhouse. Blight spores need free water to germinate and, if all the aerial parts of the grafted plant never get wet, they will not get blight. For complete safety, both methods may be used.

Some useful research, that can easily be undertaken by amateur breeders, would involve a search for alternative rootstocks that are immune to blight. Possible species include the common weed called 'thorn-apple' (*Datura stramonium*); wild species of *Solanum*, such as *S. nigrum* and *S. dulcamara* in Europe, or *S. rostratum*, known as prickly potato, or the buffalo burr, in North

America; eggplant (*Solanum melongena*); and tobacco (*Nicotiana tabacum*).

Flower Production

The potato scion will start producing flowers quite soon after grafting. Each inflorescence usually has 5-10 flowers, and they normally open one or two at a time each day (photo in preparation).

In a few potato cultivars, flowering does not occur, or the young buds are shed before opening. Some may produce pollen that is sterile. Should this happen, the parent in question should be discarded. This problem is discussed further in the next section.

Cross Pollination

Cross pollination is done in order to produce genetic variability and transgressive segregation. There are two steps in cross-pollination.

Emasculation involves the removal of the anthers so that the flower cannot self-pollinate. Emasculation is done the day before the flower opens, when the anthers are still immature and infertile. This stage is easily recognised because the petals are fully formed but still adhering to each other, so that the flower is closed. The petals must be gently separated with a needle (photo in preparation) and then each of the five anthers must be bent away from the pistil until it breaks off and falls to the ground (photo in preparation). The next day, an emasculated flower is wide open and is easily recognised by the absence of yellow anthers (photo in preparation). Each day, all the flowers that are ready should be emasculated, except those of the male parent (see next).

Cross-pollination involves the placing of pollen on the now receptive stigma of each emasculated flower. It is a good idea to use only one male parent, and a different male parent, each day in rotation, so that each parent is represented equally. The male parent flowers are wide open and are easily recognised by the presence of yellow anthers. One anther is picked with a pair of fine forceps (photo in preparation), and it is touched to the stigma of each of several emasculated flowers (photo in preparation). Make sure that the side with free pollen is used. A small dot of yellow pollen should be visible on the stigma. There are five anthers to each male parent flower and, with several flowers, this should provide adequate pollen for all the cross-pollinations to be done in one day.

Some potato cultivars are pollen-sterile, or even female sterile. If it is discovered that a male or female parent never forms fruits, its use must be discontinued. Famous cultivars that suffer sterility problems are *Russet Burbank*, *Bintje* and *King Edward*, and the use of these as parents should be avoided by amateur breeders.

Do not waste time labelling flowers, keeping detailed records, or keeping each batch of seed separate from all the others. All the true seed is going to be mixed, and sown as a single screening population.

Potato Fruits

The true fruits of potatoes are similar to a small tomato. They develop from a pollinated flower. When ripe, they are usually a green or bronze colour (see photo), and they are soft and somewhat wrinkled. Each fruit contains up to 300 true seeds. Because of the cross-pollination, these seeds will exhibit great variation in all their quantitatively inherited characteristics, including their horizontal resistances.

Seed Preparation

When the potato fruits are ripe, they should be put in a kitchen blender or food processor and covered with clean water. The blender should be switched on intermittently (the 'pulse' button) so that all the fruits are broken open, and seeds liberated. Do not over-do this maceration as the seeds themselves might be damaged. If a blender is not available, crush the fruits and then shake them vigorously in water in a sealed jar.

Now pour all the contents of the blender (or jar) into a clean plastic bowl or bucket. Leave the mixture in a warm room to ferment for about twenty four hours. Most of the fruit debris will float, and most of the seeds will sink. The debris can be removed with a coarse sieve, such as a kitchen colander, and put into another bucket. Decant the water from the first bucket into the second bucket. The seeds in the first bucket can now be put into a glass jug which is repeatedly filled with water and decanted, until the seeds are clean and free from rubbish. The seeds can now be put into a conical, paper, coffee filter, in a kitchen sieve, to drain (see photo).

When drained, the seeds should be spread out on a clean surface, such as glass, to dry. The seeds in the next two photographs came from about fifteen full jars of the blender shown above.

Potato seed often shows dormancy, which can be a nuisance in a breeding program. This process of fermentation breaks the dormancy, and all the seeds will then germinate immediately. They can either be used as soon as they are dry, or they can be stored for future use.

Soil Sieves

A set of soil sieves, designed for the mechanical analysis of soil, is a useful device for a final cleaning of dry seeds. The coarsest sieve is at the top, and finest at the bottom. The seed is shaken through the sieves, and the coarse rubbish is trapped in the upper sieves, the seed is somewhere in one of the middle sieves, and the fine rubbish is lower down, or even at the bottom. However, soil sieves do not work well with wet seed, even when used with lots of water. This is because they tend to get clogged rather quickly.

Seed Storage

The dried seed should be stored in an air-tight jar which also contains a small bag of freshly dried silica gel. These bags of silica gel are often packed with electronic equipment to keep it dry during transport. They can usually be purchased from a pharmacy, or from a scientific goods supplier. The gel is best dried in a convection oven using the vegetable dehydration cycle. Alternatively, the bag should be left in the hot sun for a few hours. Dryness is essential in seed preservation, and damp seed will not remain viable for long, even when refrigerated.

The jar should be labelled to identify both the batch of the seed and its age. If it is stored in a refrigerator at about 4°C, it will keep in a viable condition for several years.

Seed Sowing

When there is no further risk of frost, the seed should be sown in a seedbed with a minimum separation of about two inches between seedlings. Various hand-operated seed drills are available for this sort of work. The seed bed should have a very fine tilth, having been rota-tilled several times in order to germinate and kill weeds. Sow most of the seeds you have been able to produce, keeping back a few as an emergency reserve in case of disaster. It is a good idea to aim at sowing at least 100,000 seeds. In the later breeding cycles, the number of seedlings can be gradually reduced, and this is a point that will be determined by experience.

These seedlings can then be screened for horizontal resistance, and the whole idea is to let the parasites do this work for you. Remember that you will only be interested in the survivors, and there will not be many of these.

Seedling Screening

After the seedlings have been showing above ground for a few weeks, blight will begin to attack them, and Colorado beetles will begin to eat them.

In the early breeding cycles, there is a grave risk that the blight and beetles will destroy every single plant. The damage will be comparable to the destruction caused by blight, when it first appeared in Ireland. This is obviously a critical stage, and the relatively few survivors must be rescued in good timer. They should be transplanted into pots, and taken to a greenhouse where they can be nursed back to health. It may also be necessary to use crop protection chemicals, both in the field and the greenhouse, in order to save the few survivors. This is a point that should be noted by breeders working on an organic farm, who may prefer to conduct their early breeding cycles on rented land in a conventional farm, where crop protection chemicals can be used without jeopardising their organic certification.

The Later Breeding Cycles

In the later breeding cycles, the numbers of seedlings can be reduced. There may be so many surviving seedlings that the best 10-20% would have to be transplanted to a potato field, with a spacing similar to that of a commercial potato crop, before final selections can be made. Professional potato breeders reckon that about 10,000 seedlings must be screened to get a new clone of commercial quality, but this is without regard to horizontal resistance.

As the breeding progresses, therefore, and the levels of horizontal resistance increase, the number of seedlings screened can be reduced, but the amount of work required for each seedling will increase. It is at this stage that the breeding begins to get exciting.

Inoculation and Infestation

In the later breeding cycles, there will be so much resistance that inoculation may be necessary. One or more rows of susceptible modern cultivars should be planted on each side of the seedbeds (or the transplanted potato seedlings) so that blight and beetles can invade the screening populations. It is at this stage that much stronger selection pressures for other selection criteria begin to be applied. These include resistance to other parasites, such as virus diseases, as well as attributes of yield and quality. It will probably be advisable to get technical help with the virus diseases.

Number of Generations

The method of potato breeding recommended here is based on the behaviour of maize in tropical Africa following the accidental introduction of a rust disease from Central America (see *Return to Resistance*, available as a sharebook at www.sharebooks.ca for a full description). When this maize disease first appeared, the loss of crop was almost total, and the farmers had barely enough seed to sow the next crop. This represented the minimum level of horizontal resistance. There are two crops each year in this area and, after 5-7 years, the level of horizontal resistance was maximal, and the loss of crop was negligible. This indicates how many breeding cycles will be required, as well as how very effective transgressive segregation can be.

Note that this maize accumulated all the resistance it needed without any help from professional breeders or pathologists. It could do this because maize is open-pollinated, and the recurrent mass selection was effectively a natural process, assisted by the wisdom of the farmers who were persisted in trying to preserve their favourite landraces. While this accumulation of horizontal resistance was happening, an official maize breeding program was conducted to produce maize with single-gene resistances, but these vertical resistances broke down so quickly that the new lines never even reached the farmers.

Breeding potatoes for comparable levels of horizontal resistance to blight, beetle, and other parasites, may take a little longer than the African maize, because more species of parasite are involved. But the difference is unlikely to be large.

On-Site Screening

On-site screening means that the screening is conducted in the *agro-ecosystem* of future cultivation, in the *time of year* of future cultivation, and according to the *farming system* of future cultivation. This is important because the epidemiological competence of parasites varies considerably from one agro-ecosystem to another. A cultivar with horizontal resistances that are in perfect balance with one agro-ecosystem will then have too much resistance to some parasites, and too little to others, when taken to a different agro-ecosystem, or when cultivated out of season, or when cultivated with different cultivation practices.

Fortunately, with potatoes, the agro-ecosystems are usually large, and this is not a serious problem. For example, bacterial wilt (*Pseudomonas solanacearum*) is a tropical disease which lacks epidemiological competence entirely outside the tropics and sub-tropics, apparently because it cannot survive a winter. There is no need to breed for horizontal resistance to this disease in temperate regions. Equally, the temperate virus diseases of potato seem to lack epidemiological competence in the tropics, and there is no need to breed for horizontal resistance to these diseases in tropical countries.

However, the principle of on-site screening becomes important with greenhouse work. Greenhouse screening is permissible when there is a 180-day breeding cycle, but only if it is alternated with an on-site field-screening at the proper time and place.

Locally Important Parasites

Because of the need for on-site screening, a potato breeding club must be located in the area of future cultivation. The breeding for horizontal resistance can only embrace potato parasites that are *locally* important. If a parasite species is absent from the agro-ecosystem in question, or if it has a very low epidemiological competence, it is not feasible to breed for resistance to it. Nor is there any necessity to do so.

A manual such as this can accordingly make only very general remarks concerning individual species of parasite. An amateur breeding club must make itself informed in this matter, and the members should consult libraries and/or specialists. However, if a parasite is locally important, it will show up quickly enough in the screening population.

The 180-day Breeding Cycle

In the temperate regions, it is normally possible to achieve only one breeding cycle each year, with the cross-pollination and seed production undertaken in a greenhouse, during the winter, and the on-site screening conducted in the field, during the summer. With ambitious breeding targets (e.g., horizontal resistance that is complete and comprehensive against all locally important parasites), this could require 10-15 breeding cycles during the same number of years.

If, however, we could squeeze two breeding cycles into each year, the total breeding time would be halved. This would necessitate a 180-day breeding cycle, with each cycle divided into a 90-day seed production cycle, and a 90-day screening cycle. This would require a lot of careful planning, and hard work, but it is feasible. It would be achieved by considerable over-lapping of the cycles.

For example, about five times the required number of parents could be selected about two thirds of the way through the screening cycle (i.e., after 60 days of screening). These would be grafted on to tomatoes (sown well in advance) on the clear understanding that 80% of them will be discarded when the final selections are made. By the end of the screening cycle, the selected parents will be grafted, flowering, and ready for cross-pollination. This would add 30 days to the seed production cycle, which would then be effectively 120 days.

One breeding cycle would obviously have to be conducted during the winter and, in most temperate countries, this would mean a fairly large heated greenhouse, as well as the induction of both insect infestations and disease epidemics. Technical help may be needed here. The screening cycle would begin by sowing the true seed immediately after it is becomes available at the end of the seed production cycle, including seed taken from somewhat immature fruits.

In the temperate regions, one 180-day breeding cycle should start in spring, and allow an on-site screening in the summer. The second breeding cycle would start in the autumn, and this would necessitate a winter screening in the greenhouse.

Obviously, this winter screening would not be an on-site screening but, as this happened in every alternate breeding cycle, the small reduction in breeding efficiency would be acceptable, in view of the huge gain in time. (But see also: Tuber resistance).

Sources of Error

A number of common errors can occur in the understanding of horizontal resistance, and they must be clearly recognised by the amateur breeder, because they can be dangerously misleading.

The first concerns the belief, held by many organic farmers, that organic farming produces plants that have an improved resistance to many parasites. However, good nutrition affects the *physiology* of the plant, but it does not affect the *genetics* of the plant. And resistance to parasites is controlled genetically. Anyone who doubts this should try growing a modern cultivar of potatoes in, say, North America or continental Europe, using the best possible soils and nutrition, but without spraying against either blight (*Phytophthora infestans*) or Colorado beetle (*Leptinotarsa decemlineata*).

There is an important difference between a low incidence of a parasite, and resistance to that parasite. A low incidence means that the parasite is rare in the crop in question, but this could change at any time, and the parasite would then become common.

A high resistance means that the parasite is rare, and it remains rare, in that crop.

Many organic farmers can grow unsprayed potatoes reasonably successfully because of a low *incidence* of blight and beetle. This low incidence results either from their isolation, or from the fact their neighbour's potato crops are all being sprayed. And it is then very easy, and very tempting, to attribute the reduced parasitism to an increase in resistance resulting from a healthy soil and organic farming. If potatoes are grown organically in large quantities, the incidence of both blight and beetle will rise sharply, and the need for increased levels of horizontal resistance to these parasites will become critical.

A second error concerns chance escape from parasitism, and this happens most with slow-moving parasites such as virus diseases. These individuals are susceptible but, being parasite-free, they look so healthy that they are mistakenly believed to be resistant. If they are used as parents, there will be little breeding progress in accumulating horizontal resistance. There are two methods of avoiding this error. One is to select only plants that have slight parasitism, rather than no parasitism. The other is to inoculate the screening population.

A third error is to confuse vertical resistance for horizontal resistance. Fortunately, with potatoes, this is not normally a serious problem with blight, because of the presence of the A2 mating type, and because the other parasites, in which vertical resistance occurs, are rare. If a functioning vertical resistance to blight is suspected, look for the small necrotic flecks, just visible to the naked eye, which indicate that the hypersensitivity mechanism of vertical resistance is operating.

A fourth error concerns biological anarchy, which means that the natural biological controls have been severely damaged, even destroyed, by the use of crop protection chemicals. Because potato seedlings must be screened without any crop protection chemicals, the parasites will behave with a savagery that would be impossible if their biological controls were functioning fully. This is another reason for using relative measurements of horizontal resistance. It is also a clear indication that we will need less horizontal resistance than we may think, once the biological controls have been restored. The best way to restore the biological controls is to use horizontal resistance. And the best way to enhance the effects of horizontal resistance is to restore the biological controls. The two effects are mutually reinforcing.

A fifth error concerns parasite interference, which results from the fact that most parasites are mobile, and can spread from one plant to another. If a resistant plant in a screening population is surrounded by susceptible plants, parasites will move on to the resistant plant and make it appear much more susceptible than it really is. This is another reason for using relative measurements of horizontal resistance. This error also suggests that we will need much less horizontal resistance than we may think, when our seedling becomes a clone grown in a farmer's field without any parasite interference at all.

Finally, there is the error caused by 'population immunity'. This error concerns *population* growth rates which can be either positive or negative. If a population exhibits more births than deaths, the population growth rate is positive, and the population increases in size. Conversely, if the deaths exceed the births, the population growth rate is negative, and the population decreases in size. If a parasite is to cause an epidemic, its population growth rate must obviously be strongly positive. However, there may be a level of horizontal resistance such that the parasite population growth rate is close to zero, or even negative. This situation is called population immunity, because the epidemic does not develop, even though the host individuals within that population are less than immune.

The error arises when host individuals are believed to be susceptible, because the population immunity is not apparent under the conditions of measurement (e.g., in a greenhouse or plant growth chamber). Once again, we may need less horizontal resistance than we think, because population immunity can prevent an epidemic from developing in a cultivar that is less than completely resistant.

These errors have been deceiving men of science for decades. Do not let them deceive you.

Measuring Horizontal Resistance

The level of horizontal resistance can be determined only from the level of parasitism. Various factors, such as the sources of error just described, can increase the levels of parasitism very considerably in a screening population, or in research plots. For this reason, the level of horizontal resistance is likely to *appear* much less than it really is. But this appearance is deceptive. Indeed, this deception is probably the reason why professional plant breeders have ignored horizontal resistance so consistently.

It is very unlikely that we shall ever have a scale of measurement for horizontal resistance comparable, say, to the Celsius scale for temperature. In other words, we cannot make *absolute* measurements of horizontal resistance. We can make only *relative* measurements. These relative measurements are important in two situations.

First, when screening potato seedlings for horizontal resistance, it is important to select the *least* parasitised individuals, regardless of how severe their parasitism may be. When grown as a clone in farmers' fields, without parasite interference, and with restored biological controls, these apparently susceptible seedlings may well have population immunity. At the very least, they would make the best parents for the next breeding cycle. It would be tragic if such seedlings were destroyed, just because they *appeared* to be so much more susceptible than they really are.

Second, a new cultivar has to be described, and it is important that its horizontal resistances to major parasites should be accurately indicated. The only way to do this is to compare it with well-known commercial cultivars. That is, for each important pest or disease, you can say that its horizontal resistance is superior to cultivar A, and inferior to cultivar B. An alternative approach is to indicate how much spraying, if any, and with what, is needed in an average season.

Horizontal resistance can also be determined with crop loss assessment trials, but these trials are complicated and they are not recommended for amateur breeders. Such determinations enable you to say what sort of yield loss each parasite might cause in an unsprayed crop, in an average season.

Tuber Resistance

Blight, as well as a number of soil-borne pests and diseases can attack the tubers. Tubers of the more promising parents, particularly in the later breeding cycles, should be kept and cultivated as small clones. Tuber resistance to these various parasites can then be assessed fairly easily. Clearly, tubers that rot quickly in store are not very resistant, and they are not very useful, either. But, here again, all measurements of resistance must be relative measurements.

This need for measuring tuber resistance will require a longer breeding cycle and, at this stage, it may be as well to revert to the one-year breeding cycle. But this is a decision that can be made later, and it should not deter you from starting a breeding program.

Tuber Quality and Yield

Visible characteristics of tuber quality include tuber shape and size, and the depth of eyes, deep eyes being difficult to peel. The colour of the skin and flesh can vary considerably, and local preferences can have a big effect on sales. For example, people in England generally prefer white flesh potatoes, while people in Holland prefer yellow flesh.

Tuber yield is related to the number of tubers, and the size of tubers. Generally speaking, fewer large tubers are preferable to the same weight of smaller tubers. Manufacturers of French fries like large, long tubers. Tubers are sorted by size with a ‘riddle’, which is a coarse sieve, and the smaller tubers can be kept for ‘seed’.

Note that a true seedling never yields as much as a potato plant grown from a seed tuber. Comparisons of tuber yield must consequently be made between seedlings and, at this breeding stage, they should not be made with commercial cultivars.

At a later date, as potential new cultivars are being vegetatively multiplied and assessed, more accurate yield measurements can be made. However, it must also be remembered that research plots usually yield considerably more than commercial fields, and the variation between research plot assessments is also considerable. Care should be taken not to make exaggerated claims that cannot be substantiated later.

Cooking Characteristics

Cooking tests can be made only after a sizeable quantity of tubers from each promising seedling has been accumulated by vegetative propagation. These tests include taste, tuber colour (white or yellow), texture (floury or soapy), and specialised uses, such as salad potatoes, which must not turn black when cold, French fries, roasting, baking, boiling, and starch production. Most of these characteristics are quantitatively variable. The demands of commercial markets can be important, as with French fries in fast food outlets, and the manufacture of potato crisps.

Many industrial countries have special laboratories that can make an official report on these matters, including dry weight, starch content, protein content, vitamin C, glyco-alkaloids, etc. Depending on the country, this reporting can be expensive, but it is very useful during the process of registration.

Agronomic Suitability

The two principle characteristics of agronomic suitability are stolon length and leaf spread. Short stolons are necessary for mechanical harvesting. They are less necessary for subsistence cultivars but, even so, short stolons make hand harvesting easier.

A good spread of dense leaves is a valuable aid to weed suppression and, for this reason, potatoes are often called a cleaning crop. However, such a leaf spread will normally develop only from a seed tuber, and it cannot be expected from a true seedling. A mass of leaves is also a useful screening character, because a mass of *green* foliage is a very good indication of resistance. While a mass of foliage does not necessarily indicate a high yield of tubers, it is usually a prerequisite for such a high yield.

Flowering in Potato Crops

Many potato cultivars produce flowers and fruits in cultivation. These fruits constitute a ‘physiological sink’ which take a large share of the nutrients being produced by the ‘physiological source’ of the leaves. Cultivars that flower early and profusely, and set many fruits, will yield fewer and smaller tubers. Consequently, the character of ‘late flowering’, or ‘no fruits’, or even ‘no flowering’ is a useful, selection criterion, even though it might lead to difficulties in breeding.

Rapid Multiplication

A promising new selection should be multiplied as rapidly as possible in order to provide material for various tests, and registration. A useful rapid multiplication technique involves green stem cuttings. A piece of potato stem is used as a cutting. It is put in a mist propagator for about five days until roots develop (photo in preparation). It is then planted in soil, in a pot, still in a mist propagator, until vigorous growth commences.

In the meanwhile, the stem from which the cutting was taken will produce two new side-shoots, which can also be used as cuttings. These parent stems will then develop four new shoots, and so on until the parent plant looks like a candelabra (photo in preparation). This technique has even been called the ‘candelabra technique’. The rooted cuttings will themselves produce cuttings, and begin to resemble candelabra. All these plants will also produce tubers that can be used for rapid multiplication, in both the greenhouse and the field.

Mist Propagation

Cuttings are most likely to form roots if: (i) they have plenty of leaf; (ii) they are exposed to strong light; (iii) they have a rooting medium that is biologically and nutritionally inert; and (iv) they are kept in a 100% humidity. These conditions are met in a simple apparatus called a mist propagator. When the cuttings have plenty of leaf, and plenty of light, they can manufacture all the carbohydrates they need in order to grow roots. But they must be kept moist until they are able to produce enough root tissue to absorb water from the rooting medium. The rooting medium must be biologically and nutritionally inert to prevent rot-causing fungi and bacteria from attacking the cuttings.

The mist propagator consists of a tray containing the rooting medium. A good rooting medium is polystyrene granules mixed with sand in a ratio of about 4:1. If polystyrene granules are not available, use plain sand, or sand mixed with vermiculite or perlite. The tray is enclosed in a tent of transparent plastic film, and it may be exposed to full sunlight, at least for part of the day (photo in preparation). A domestic humidifier is used to continuously pump a fine water mist into the tent. Alternatively, a hand sprayer can be used every hour or so during the day, in order to keep the inside of the mist propagator permanently moist. A more simple apparatus consists of a plastic bag tied over the top of a flowerpot and supported by sticks (photo in preparation).

Under mist propagator conditions, potato cuttings will form roots in 5-10 days (photo in preparation). They can then be transplanted into pots of soil, and protected by a plastic bag cover for a few days. Once they are growing vigorously, they can be transplanted into larger pots or into the field.

Day-Length

Potatoes originated in the high altitude tropics of South America, where the days and nights last for about twelve hours throughout the year. Consequently, they are 'short-day' plants. This means that various growth processes such as flowering and tuber initiation will occur only under the influence of a twelve-hour day. Such potatoes cannot be cultivated in the temperate regions because tuber initiation does not occur until the autumn equinox in late September (or late March in the southern hemisphere), and the plants are killed by winter before they are ready to harvest.

About two centuries of both natural and artificial selection in Europe produced day-neutral plants that are able to initiate tuber formation in the long days of a temperate summer. These are day-neutral plants rather than long-day plants. They can be successfully cultivated in the tropics, but they are likely to very susceptible to the tropical disease called bacterial wilt (*Pseudomonas solanacearum*).

It follows that amateur breeders in temperate countries should use only day-neutral plants in their breeding program. But amateur breeders in the tropics may use potatoes with any degree of photoperiod sensitivity.

Glyco-Alkaloids

Potato leaves and fruits are poisonous, because they contain toxins known as glyco-alkaloids (i.e., leptinines, leptines, solanine, and chaconine). Sometimes, the tubers contain sufficient concentrations of glyco-alkaloids to prevent their registration as new cultivars. Without worrying about this too much, potato breeders should keep an eye on glyco-alkaloid concentrations, and clones with high levels in the tubers should not be used as parents.

Testing for glyco-alkaloids is not difficult, but it must be done in a professional laboratory, such as a university or a commercial company, usually for a fee.

Widening the Genetic Base

In the later breeding cycles, the rates of gain in quantitative variables, including horizontal resistances, may decline before the breeding targets have been achieved. This would happen because the genetic base of the original parents was too narrow. Such an error is easily corrected by adding new genetic material to the breeding program. This is likely to lead to a small loss in various quantitative variables, but these losses will soon be made up, and the breeding ceiling will be raised considerably. The use of neo-tuberosum material is recommended for such widening.

However, it must be clearly recognised that there is a limit to every quantitative variable and, once that limit is reached, no further progress is possible. Most of these limits are unknown because so little quantitative breeding has been undertaken in potatoes. But the amateur breeder may safely assume that these limits represent levels of horizontal resistance that are vastly superior to those of modern cultivars. The limits to other variables, such as yield and quality, are also unknown, but modern cultivars are obviously much closer to them than they are in their horizontal resistances.

Old Encounter, New Encounter, and Re-encounter Parasites

My old friend Ivan Buddenhagen first proposed that parasites come in three categories, according to their history. *Old encounter* parasites evolved with their host, and they have been in contact with it since its original domestication. This happens in the centre of origin as well as in new areas, when both the host and the parasite were taken there together.

New encounter parasites evolved on a botanical relative, but they remained out of epidemiological contact with their domesticated host. They were brought into contact with their domesticated host by people.

Re-encounter parasites evolved with their host, but they were separated from it when people took the host to another part of the world, leaving the parasite behind. At a later date, the parasite is inadvertently introduced to the new area where it re-encounters its host.

Blight, Colorado beetle, and the temperate virus diseases are new encounter parasites of potato. This may mean that a few more breeding cycles will be necessary than if these were old encounter parasites. However, it would be quite wrong to conclude that it is impossible to obtain adequate levels of horizontal resistance to new encounter parasites. High levels of horizontal resistance to blight have been clearly demonstrated. The fact that no one has achieved high levels of horizontal resistance to Colorado beetle is because such breeding is only now being attempted (see Fisher *et al*, Recommended Reading). And it seems that no work has been attempted with horizontal resistance to the temperate virus diseases of potato.

Most other potato parasites are re-encounter parasites. The host tends to lose resistance in the absence of a parasite. If the separation between host and parasite has been lengthy, the loss of horizontal resistance may be considerable. The classic example of this occurred with the maize of tropical Africa.

Blight

Potato blight, caused by the microscopic fungus *Phytophthora infestans*, is by far the most important disease of potatoes, and it now occurs in every potato growing area of the world. In about 1840, the potatoes on a ship travelling from Mexico to New York mysteriously rotted. This ship was inadvertently carrying the blight fungus from its centre of origin in Mexico to the temperate Northern Hemisphere. Shortly after this, the cook on another ship, travelling from New York to Rotterdam, also found that all his potatoes were rotten. This ship carried the blight from the New World to Europe. The fungus then spread rapidly and, by 1845, it had reached Ireland.

The damage it caused was incredible, and potato crops all over Europe were reduced to a black, stinking mush. This was the first devastating plant disease known to history, and it was devastating because it was a 'new-encounter' disease. The potato had evolved and been domesticated in South America, while the fungus had evolved on botanical relatives in Mexico, and they had been brought together by people. The potato had very little resistance to the fungus.

In Ireland alone, about one million people died of starvation, and another one and a half million emigrated, mainly to North America. This loss of people reduced the population of Ireland by one third. It is thought that another million people died in the rest of Europe. The decade became known as "The Hungry Forties". A more detailed account is given in *Return to Resistance* (available as a free download at www.sharebooks.ca).

Then, after two or three years, the blight epidemics declined. For the next forty years, potatoes were cultivated all over Europe and North America. Although blight limited the yields, potatoes remained one of the most important food crops in the Northern Hemisphere.

The reason for this decline in the epidemics was the rapid and complete elimination of all the most susceptible clones of potato. Only relatively resistant clones remained. Furthermore, all new potato breeding automatically produced resistant clones, because every susceptible seedling was killed by blight. This was horizontal resistance, and it enabled massive potato cultivation to continue without any spraying with fungicides. Indeed, no fungicides were known at that time. Equally, no vertical resistances were known at that time.

In 1882, Millardet, in France, discovered the fungicide that he called *bouillie bordellaise*, or Bordeaux mixture, which consisted of a mixture of copper sulphate solution and newly slaked lime. He used it to control downy mildew of grapes, which had also been accidentally imported from the New World, and was threatening the wine industry with ruin. And it was quickly discovered that this fungicide would also control potato blight. This made potato cultivation easier and more profitable. But it ruined potato breeding. This was because the breeders could now spray their screening populations, and this made the breeding very much easier. All the most famous potato varieties were produced during this period which lasted another forty years.

Unfortunately, during this breeding, the accumulation of blight resistance not only stopped. It went into reverse, and horizontal resistance was gradually lost because of the ‘vertifolia effect’. This loss of resistance was not recognised at the time and, even if it had been, it would have been considered unimportant, because the crops could be sprayed with Bordeaux mixture. The slow loss of quantitative resistance was not even noticed, and potato varieties bred after about 1885 became increasingly susceptible.

During World War I, Germany was critically short of many commodities but, in particular, copper was scarce. Copper was needed for making Bordeaux mixture. But it was also needed for making brass shell cases for the rifles and field guns. Because of the war, the military had priority, and the potato crops went unsprayed. The winter of 1917 was known as the ‘turnip winter’. Germany lost the war mainly because of food shortages, and several countries decided that potato blight had military significance.

When the war was over, they began to breed potatoes for resistance to blight. And they used the most modern techniques available. They used single-gene resistances that obeyed the recently recognised Mendel’s laws of inheritance. In a word, they used vertical resistance.

For the next forty years, there was great optimism, as scientists believed they would eliminate blight forever. But these unstable vertical resistances failed again and again. And, during the 1960s, the breeders decided that it was a waste of time breeding for vertical resistance to blight. They should have tried horizontal resistance but they did not, probably because they were so badly misled by various sources of error.

A notable exception to this rule was John S. Niederhauser, who was working in Mexico. He was the first scientist who deliberately avoided the use of vertical resistance and worked with horizontal resistance. He was very successful and, in 1991, he was awarded the World Food Prize, which is the agricultural equivalent of the Nobel Prize.

The A2 Mating Type of Blight

For about a century, scientists were baffled by the fact that the blight fungus apparently had no sexual reproduction. The problem was solved by Jorge Galindo, a famous Mexican scientist.

Galindo showed that the blight fungus has two mating types. Each mating type is hermaphrodite (i.e., it has both sexes) but it is self-sterile. This means that both mating types must be present if the blight fungus is to reproduce sexually. Sexual reproduction has two advantages for the fungus. First, it produces great variation in the fungal population and, second, it produces very tough 'oospores' that can survive outside the host during a winter, a drought, or an otherwise rough environment, without being killed. If only one mating type is present, the fungus can only reproduce vegetatively, by means of very fragile, asexual spores. It can then produce variants by mutation only, and it can survive a winter only inside its host. That is, it can survive only in potato tubers.

When the blight fungus was taken from Mexico to New York, and then to Europe, it was taken as one mating type only, now known as A1. For about 150 years the entire population of the blight fungus in the temperate regions consisted of this one mating type only. But, recently, the second mating type, discovered by Jorge Galindo, and now known as A2, was accidentally taken from Mexico to Europe. Before its presence was detected, it had been spread all over the northern hemisphere in certified seed potatoes.

The presence of A2 means that the blight fungus can now form oospores in huge numbers. This has several effects on the blight epidemics.

- First, the greatly increased variability in the fungus means that vertical resistances will break down even more quickly, and that they are even less useful than before. And modern synthetic fungicides, such as glyphosate, will also break down more quickly.

- Second, when only A1 was present, the blight could survive a winter only in potato tubers. Blighted tubers were relatively rare, and this meant that the initial inoculum was small, and the epidemics required more time to develop fully. The disease was known as ‘late blight’ for this reason. But, with huge numbers of oospores in the soil, the initial inoculum becomes very large, and the epidemics start earlier, and they are more serious. This means that higher levels of horizontal resistance will now be necessary if the blight is to be controlled by breeding.
- Third, when only A1 was present, tomatoes could get blight only from diseased potatoes, and this made it ‘late blight’ on tomatoes also. But tomatoes can now get blight directly from oospores, and they get it much earlier. The disease is now much more severe on tomatoes, and some plant breeding clubs might care to breed tomatoes for comprehensive horizontal resistance, in parallel with their potato breeding.
- Fourth, areas that are still free of the A2 mating type should be very careful not to import it. It is certain to reach all such areas eventually, but any delay will be useful, until such time as local cultivars with adequate resistance to blight have been produced.

There are two advantages obtained from the presence of the second mating type. First, a dangerous crop vulnerability has been realised and, once overcome, it will be permanently eliminated. Second, the inactivation of vertical resistances to blight is so rapid that the one-pathotype technique is no longer necessary during potato breeding.

Colorado Beetle

As settlers moved west, in the U.S.A., during the second half of the nineteenth century, they eventually reached the State of Colorado. A harmless beetle that parasitised the wild *Solanum rostratum*, known as prickly potato, or the buffalo burr, moved into their potato crops and it became one of the worst crop parasites ever known. Like blight, it is a ‘new encounter’ parasite. Its Latin name is *Leptinotarsa decemlineata*, and it was given the English name of Colorado beetle, after its home state, and its centre of origin.

There are many areas, such as the United Kingdom, Africa, Central and South America, and the Pacific Northwest of North America, where the Colorado beetle does not occur. Anyone breeding potatoes in such areas obviously cannot accumulate horizontal resistance to this insect pest. And any new potato cultivars produced in such an area will have a commercial value limited to those beetle-free areas. Conversely, beetle-resistant potato cultivars will be useful in beetle-free areas, even if their resistance is unnecessary. These limitations should be borne in mind by anyone thinking of starting a potato-breeding club.

David Fisher (see Recommended Reading) is breeding potatoes with success, in the U.S.A., for horizontal resistance to Colorado beetle, and one of his colleagues has shown that the horizontal resistance is not due to a high glyco-alkaloid concentration. He also makes the useful observation that, because potatoes can lose up to one third of their leaf tissue without significant yield loss, it may be economically feasible to control the losses caused by Colorado beetle with levels of horizontal resistance that are far from maximal.

Some insect larvae, such as the Monarch butterfly, which feeds on poisonous milkweed, and the Colorado beetle, which feeds on poisonous potato leaves, are able to isolate these poisons in a special sac inside their bodies. This makes both the larvae and the adults poisonous to insect-eating birds. From their colouring, insect-eating birds recognise these poisonous insects and avoid them. Consequently, putting chickens in the potato patch will not provide a biological control of Colorado beetle. (Frogs and toads do not have this instinct, and they die if they eat these insects).

Virus Diseases

A review of the scientific literature reveals that little potato breeding has been undertaken for resistance to virus diseases. The reason is fairly simple. Single-gene resistances to these diseases are relatively rare, and even when they exist, they provide unstable resistance. It was also argued that the use of certified seed potatoes made their development unnecessary. There was also a fear that their development would damage the certified seed industry. Additionally, potato breeders were not working with quantitative resistance. Virus diseases spread relatively slowly in a screening population, and any plant that got a virus diseases would be discarded, on the grounds that it was susceptible. The potato seedlings that were kept were not resistant, however. They were all susceptible 'escapes'.

Consequently, there is immense scope for amateur potato breeders to produce cultivars that are largely unaffected by these viruses, or any other tuber-borne diseases. Farmers can then keep some of their own harvest for seed. This would reduce the costs of potato production enormously. The certified seed potato industry would then be reduced to providing elite seed stocks of new cultivars, certified as to identity and purity of variety only. Anyone who doubts that this is possible should visit Kenya, where some potato cultivars have been grown for more than sixty vegetative generations without any renewal of seed stocks.

The major seed tuber-borne diseases are:

Potato Leaf Roll Virus. Insect transmitted by *Myzus persicae* and other aphids. The leaves roll into cup shapes, even cylinders, and become brittle.

Potato Virus X. Mechanical transmission.

Potato Virus Y. Also known as 'Leaf Drop Streak'. Main spread in field is by *Myzus persicae* but also sap-transmissible.

Spindle Tuber Viroid. Transmitted in true seed.

Other Potato Viruses. Generally unimportant.

Other Tuber-Borne diseases.

Readers should consult *The Compendium of Potato Diseases* (see Recommended Reading). Screening for horizontal resistance to tuber-borne diseases is done by visual symptoms on the tubers, and by tuber-rotting in store. These diseases include:

Ring rot (*Corynebacterium sepidonicum*).

Black Leg (*Bacterium carotovorum*).

Common Scab (*Actinomyces scabies*).

Powdery Scab (*Spongospora subterranea*).

Wart Disease (*Synchytrium endobioticum*).

Golden nematode (*Globodera rostochiensis*).

Bacterial wilt (*Pseudomonas solanacearum*).

Other Diseases

Readers should consult *The Compendium of Potato Diseases* (see Recommended Reading). There are about fifty other diseases but most of them are relatively unimportant.

Other Pests

There does not appear to be a book on the insect pests of potatoes, comparable to *The Compendium of Potato Diseases.* Amateur potato breeders should consult an agricultural advisor, or visit an agricultural library. The Entomological Society of America (www.entsoc.org) may be able to help.

In addition to the Colorado beetle, the principle pests of potatoes are the aphids (*Myzus persicae* and *Macrosiphum euphorbiae*) which are vectors of virus diseases, the potato flea beetle (*Lema trilineata*), and the potato tuber moth, also known as the potato tuber worm, (*Gnorimoschema operculella*) which is a gelechiid moth related to the pink bollworm of cotton.

Epidemiological Competence

Epidemiological competence is the ability of a parasite to produce an epidemic. The epidemiological competence is usually quantitative, in the sense that it can vary between a minimum and a maximum. This occurs with bacterial wilt (*Pseudomonas solanacearum*) of potatoes, for example. The epidemiological competence of this bacterium is maximal in the tropics, and it declines steadily towards the subtropics. In a region with frost in the winters, the epidemiological competence is lost entirely. Equally, the temperate virus diseases seem to lack epidemiological competence in the tropics.

Variation in epidemiological competence is the reason for on-site screening. New cultivars must have horizontal resistances that are compatible with the epidemiological competence of all the local parasites in the agro-ecosystem of future cultivation. If the new cultivar was selected in a different agro-ecosystem, it will have too much resistance to some parasites and too little to others, when brought to its new agro-ecosystem. Having too much resistance does not matter, but having too little resistance represents a failure of the breeding program.

Fortunately, most potato agro-ecosystems are large, and a new potato cultivar is likely to be agriculturally suitable over a considerable area.

The One-Pathotype Technique

This is a technique for ensuring that vertical resistances are inactivated during screening for horizontal resistance. Amateur breeders are unlikely to need this technique because the A2 mating type makes it unnecessary with blight, and other diseases with vertical resistances (e.g., wart disease, golden nematode) are unlikely to feature in amateur potato breeding programs. Should they need it, a full description of this technique is available in *Return to Resistance* (available as a free download at www.sharebooks.ca).

Illegal Parasites

Some potato parasites are the subject of legislation and it may be illegal to work with them. These include areas where Colorado beetle is still absent, such as the United Kingdom, Mexico, and the Pacific Northwest in North America. Wart disease (*Synchytrium endobioticum*) and golden nematode (*Globodera rostochiensis*) are also controlled by legislation is many countries.

Crop Vulnerability

Crop vulnerability means that a crop is susceptible to a foreign parasite which, however, is absent from the region in question. When that parasite is accidentally introduced, the vulnerability is manifested, and potential parasitism becomes actual parasitism. Crop vulnerabilities can vary from the trivial to the catastrophic.

Historically, two of the worst crop vulnerabilities were the potatoes of Europe prior to the introduction of blight and Colorado beetle. Two more were the European wine grapes susceptible to *Phylloxera* and downy mildew, which were both new-encounter parasites accidentally imported from the New World.

Crop vulnerability is important to amateur plant breeders in two ways. First, they should make themselves aware of the crop vulnerabilities in their region, and they should be very careful not to introduce foreign parasites on imported breeding stocks. They should familiarise themselves with their country's phytosanitary regulations and take great care to obey them. This is particularly true of breeding clubs in island nations, such as the United Kingdom, Australia, Madagascar, etc.

Second, a serious crop vulnerability may be realised during the breeding activities of a club, and their new cultivars would then be susceptible to the foreign parasite. This can be very disappointing as promising new cultivars would be ruined. However, the club members should immediately make horizontal resistance to the new parasite one of their selection criteria, provided that this was legal. They may well be the first to solve this new problem, and to provide a valuable service to their region.

Cultivar Formation

The biological formation of a new cultivar of potato is easy because this crop is cultivated as a clone, propagated by tubers. However, the tubers emerging from a breeding program will be either infected or contaminated with pests and pathogens, including virus diseases. In the industrial countries, potato seed legislation will usually demand propagating material shown to be free of many specified pests and pathogens. In practice, this usually necessitates a technique called ‘meristem culture’, in which new plants are produced from parasite-free ‘stem’ cells. This is not a technique for amateur breeders, and it would normally be undertaken by the registering authority.

These days, cultivar identification is usually done by DNA-fingerprinting, and this process also is undertaken by the registering authority.

Cultivar Registration

The legal requirements of cultivar formation concern registration of the cultivar, licensing of seed growers, collection and payment of royalties, etc. These requirements vary from country to country, and you should familiarise yourself with your own country's legislation.

Many tropical countries have no legislation of this kind and the amateur breeder must give his new cultivars to farmers for trial and approval. Successful cultivars will spread rapidly.

Royalties

The payment of breeders' royalties is based on the sale of certified seed tubers of a registered cultivar. Both the duration of the copyright, and the amount of royalties vary from country to country. But even a moderately successful potato cultivar will be grown on many acres, and could earn many thousands of dollars a year in royalties.

In the non-industrial world it is often impossible to register a cultivar, or to collect royalties, because there are no certification schemes, and no mechanisms for collecting royalties. And a breeding club should not want to earn royalties from subsistence farmers. As a general rule, breeding clubs in the Third World cannot expect to earn royalties, and their efforts should be entirely altruistic.

Potato breeding clubs should work for both the elimination of certified seed, and the elimination of crop protection chemicals. Ironically, the more successful they are in these targets, the more they will reduce their potential royalties. However, potato breeding clubs are intended to function for the betterment of humankind, rather than for the gaining of filthy lucre.

Farmer's Privilege

In the plant breeders' rights legislation of most countries, there is a clause called 'farmer's privilege'. This means that a farmer is entitled to keep some of his own harvest of a copyrighted cultivar for seed, but only for his own use. He may not sell any of this seed unless licensed to do so.

Breeder's Privilege

In most countries, plant breeders are allowed to use copyright cultivars as parent material. If in doubt, check with your agricultural authorities. In some countries, where single genes are still considered important, it is possible to patent a single gene. This is of no interest to amateur breeders who will normally be working exclusively with quantitative variation (i.e., polygenes).

Seed Certification

There are two kinds of potato seed tuber certification. The traditional certification is undertaken by government inspectors who confirm that crops grown for seed, on licensed seed growers' farms, are free from virus diseases. They also check the trueness and purity of variety. The second kind of certification concerns freedom from synthetic chemicals in seed tubers for organic farmers. In many countries it is becoming possible to have a double certification covering both aspects of the guarantee.

The Elimination of Certified Seed Tubers

The cost of certified seed tubers is high, and is probably the largest single input in potato cultivation. If amateur breeders produce new cultivars so resistant to tuber-borne parasites that they do not need certified seed tubers as a means of parasite control, farmers need buy certified seed only if they want to introduce a new potato cultivar to their farm. This will bring down the cost of potato cultivation dramatically, and this should be one of the main aims of plant breeding clubs.

Obviously, this use of resistance will largely eliminate the certified seed industry. However, given proper potato breeding, this industry should never have been necessary in the first place. Nor should the very high cost of potato cultivation have been necessary during the past century or longer. In any event, the certified seed industry is being given plenty of notice, because it will inevitably be some time before such resistant cultivars become available.

A second consideration, already mentioned, is that this elimination of certified seed as a means of parasite control will eventually reduce the breeders' royalties to almost nothing. These royalties are calculated on the basis of sales of certified seed. However, this should be regarded as proof of success, because most plant-breeding clubs will be working primarily for the benefits of food that is both cheap and free from crop protection chemicals. Royalties should be a secondary consideration.

The Elimination of Crop Protection Chemicals

The cost of spraying potato crops with crop protection chemicals often equals or even exceeds the cost of using new certified seed for each crop.

The frequency of spraying potato crops, and the complexity of the chemical mixtures be applied, have both been increasing during the past decades. This is partly due to changes in the parasites, such as the development of increasing pesticide-resistance, or the A2 mating type of blight. It is also due to the susceptible nature of the potatoes themselves.

Breeding for horizontal resistance is cumulative and progressive. This means that there will be many quantitative improvements in resistance, and the amount of spraying will gradually be reduced as better and better cultivars become available.

If the amateur potato breeding clubs are successful, their new cultivars will eventually be so resistant that they will need very little spraying or, possibly, none at all. This will make a dent in the markets of the big chemical corporations. However, given good potato breeding, this spraying should never have been necessary in the first place. And the chemical corporations are being given plenty of notice.

Nevertheless, we should expect some quite fierce opposition from the chemical manufacturers. It will probably be covert opposition, and it is most likely to appear in the form of refusing research grants to universities that work with horizontal resistance. This is one of the reasons that amateur breeding clubs are so necessary.

Other Crops, Other Manuals

This is the first amateur breeders' manual to be published as a 'sharebook'. More are planned. Anyone who would like to write a new manual for a specific crop, or a group of closely related crops, or has suggestions for existing manuals, should contact the editor at www.sharebooks.ca.

Technical Assistance

There will inevitably be questions that a manual such as this does not answer. Never hesitate to seek technical help. Technical questions not addressed by the author's book Return to Resistance may be obtained over the Internet, at the author's website: www.sentex.net/~raoulrob. Alternatively, a local agricultural advisor may be able to help. A further possibility is a university that has an agricultural department and, possibly, a university breeding club. With a little perseverance, it should be possible to find a sympathetic expert who is willing to advise and assist.

Recommended Reading

Books:

Compendium of Potato Diseases (Second Edition, 2001), published by the American Phytopathological Society (ISBN 0-89054-275-9), 144 pages, 193 coloured photos, US $47.00. This book can be purchased online at www.cplpress.com or by phone at +44-1635-817408, or by mail at CPL Press, Suite 36, Liberty House, The Enterprise Centre, New Greenham Park, Newbury, RG19 6HW, United Kingdom.

Return to Resistance by Raoul A. Robinson, available as a free download from www.sharebooks.ca. This book is in three sections called Explanations, Examples, and Solutions. It explains in non-technical language why modern crops are so susceptible to their many parasites, and it gives some classic examples from around the world. The section on solutions recommends the formation of plant breeding clubs made up mainly of amateur breeders, so that plant breeding can become democratic rather than autocratic. A useful companion to the present manual.

Amateur Plant Breeder's Handbook by Raoul A. Robinson, available as a free download from www.sharebooks.ca This handbook defines 1,750 terms, and both Latin and vernacular names, with a high density of internal hyper-links. A useful companion to both *Return to Resistance* and the present manual.

Scientific papers:

Fisher, D.G., Deahl, K.L., & Rainforth, M.V. (2002); Horizontal Resistance in *Solanum tuberosum* to Colorado Beetle (*Leptinotarsa decemlineata* Say). *Amer. J. of Potato Res*. **79**: 281-293.

Simmonds, N.W. (1976); 'Neo-tuberosum and the genetic base in potato breeding.' *ARC Res. Rev*., **2**, 9-11.

Simmonds, N.W. (1991); Genetics of Horizontal Resistance to Diseases of Crops. *Biol. Rev*., **66**: 189-241.