Plant breeding for stable agriculture: Presidential Address 1994

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Introduction

Plant breeding contributes to stable agriculture by improving adaptation of plants to the agricultural environment. There are many successes and failures in modern plant breeding - the key is to learn from the mistakes and build on the successes.

It is my privilege to talk on the subject of plant breeding and its role in developing stable agricultural systems. Plant breeding has fascinated the human race and has been pivotal to its development since the early hunter-gatherers selected the first domesticated plants about 10,000 years ago (Duvick 1996). Plant breeding may also provide a key to survival of the human species. There is a widely held view that agriculture is intrinsically unstable and that plant breeding can do little to help, especially with regard to disease resistance. My talk challenges this view and provides a more optimistic outlook for agriculture. In order to be "stable", agricultural systems must be dynamic, have minimal impact on the surrounding environment, and be well buffered against attacks of pests and diseases. I believe that plant breeding will underpin future progress towards stable agriculture by developing crops that are better adapted to their environment and have more durable disease resistance. However, some changes in the approach to plant breeding may be needed.

Plant breeding is a very public activity, and the result of a plant breeder's labour - a new crop variety - is subject to more critical review by the public than results of most other biological science professions. There have been some spectacular failures in modern plant breeding, most notably the failure of disease resistance genes. This has over-shadowed the steady progress in yield and quality that continues to be made in modern plant breeding. I define "modern plant breeding" as the era of Mendelian genetics from the early 1900's to the present day. Resistance to rust in wheat was one of the first economically important characters proven to be under the control of a single gene. Such genes had major qualitative effects that followed Mendel's Laws. There was much excitement with the discovery of the gene as the basic unit of inheritance, and zealous Mendelian crusaders used disease resistance genes to verify the importance of their theory, and to criticise the proponents of Darwinian "gradualism" (Robinson 1996).

It was soon learned that some characters were not controlled by single genes, and that not all genetic effects were qualitative. Some characters displayed quantitative rather than discrete variation. Bitter arguments erupted between the new Mendelian geneticists and followers of Darwinian "gradualism", and these arguments were not resolved until the development of the science of population genetics. Population genetics theory explained the movement of genes in populations, and also explained the genetic control of quantitative characters. Such characters did not form discrete groups in Mendelian tests, and were influenced by the environment. Biometricians developed the statistical theory that formed the basis of population breeding methods in animals and cross-fertilising plants such as lucerne. However, breeders of self-fertilising crops remained largely locked into pedigree breeding procedures developed by the early Mendelian geneticists 90 years ago - especially with respect to disease resistance (Robinson 1996).

In many crops, single "Mendelian" genes for disease resistance have often "broken down" due to the development of new races of the pathogen. The situation with wheat stem rust and potato late blight is documented and discussed by Vanderplank (1963). This has happened so many times and in so many crops in the past 90 years that most farmers and scientists alike have come to believe that all disease resistance is temporary - that eventually all disease resistance breaks down. There is no doubt that Mendelian disease resistance genes have been of great economic value in some crops, although the hidden costs of such breeding may be high. Nevertheless, the failure of some types of disease resistance genes have prompted many authors such as Vanderplank (1968) and Robinson (1987) to promote alternative approaches to breeding for durable resistance.

Plant breeders are reluctant to change from pedigree breeding methods because they continue to make breeding progress with these methods (Kannenberg & Falk 1995). In pedigree breeding, selfing occurs for several generations to allow selection on near-homozygous and uniform lines. The tendency is to restrict parents to a few "tried and proven" varieties, and cycles of crossing and selection are long (10 to 15 year cycles). This has lead to narrowing of the genetic base in modern cultivars, which is a concern for many breeders (Shands & Weisner 1991, 1992). In the common bean there has been no yield progress for several decades due to the narrow germplasm base (Silbernagel & Hannan 1992; McClean *et al.* 1993).

Population breeding, on the other hand, draws on a broad genetic base and employs rapid cycles of crossing and selection (1 to 4 year cycles). Parents may be heterozygous early generation lines rather than "tried and proven" varieties. The introduction of new germplasm raises the genetic ceiling on yield improvement, improves ecological adaptation, and decreases vulnerability to pests and diseases (Kannenberg & Falk 1995). Population improvement is a powerful procedure for breeding programs to exploit genetic variability (Frey 1983). Population breeding methods have been shown to

improve polygenic and durable resistance, and to secure long-term improvements in yield and adaptation (Carver & Bruns 1993; Cassler & Pederson 1996; Robinson 1987). Such methods should contribute to the long term stability of agriculture.

Stable agriculture - past and present

Instability in agricultural systems has caused major social and environmental problems since the beginning of civilisation. Despite this, some stable agricultural systems are evident and some have involved lupins.

Is stable agriculture possible? To answer this question, it is important to examine the factors that have rendered agriculture unstable. These include genetic vulnerability in crop plants (usually referring to vulnerability to new diseases or changes in strains of pathogens), cultivation techniques or grazing pressures that cause soil erosion by wind or water, rising water tables and salinity caused by land clearing or irrigation, continuous cropping leading to soil acidity and depletion of soil fertility and structure, and more recently, chemical contamination of ground water and produce and development of pesticide resistance.

The genetic vulnerability of crop plants to disease was highlighted as the level of international trade increased in the 18th and 19th century. Potatoes provide an interesting example of extreme susceptibility in a crop plant that is exposed to a new pathogen for the first time. Potatoes were introduced into Europe from South America by the Spanish in the 16th century. Two centuries of selection by European horticulturalists altered the potato from a tropical plant to a long-day plant that matured before the frosts of winter (Robinson 1996). Potatoes grew particularly well in Ireland where the climate was moist and there was little frost. Social changes at the time of the industrial revolution demanded plentiful supply of cheap food, and potatoes became cheaper than bread. In Ireland, where it was difficult to grow cereals, the population flourished as the potato flourished. However, the potato in South America (where the European potato originated) had never encountered the late blight fungus, and when the late blight fungus arrived in Europe from Mexico in the 1840's, it rapidly spread through vast regions of uniformly susceptible potato crops - with devastating consequences (Large 1940) . Ireland's social structure and economy collapsed as millions died or emigrated to the USA or Australia.

Instability in agriculture in WA is very evident as a result of rising water tables and salinity following land clearing. This is a major threat to long-term sustainability of agriculture. Increasing water use from agricultural lands and nature reserves is a major priority for reducing the problems in WA (George *et al.* 1996). Alley farming and agro-forestry will help to lower salt-laden water tables and provide useful shelter for stock and wind breaks for crops (Lefroy & Scott 1994). The cost of revegetation will be large, and must be accompanied by the development of profitable and sustainable cropping systems on the best soils.

Some agricultural systems have remained relatively stable for many years - take for example cork oak plantations in Portugal (Pinto 1994). The cork oak soils in southern Portugal are very poor - not unlike soils in the south-west of WA. Cork is harvested from the trees every nine years. During this nine year cycle, up to two crops of semi-bitter yellow lupins (*Lupinus luteus)* with shattering pods are planted and allowed to self-seed for a second year. Sheep graze the lupin seed and stubble at the end of each year. Cultivation occurs only to plant the lupin and to control flammable vegetation. This agro-ecosystem has survived without chemicals or fertilisers and has proven to be a very sustainable and low-input agricultural system (Pinto 1994).

Plant breeding and stable agriculture

Despite the repeated break-downs in disease resistance, modern plant breeding has resulted in steady improvements in yield and quality of many crops However, genetic diversity in modern crops is low and rates of improvement may fall. Population breeding methods may improve the yield and stability of crops through more diversified gene pools and durable polygenic disease resistance.

Plant breeding should underpin progress towards stable agriculture by providing farmers with well adapted and high yielding crop varieties. But how well has plant breeding achieved stable improvements in the past, and how should breeding practices be altered to maintain or accelerate these improvements in the future? Examples will be given to show that improvements in grain yield have been occurring steadily in most crops since modern plant breeding began about 90 years ago. Biotechnology will be one more addition to the tool kit of plant breeders to help them to continue this progress into the future (Duvick 1996).

In the process of achieving these improvements, plant breeders have restricted their genetic diversity to a narrow range of elite parents. There is a growing concern that genetic diversity is dangerously restricted in modern crop cultivars (Shands & Weisner 1991, 1992). Crops that demonstrate continued improvements with modern plant breeding have achieved this progress in the early cycles of selection. In most crops only 5 to 8 "effective" cycles of selection have occurred since the early 1900's. There is a strong incentive to restrict the crossing parents to tried and proven varieties in pedigree breeding and pure line methods. It is very difficult to find improvements in single crosses outside of the main adapted cultivars. It is possible that many crops have not yet reached a yield plateau because of these slow cycles of selection. The yield plateau in common bean (Silbernagel & Hannan 1992; McClean *et al.* 1993) provides a timely warning - there is an urgent need to introduce additional genetic variability into breeding systems (Kannenberg & Falk 1995).

Yield improvements in modern crop cultivars are often dependent on major genes for disease and pest resistance, and the extensive use of pesticides. Pedigree breeding attempts to maintain disease resistance through a procedure known as backcrossing, whereby new disease resistance genes are transferred from a "good source" into the elite cultivar following the "break down" of previous resistance genes (Robinson 1996).

In order to contribute to stable agriculture, plant breeding should improve yield and quality in target en-

vironments in tandem with durable disease resistance. Most economically-important traits, including yield, quality and disease resistance, may be considered as polygenic characters that are subject to the laws of population genetics (rather than Mendelian genetics). In many cases, the rate of yield improvement may be increased and genetic vulnerability decreased by the application of population breeding methods. Recurrent selection is a common population breeding method that increases the frequency of favourable genes in a population (Frey 1983). The rate of improvement depends on genetic diversity, selection pressure and the duration of selection cycles. Population breeding methods should enhance the development of favourable combinations of genes that are likely to contribute to the long-term stability of agriculture.

Plant breeding progress

Breeding progress has been apparent in the major crops in most countries over the past 90 years. Examples include wheat, barley, soybean, cotton, sorghum and corn.

Grain yield of soft red winter wheat varieties in Ohio increased by 2259 kg ha^{-1} from 1910 to 1991 (1.3% per year from 1947-1987), based on historical variety trials conducted at high rates of fertilisation but without fungicides (Fig 1). Higher yields were associated with earlier flowering, reduced height, and greater resistance to lodging in modern varieties (Berzonsky & Lafever 1993).

Yield of barley varieties in Eastern Canada increased steadily by 1.0% per year from 1956 to 1988, with no signs of a yield plateau. Harvest index increased from 0.44 to 0.51, and biomass also increased. Modern cultivars are heavier, have stronger stems and tend to be shorter, with greater lodging resistance (Bulman *et al.* 1993). Similar genetic improvements are noted in yield of corn (Tollenaar *et al.* 1994), soybean, sorghum, cotton and wheat in the USA (Fehr 1984), and in yield and quality of wheat in South Africa (van Lill & Purchase 1995).

It is important to remember that varieties bred in one country are not necessarily adapted in another. Estimations of breeding progress are affected by the locations of historic variety trials. Genotype *x* environment interactions affect estimates of breeding progress, or to use an analogy, there are "horses for courses" - each variety has its preferred region of adaptation. The "horses for courses" analogy applies at the international level as well as at the regional level within WA. Genetic improvement must be measured in relevant environments.
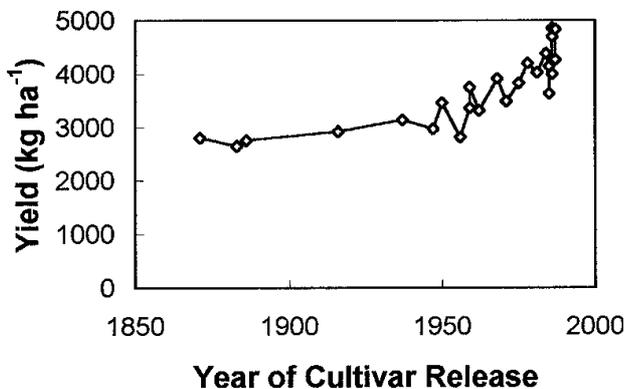
Breeding progress in WA

Plant breeding in WA has an impressive record of crop improvement in recent years. Breeding progress is usually measured in historic variety trials, and the results are highly dependent on how, where and what measurements are made. Improvements in lupins, barley and wheat in WA demonstrate these points.

The techniques chosen to estimate breeding progress can have a major influence on the outcome of the experiments. In 1991 and 1992, I conducted a series of historic variety trials in the cropping region of southwest WA using an historical set of narrow-leafed lupin (*L. angustifolius*) varieties released earlier by Dr John Gladstones. Each variety was sown at a wide range of seeding rates. Merrit, released in 1991, was significantly higher yielding than Unicrop, released in 1973. At a target density of 70 plants m^{-2}, the yield of Merrit was 43% higher yielding than Unicrop, a yield improvement of 2.4% per year from 1973 to 1991 (Cowling & Speijers 1994). At a seeding rate of 120 kg ha^{-1}, the estimate of breeding progress was 1.9% per year between Unicrop and Merrit. However, at low seeding rates of 30-40 kg ha^{-1}, there was no difference in yield between the two varieties, and no apparent progress in yield improvement (Fig 2).

It follows that estimates of breeding progress depend on the seeding rates at which varieties are tested. As with lupins in WA, modern varieties of corn perform better than older varieties at high densities (Tollenaar *et al.* 1994). It makes good economic sense for a farmer to

Figure 1. Grain yield (kg ha^{-1}) of soft red winter wheat varieties in Ohio based on historical variety trials (Source: Berzonsky & Lafever 1993).
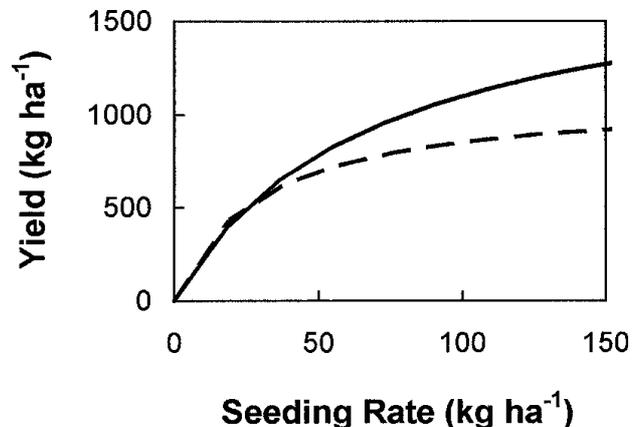
Figure 2. Influence of seeding rate (kg ha^{-1}) on yield (kg ha^{-1}) of narrow-leafed lupin cultivars Merrit (solid line; released in 1991) and Unicrop (broken line; released in 1973) in historic variety trials in Western Australia. (Source: Cowling & Speijers 1994).
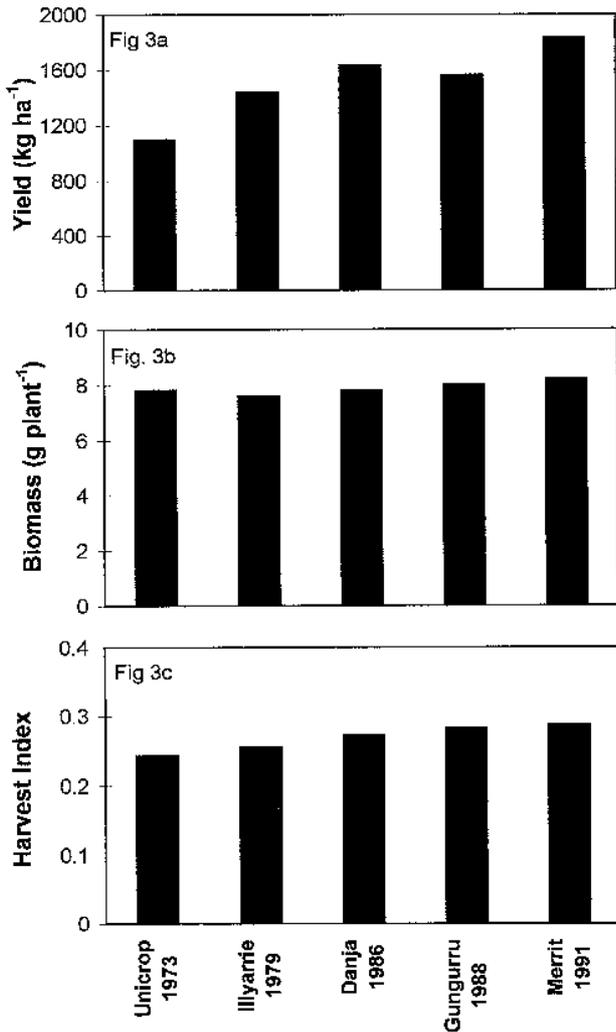
Figure 3. Results of historic variety trials in Western Australia of narrow-leafed lupin cultivars Unicrop (released 1973), Illyarrie (1979), Danja (1986), Gungurru (1988) and Merrit (1991): **A** Relative yield (kg ha^{-1}) at predicted maximum yield; **B** Biomass (g plant^{-1} dry weight) at harvest; and **C** Harvest Index. (Sources: Cowling & Speijers 1994, and Tapscott *et al.* 1994).

sow Merrit lupins at higher seeding rates than Unicrop. Conversely, any factors that decrease the plant density of Merrit, such as poor germination or root rot disease, will decrease its relative yield advantage.

While there has been a progressive improvement in yield of lupin varieties from Unicrop to Merrit (Fig 3A), total plant weight or biomass of the historical cultivars has not changed (Fig 3B) over this 18 year period (Tapscott *et al.* 1994). Total weight includes seed, leaves and stems at harvest. Harvest index, or the proportion of the mature plant dry weight in seed, has increased steadily from Unicrop to Merrit (Fig 3C) (Tapscott *et al.* 1994). Merrit is more efficient at converting vegetative mass to seed than Unicrop. However, harvest index is still low in comparison with other grain legumes, and harvest index of lupins in WA may be higher in future higher-yielding varieties.

Estimations of breeding progress are also affected by locations of variety trials. In this example, some barley

varieties perform better in low rainfall regions, others perform better in high rainfall regions of WA (R F Gilmour, *pers. comm.*).

In the high rainfall region, progress in barley breeding in WA has been very impressive - yield has improved by 2.5% per year from Dampier (released 1966) to Onslow (released 1990). Onslow yields more than twice that of Prior, released in 1900 (Fig 4A). In the low rainfall region, yield improvement has not been as rapid, but is still very reasonable (Fig 4B), increasing 1.5% per year from Dampier (1966) to O'Connor (1984). Onslow is not adapted to low rainfall regions, and yields less than Prior in low rainfall! It would be quite misleading to measure breeding progress in barley based on the average yield of these varieties across rainfall regions. Breeding progress in barley is occurring in different gene pools in the high rainfall than in the low rainfall.

When estimating breeding progress, it is also important to define what is being measured. The wheat breeding program in Agriculture WA is the first in the world to breed a variety specifically for the Japanese noodle market. The variety Cadoux was released in 1992. Cadoux is higher yielding than its predecessor, and gives WA a competitive edge in the Japanese noodle market over its rivals in Canada and the USA. Growers receive a price bonus for Cadoux wheat. This is equivalent to 10-20% yield improvement in normal Australian Standard
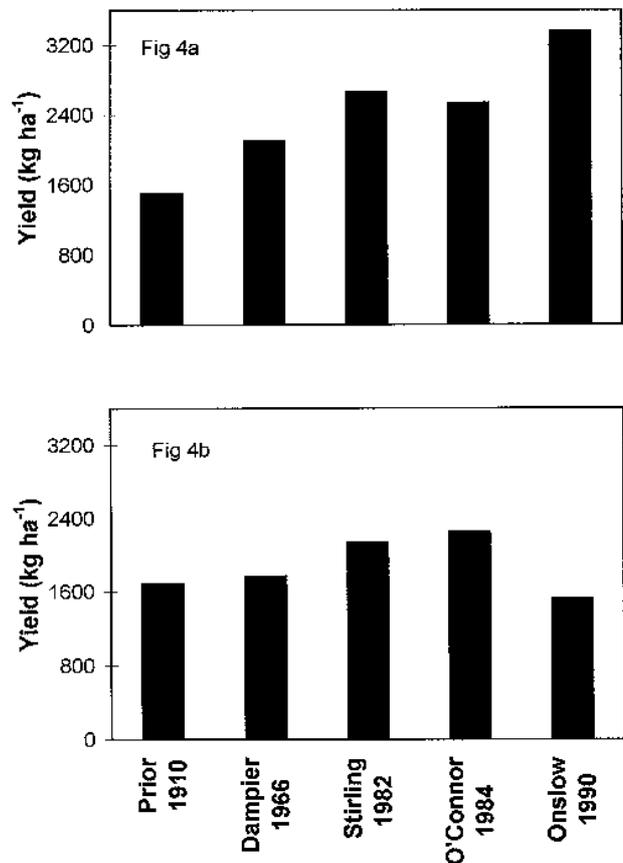
Figure 4. Yield (kg ha^{-1}) of barley varieties in historic variety trials in high rainfall (**A**) and low rainfall (**B**) regions of Western Australia (Source: R F Gilmour, *pers. comm.*).

White varieties. The market potential was recognised by the breeders and cereal chemists at least 10 years in advance. Selection techniques for Japanese noodle qualities had to be developed and working effectively long before the new wheat was released (G Crosbie, pers. comm.). The Japanese noodle wheat has lifted the profitability of cropping and provided cash for stability projects on the farm.

Lupins and stable agriculture in WA

Lupins have rapidly expanded in area and production in WA over the past two decades. Lupins filled the need for a productive legume in rotations with cereal crops on light sandy soils. Improvements in crop rotations due to lupins will improve the profitability and stability of agriculture. Improvements in farm profits may allow increased expenditure on land and soil conservation measures.

Narrow-leafed lupin production increased exponentially during the 1980's in WA to more than one million tonnes per annum by the early 1990's. Average lupin yield per hectare in WA improved by about 20% during the 1980's (Fig 5). This was partly the result of better lupin agronomy and partly due to better lupin varieties. Lupins are now the second largest crop in WA based on area of production (Australian Bureau of Statistics 1996). Farmers have responded quickly to incorporate this legume into their farming systems. In doing so, they have improved their economic viability and the long-term stability of agriculture.

Lupins provide a direct benefit for the stability of agriculture in WA, mostly through improvements in crop rotations with cereals. Wheat following lupins is higher yielding, has lower disease levels, fewer weeds and higher grain protein than wheat following another cereal or poor pasture (Nelson 1994). Consequently, the crop rotation is more profitable and more stable in the long term when lupins are included in the system.

Lupins also improve soil structure and fertility, are a cash crop in their own right, and the stubbles and seed provide valuable on-farm feed for livestock over summer. Lupins lift whole-farm profitability and help to pro-

vide farmers with the extra cash needed to help them modify their farms for long-term stability.
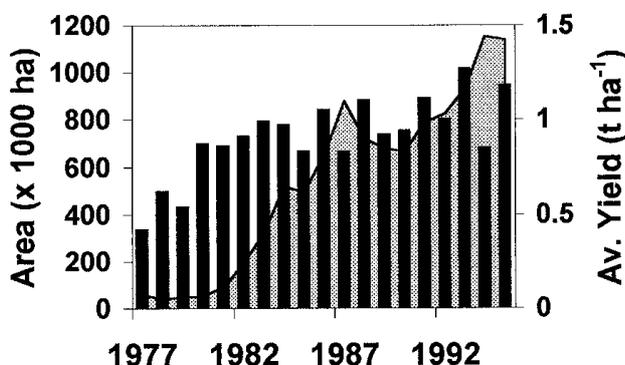
The total biomass production of a lupin:wheat rotation exceeds that of continuous cereal cropping or cereal crop following poor grassy pasture; as a result, the lupin:wheat rotation should use more of the available soil moisture and there should be less recharge to the water table. The introduction of lupins into the rotation should reduce potential problems from rising water tables and salinity (George *et al.* 1996).

Recently, yellow lupins (*L. luteus*) have been found to be very well adapted to the very acidic soils of the eastern wheatbelt of WA (Sweetingham *et al.* 1994). Yellow lupins are resistant to brown spot (Yang *et al.* 1996) and *Pleiochaeta* root rot (Sweetingham *et al.* 1994) and yield more than narrow-leafed lupins on these very acidic soils. This is the first legume crop for very acid soils, and as with the narrow-leafed lupin, yellow lupins will increase productivity of crop rotations on these soils.

Lupins, as with any legume or nitrogen fertiliser, contribute to soil acidity. This is an increasing problem on WA soils, but fortunately there is a remedy - the application of lime to the soil. The added cost of lime should be funded by the increased profitability of lupin:wheat rotations on acid soils.

Lupins and new approaches to plant breeding

Lupins are a new crop for modern agriculture and are in an ideal position to test some new approaches to plant breeding.

Lupinus is a large genus in the Leguminosea with a great diversity of forms in the Americas, the Mediterranean basin and northern Africa. Perennial lupins are found above the snow-line in Alaska and along the California coast, annual types on the fringe of the Mediterranean sea and in the highlands of equatorial Africa, and simple-leafed types on the coastal plains of Paraguay, Argentina and in southern Florida (Allen & Allen 1981; Monteiro & Gibbs 1986; Planchuelo 1994; Gladstones 1974).

Lupins provide an interesting example of the parallel domestication of plants by two geographically and culturally isolated human civilisations. Lupins were developed independently as a food crop by Greek/Roman civilisations in the Mediterranean region and by native American civilisations in the high Andes mountains of South America (Hondelmann 1984). There are frequent references to lupin cultivation in early Greek and Roman literature (Hondelmann 1984). Lupini beans (*L. albus*) are consumed to the present day after debittering by traditional methods in Italy, Greece, Spain, Portugal, and in the Arabic cultures of the eastern and southern Mediterranean and northern Africa. Cultivated types of the Andean lupin (*L. mutabilis,* known as "tarwi") were selected independently by Indian civilisations in South America. One of the early Spanish conquerors noted the similarity between the lupin eaten by the Incas and those eaten in Spain (Hondelmann 1984), and it is certain that the technology to debitter lupins was developed by both cultures independently of one another.

Figure 5. Average yield (solid bars; tonne ha^{-1}) and area of production (stippled area; x 1000 ha) of narrow-leafed lupin in Western Australia from 1977 to 1995 (growing seasons). Source: Australian Bureau of Statistics (1996) and earlier publications of the same series.

As a modern crop plant, lupins have a relatively short history. Researchers in Germany in the 1920's and 1930's were convinced that low alkaloid (sweet) forms of lupins could be found. They proceeded to select sweet forms of *L. angustifolius*, *L. albus* and *L. luteus* and were able to fully domesticate the latter two species. Sweet narrow-leafed lupins were not fully domesticated (with sweet and soft seeds and non-shattering pods) until the 1960's by Dr John Gladstones in WA (Gladstones 1982). The history of narrow-leafed lupin production in WA since the 1960's is a story of successful collaboration among lupin breeders, researchers, advisers, marketers and growers in WA (Nelson 1994).

There are few other breeding programs for *L. angustifolius* in the world, and most of those are based on varieties released in WA, so the domesticated gene pool is relatively small. All improvements in narrow-leafed lupins of relevance to southern Australia for the near future will depend on breeding material developed in WA (Cowling 1994).

Wild lupins are an important source of new genetic variability, and a significant proportion of the lupin breeding effort in WA is allocated to conserving and evaluating the genetic resource in the "International Lupin Collection" at Agriculture WA in South Perth (Cowling 1994). It is necessary to cross advanced breeding lines with wild plants to expand the domesticated gene pool. Crosses with wild narrow-leafed lupins from Spain, Morocco, Portugal, Israel, Italy, and Greece have formed the backbone of genetic improvements in lupins in WA and such crosses will continue to be important for some time (Gladstones 1994).

It takes several years to reselect fully domesticated progeny from crosses with wild lupins, and these "first-cross" lines may not be suitable for release due to flaws in yield, quality or agronomic characteristics. Nevertheless, they may have particular features (such as improvements in disease resistance) that may contribute to crop improvement. I have used recurrent selection to simultaneously improve disease resistance, yield and quality in such breeding material (Cowling 1994). In 1984 when I began breeding for resistance to brown spot (caused by the fungus *Pleiochaeta setosa*) in narrow-leafed lupins, there was no known "strong source" of resistance. Recurrent selection seemed the best choice of methods for this crop and this disease (see below; "Brown Spot Resistance in Lupins: a Case History of Recurrent Selection").

Recurrent selection is a form of population breeding that is the accepted standard method in cross-pollinating forage plants (Casler & Pederson 1996), but has yet to be fully exploited in self-pollinating plants. Durable disease and pest resistance should result from the application of population breeding methods to resistance (Robinson 1987, 1996). The lupin recurrent selection program in WA is one of few applied breeding programs of self-pollinating plants to use population breeding methods.

Population breeding methods

Population breeding methods, although not new, offer long-term solutions to some serious problems with modern plant breeding.

I discussed earlier the seriousness of the problems of

narrow gene pools, slow selection cycles and the unreliability of Mendelian genes for resistance in modern plant breeding. To overcome some of these problems, it is necessary to use population breeding methods. Such methods should improve long-term progress in plant breeding by (i) increasing genetic variance (diversifying the gene pool in order to increase the potential for long-term genetic gain), and (ii) accelerating cycles of selection (decreasing the time between crossing of parents and crossing of progeny). Success depends on high selection pressure which results from accurate and reliable yield measurements, uniform disease pressure, and relevant quality measurements.

Population breeding methods are designed to improve traits under polygenic control, such as yield, quality and disease resistance. Genes are mixed and re-arranged to form so-called "adapted gene complexes", and the frequency of favourable alleles in the population is increased through transgressive segregation (Frey 1983). Transgressive segregation is said to have occurred when, after some cycles of crossing and selection, many lines in the final generation are higher yielding or more disease resistant than the original parents.

In recurrent selection, recurring cycles of crossing and selection allow favourable genes or gene combinations to be accumulated in the population. Recurrent selection has been used extensively (Frey 1983) in cross-pollinating crops (such as maize) and pasture plants (for example sweetclover and alfalfa). More recently, it has been applied to several self-pollinating crops such as wheat, oats, barley, soybean, sorghum, bean, tobacco, and cotton (Kervella *et al.* 1991; Goldringer & Brabant 1993). In most references in these two review articles, recurrent selection was used to improve polygenically-controlled traits such as yield, seed size, protein, and oil. There are relatively few references in the literature to improvements in disease resistance by recurrent selection, mostly because the research required for publication has not been done.

Recurrent selection in self-pollinating plants begins with a partial diallel cross among the selected parent lines, and selection normally takes place on F_2-derived lines. The best progeny are selected by the F_2, F_3 or F_4 for inter-crossing to begin the next cycle. If the parents themselves are F_2-derived and quite heterogeneous, it is possible to begin selecting in the F_1 (called S_0 in breeding of cross-pollinating plants). The population may be kept "closed", that is, without introducing new genetic lines to the population after the initial diallel cross, or new lines may be added to crossing in the following cycles.

Carver & Bruns (1993) in their review found that recurrent selection in self-pollinating crops has resulted in yield improvements of 3-4% per year, and quality improvements of 5.3% per year. This compares very favourably with the breeding progress for yield in traditional breeding programs around the world referred to earlier (1-2% per year).

Pedigree plant breeding may be regarded as a form of recurrent selection, but the long-term genetic gain is limited by the slow cycles, the high number of selfing generations before intercrossing, and the narrow genetic base (Kervella *et al.* 1991). The chances of improving polygenic resistance are very low using traditional pedigree breeding in self-pollinating crops.

Breeding for polygenic disease resistance by recurrent selection

Recurrent selection has been shown to increase disease resistance (presumed to be polygenic) by transgressive segregation. Polygenic resistance developed by these techniques is durable. Horizontal and vertical resistance are descriptive terms to describe (i) polygenic resistance that is normally durable (horizontal) and (ii) major gene resistance that belongs to the "gene-for-gene" system of plant disease resistance (vertical).

In 1954, a small but significant article appeared in the American Potato Journal. It was one of the first reports of the deliberate use of population breeding methods for disease resistance, carried out by John Niederhauser and coworkers in Mexico against late blight on potatoes. Niederhauser *et al.* (1954) saw that major gene resistance to late blight was of little use in Mexico, and proceeded to select partial resistance by population breeding methods - deliberately eliminating simple major gene resistance. The partially resistant varieties remained greener in field trials than plants with "broken down" major gene resistance, which were completely dead. In addition, the partial resistance developed by population breeding was not specific to one race of the pathogen: "in the field [these varieties] show a degree of resistance that is exhibited equally toward all races of the pathogen" (Niederhauser *et al.* 1954). Niederhauser produced several cultivars with high levels of partial resistance, accumulated by population breeding methods. His cultivar "Atzimba" is the standard against which other cultivars are measured in Mexico (Robinson 1987).

A similar approach was used by Robinson in Kenya in the 1950's and 1960's against late blight and bacterial wilt of potato, and Robinson's potato varieties remain resistant and are grown on a wide scale in Kenya to this day without the need for expensive seed potato schemes (Robinson 1987, 1996).

Several studies have demonstrated improvements in disease resistance beyond that seen in the parents, achieved by transgressive segregation. Transgressive segregation was shown for resistance to yellow rust in wheat (Krupinsky & Sharp 1979; Wallwork & Johnson 1984), leaf rust in wheat (Lee & Shaner 1985) and net blotch barley (Cherif & Harrabi 1993). Parlevliet & van Ommeren (1988) used recurrent selection to increase resistance to leaf rust and powdery mildew in barley. By the third cycle of recurrent selection, leaf rust resistance had improved substantially from very susceptible to "sufficiently resistant" (Parlevliet & van Ommeren 1988). All the original parents were considered to be very susceptible. No major genes for resistance were present. The third cycle selections were not immune, but had adequate resistance for protection of barley from leaf rust.

Recurrent selection has been used to improve resistance to several diseases of wheat in Brazil (Beek 1983), purple leaf spot in orchardgrass (Zeiders *et al.* 1984), *Phytophthora* rot in soybean (Walker & Schmitthenner 1984), barley yellow dwarf virus in oat (Baltenberger *et al.* 1988), scab in wheat (Jiang *et al.* 1994) and powdery mildew in rye (Lind & Züchner 1985). It is likely that such resistance is oligogenic or polygenic in nature, and should be durable in agriculture.

In these examples, the breeders were not using the traditional "good sources" of resistance. They used recurrent selection to improve resistance by transgressive segregation. I am not aware of reports of "break down" of polygenic resistance. Worthwhile disease resistance can be achieved without demanding immunity in plants. It is unfortunate that decades of breeding for immunity has resulted in the pessimistic attitude that resistance always breaks down and that breeders will always be one step behind the pathogen.

It is difficult for population geneticists to understand why plant breeders and pathologists have argued emotionally for four decades about the value of this general type of resistance, that Niederhauser *et al.* (1954) termed "partial" and Vanderplank (1963) later called "horizontal". The words horizontal and vertical resistance have invoked hostile reactions in many quarters (Robinson 1996). Even today, there are very few applied breeding programs where population breeding methods are used to increase disease resistance and other important attributes in the production of new cultivars.

In order to adopt population breeding methods for polygenic resistance, it is necessary for breeders to overcome 90 years of bias against polygenic resistance. They must accept that;

- it is not necessary to locate a "good source" of disease resistance;

- disease resistance can be improved to levels far in excess of the parents by population breeding methods, simultaneously with improvements in yield and quality;

- it is rarely necessary for a crop to be immune to disease (in fact, mild disease resistance may be preferable to immunity due to lower selection pressure on the pathogen, and may prevent economic loss in combination with other disease control measures);

- disease resistance does not always break down (in fact, polygenic resistance is likely to be very stable); and

- there is no yield penalty associated with polygenic disease resistance.

The terms vertical and horizontal resistance have been defined and refined for 30 years since Vanderplank (1963) first introduced them. There are many other terms that have been used, but since Vanderplank was the originator of the concept that differentiated the two forms of resistance, Robinson (1996) argues that his terms should take precedence.

Vertical resistance genes belong to the "gene-for-gene" system of plant-pathogen interaction (Robinson 1996). Vertical genes often completely protect plants from disease; however, the protection offered by vertical resistance genes may not be durable. New races of the pathogen, with matching virulence genes, cause vertical resistance to "break down". The resistance gene inside the plant has not changed - it simply is no longer effective as a resistance gene.

The gene-for-gene system is a highly evolved and complex system of disease resistance, almost as complex as the immune system in mammals. In the gene-for-gene system, for every resistance gene in the plant population,

there is a matching virulence gene in the pathogen population. Sooner or later, the pathogen population will respond to the introduction of a vertical resistance gene in a crop variety by developing (under strong selection pressure) high frequencies of its matching virulence gene to overcome the resistance. Vertical resistance is well adapted to wild ecosystems where the host tissue is discontinuous in space and time (for example, in wild cross-pollinating annual grasses), but it is not well adapted to modern agriculture where there are large areas of genetically uniform self-pollinating crops.

Plant breeders normally react to the break down of resistance by introducing new vertical resistance genes. Breeding for vertical resistance is well suited to traditional pedigree and backcross methods of breeding. In many developed countries, such as Australia, the wheat crop continues to be protected from rust diseases by a complex combination of vertical resistance genes. Many developing countries simply cannot afford such costly disease resistance schemes (Robinson 1996).

Horizontal resistance, on the other hand, is presumed to be effective against all races or strains of the pathogen. In practice this is difficult to prove, but the main feature of horizontal resistance is that it is normally polygenic and durable, although it usually provides incomplete protection and not immunity.

Horizontal resistance is not the "good source" of resistance that plant breeders and pathologists traditionally seek. Horizontal resistance may be increased to useful levels by population breeding methods within an adapted gene pool. Breeding for improvements in horizontal resistance is cumulative. Small additive improvements are accumulated over several cycles of crossing and selection.

In many cases, horizontal resistance is moderately to highly heritable. Resistance to brown spot in lupins was not strong in its effect, but was expressed very consistently across sites and years with high broad sense heritability (Cowling *et al.* 1997). It is possible to breed for resistance, quality and yield at the same time (Cowling 1994). However, it is not possible to breed for horizontal resistance in the presence of vertical genes - horizontal
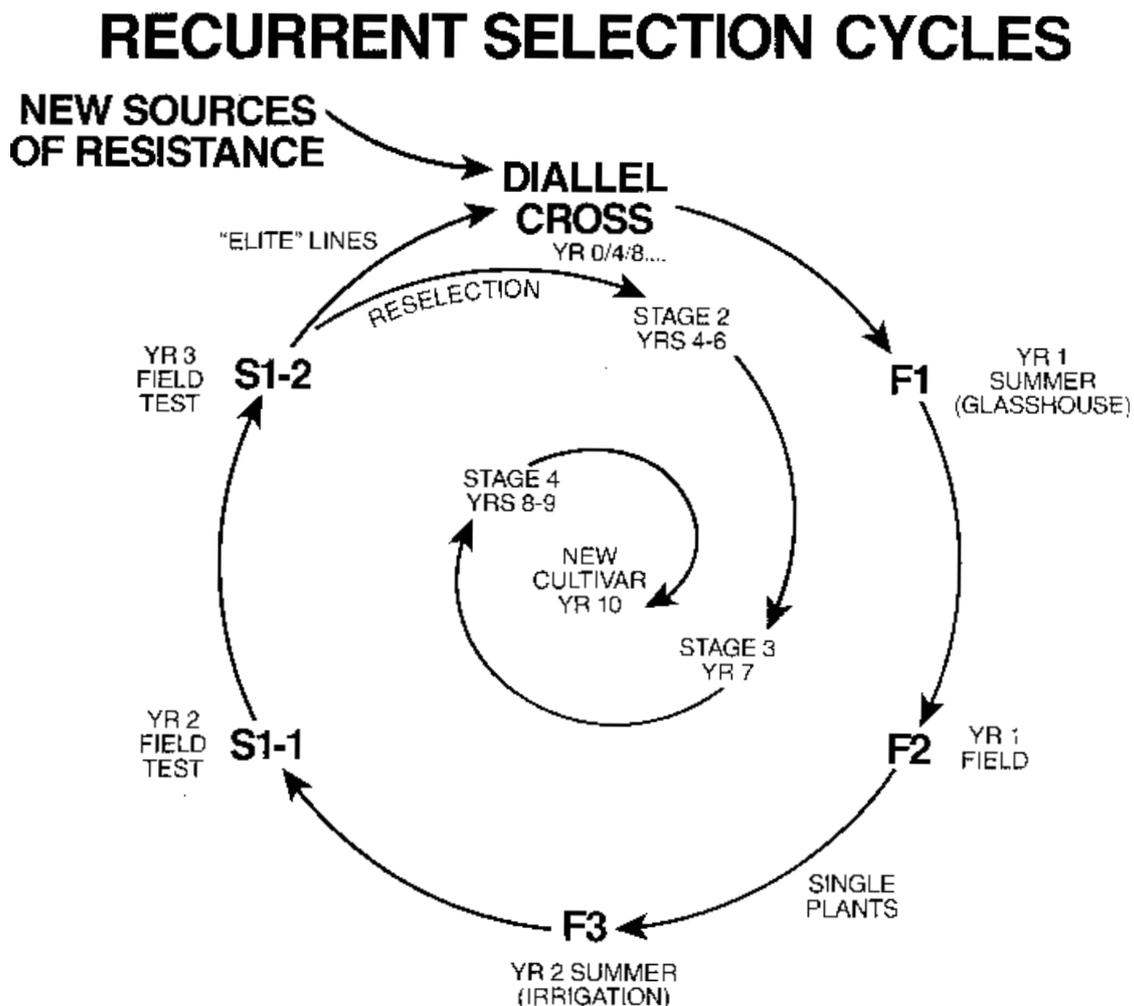
Figure 6. Recurrent selection cycles for improving yield, quality and resistance to brown spot in narrow-leafed lupins in Western Australia. Cycles last 4 years from crossing to selection of F_2- derived progeny for the next cycle of crossing, during which time two years of field testing is carried out in replicated yield trials. Reselection at the F_5 allows superior lines to be tested for potential release as new varieties.

resistance is masked by vertical resistance genes. Breeding for horizontal resistance must occur in the absence of vertical genes, as John Niederhauser discovered in 1954.

Robinson (1987) discussed procedures for breeding for horizontal resistance against disease. These include: look for moderate, but not strong, resistance in parents; nullify vertical resistance genes (use virulent races of the pathogen); use population breeding methods (recurrent selection); breeding must be "holistic" - against all important diseases, in the target environments; care must be taken to detect "escapes" (susceptible types); select the most resistant off-spring - it is the relative difference in disease levels that is important in early generations.

Stable agriculture may depend on the development of stable disease resistance in crop plants. Population breeding methods may provide the means to develop stable resistance.

Brown spot resistance in lupins: a case history of recurrent selection

Recurrent selection is described in lupins in WA, where closed populations of lupins have been bred with simultaneous improvements in yield, quality and disease resistance.

I have adopted recurrent selection as one of my breeding strategies in lupins. Closed populations undergo early generation selection (as F_2-derived lines) for yield, disease resistance and quality. Parents are crossed in all possible combinations (a diallel cross) to begin cycle 1 (Fig 6). After quickly proceeding through early generations, including over-summer generations where possible, F_2-derived lines are tested for yield, disease resistance and quality in replicated field trials in the second and third year. The best of these are selected as parents to begin the next cycle of recurrent selection, and are reselected for further testing and possible release as new varieties.

I have bred lupins for resistance to brown spot by recurrent selection. Brown leaf lesions cause the leaves to fall off prematurely, and if seedlings are attacked early in the season they may be killed. Yield is often reduced by brown spot disease, and it is present in nearly all lupin crops.

Improvements in resistance to brown spot have occurred in a closed population during three cycles of recurrent selection (Fig 7). The vertical axis represents defoliation due to brown spot, measured relative to a control variety Danja which is set at 100%. Along the horizontal axis are the parents used to begin the first, second and third cycle of recurrent selection. All parents were grown together in the same experiment repeated at several sites in WA from 1990 to 1992.

There was a significant decrease in defoliation due to brown spot in the parents of cycles 1 (1984), 2 (1988) and 3 (1992) (Fig 7A). Even more importantly, the best parents in 1992 were more resistant than any of the parents crossed in 1984. Without adding any new resistance genes, resistance is now stronger than in the original parents.

The lines were also selected for yield and other characters during the selection process. Yield increased

gradually from cycle to cycle, with some 1992 parents out-yielding the best of the 1984 parents (Fig 7B). Improvements were made to both disease resistance and yield at the same time, in the same breeding material, without adding any new genes. There was no yield penalty for improving disease resistance.

After completing two cycles of recurrent selection in lupins, the following improvements were evident; compared with control cv Danja, brown spot resistance increased 10-14% per cycle, yield increased 5-6% per cycle, Phomopsis resistance increased 30-50% per cycle (this was an added bonus, and unexpected), and average seed alkaloid levels also dropped markedly (Fig 7C). New varieties of lupins in Australia must be lower than cv Danja in seed alkaloids.

As a result of the first cycle of recurrent selection, a new lupin variety with a moderate level of resistance to
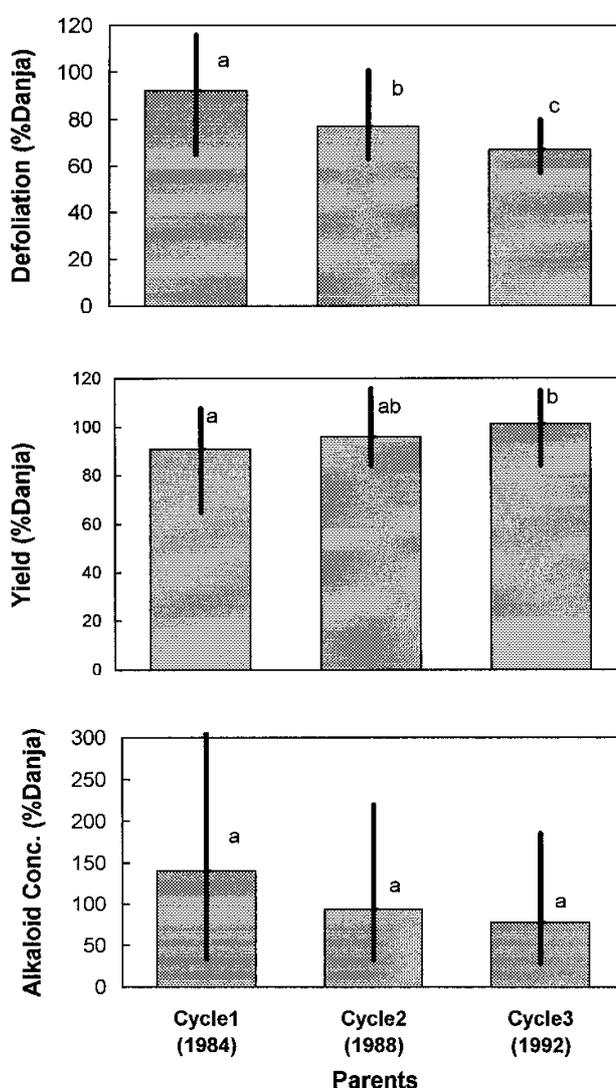
Figure 7. Improvements in resistance to brown spot (**A**), grain yield (**B**) and seed alkaloid concentration (**C**) in parents of the first three cycles of recurrent selection in a closed population of narrow-leafed lupins, compared with control variety Danja (bars represent the range from hightest to lowest parent; letters represent significance of difference between cycles at *P* = 0.05). Source: Cowling (1994).

brown spot (cv. Myallie) was released in 1995 (Anon. 1996). Myallie also has strong Phomopsis resistance, competitive yield (especially in low rainfall areas of WA where brown spot is most damaging to lupins) and low seed alkaloids. These results are significant on a global scale, because very few breeding programs of self-pollinating crops have released commercial varieties from recurrent selection programs. Until recently, recurrent selection has been restricted to specific research projects (usually PhD research projects) or to breeding of cross-pollinating forage crops.

The future of plant breeding and stable agriculture

There are many strategies that plant breeders can adopt to improve their chances of contributing to the long-term stability of agriculture.

What strategies should plant breeders adopt in order to contribute to stable agriculture in the future?

1. Diversify the gene pool: Invest in the future - create diverse populations in addition to the elite material in the program. Add new genes from new varieties bred elsewhere, or use wild types or landraces from genetic resource collections. Cross into elite lines, and reselect for the quality or adaptation that is required.

2. Introduce exotic genes: interspecific crosses, mutation or genetic engineering. Any source of germplasm is potentially valuable. However, for disease resistance, beware of major genes that may not be durable, or that prevent progress in breeding for polygenic resistance.

3. Use population breeding methods: As demonstrated here, population breeding methods have contributed to increases in disease resistance, yield and quality simultaneously. Disease resistance developed by these methods is usually polygenic and durable.

Crop plants have been evolving since the beginnings of agriculture 10,000 years ago. We may be witnessing a period of "punctuated equilibrium" in the evolution of crop plants, as proposed for evolution in nature (Gould & Eldredge 1993). Wheat and maize have evolved away from their wild relatives in the past 10,000 years due to human intervention (Duvick 1996). Lupins are just beginning to do so. In the Mediterranean region, *L. albus* var. *albus* has been cultivated for thousands of years and is relatively remote from its wild ancestor *L. albus* var. *graecus* in morphology, colour and seed size (Gladstones 1974).

Plant breeders therefore have a great responsibility to lay strong foundations for the future evolution of crop species. The genetic diversity that is now created will become the future gene pool of several new man-made species, which, like wheat or maize, are so remote from their wild ancestors that little introgression from wild relatives will be possible.

I believe that stable agriculture may be achieved if crop rotations are profitable and adapted crop species and varieties are available for growing on each soil and in each climate. Land conservation measures will be an essential component of stability, and another essential component will be the breeding of crop plants with du-

rable disease resistance, low pesticide requirement, high yield and quality, and adaptation to regional environments. Regional adaptation will become more and more important, and the universal crop variety will become a thing of the past. Barley in WA is bred in different gene pools for high and low rainfall environments - a similar situation is likely to develop for lupins over the next several decades.

Breeding programs must have short-term and long-term goals. Given the current push towards privatisation at all levels of Government, it is important to ask: who will take responsibility for the long-term maintenance of genetic diversity in crop breeding? I have indicated that diversity is essential for long-term breeding progress. In Europe and the USA, very few private breeding programs have taken on this role in the case of the common bean, and the gap between the identification of useful characters in exotic germplasm and the transfer to cultivars has widened (Silbernagel & Hannan 1992).

Population breeding methods help to generate genetic diversity, but are still not the favoured procedures in self-pollinating crops. Farmers and plant breeders alike need to ask themselves; what level of disease resistance is sufficient? Do I really need immunity? In most cases, a moderate level of resistance is sufficient, when combined with agronomic or other management packages. Population breeding methods are most ideally suited to long term genetic gains and sufficient lead-time must be allowed to achieve significant gains.

Intuitively, plant breeders will use whatever genetic variation is available to them to improve adaptation of plants to the environment. The future stability of agriculture depends, to some extent, on how successful they are in producing stable varieties, with stable yield, thereby improving the stability of crop rotations, leading to stable profits, and allowing further investment in stable agriculture.

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