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BREEDING LONG-LIVED PERENNIALS — FRUSTRATIONS, TEMPTATIONS, OPPORTUNITIES

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ABSTRACT

Long-lived perennials typically show at least some of the following characteristics: long generation intervals, protracted evaluation times, heavy capitalisation of crops, high costs of breeding inputs, slow and irreversible maturation, and insidious viral infections. These features reduce margins for error in breeding, and necessitate carefully integrated breeding strategies to assure continued genetic gains.

Emphasis must be placed on developing efficient propagation technologies, shortening generation times, and quicker and improved screening methods.

Prospective methods of genetic manipulation are attractive, but more as a complement to classical breeding methods and management of genetic resources than as a substitute.

KEYWORDS

Breeding strategy, mutation, selection criteria, selection methodology, screening, *Pinus radiata*.

INTRODUCTION

Long-lived perennials (LLPs) are taxonomically diverse, but their classical features are: long generation time, delays in evaluation of genotypes, high costs of replacement or re-establishment of crops, requirement for considerable space and other resources in breeding work, susceptibility to insidious effects of viruses etc, and/or somatic mutation, and slow and essentially irreversible maturation.

The resulting problems, while not qualitatively different from those in other areas of plant breeding, can be acute, especially when the features occur in combination. Mercifully, few LLPs show all these features. The relative importance of the respective features is shown for some plant species in Table 1. By contrast, practically none of these features are a problem in crops like cereals.

The problems reduce margins for error. Genetic gains per generation should be maximised, yet without compromising improvement in future generations. Careful choice of mating designs, good screening procedures, efficient selection methodology and appropriate propagation technology coupled with good genetic information are required. Market risks and biological risks are especially important.

All these factors accentuate the need for coherent and well-structured breeding programmes. Yet with many species there is little management or market experience to focus worthwhile breeding effort on individual species.

PROPAGATION TECHNOLOGY AND BREEDING METHODS

The propagation characteristics of a species impose

Table 1. Approximate relative importance for plant breeding, of different features of perenniality in a range of long-lived perennials. (Note: this is intended to illustrate contrasts among species rather than to attempt definitive statements for each case)

Problem feature	*Pinus radiata*	Apples	Kiwifruit	Perennial ryegrass	Lucerne	Wine grapes
Generation interval	***	**	**		*	*
Evaluation time	**	***	***	*	*	****
Space requirement etc	***	***	***	*	*	**
Crop replacement costs	***	**	**	*	**	***
Maturation (irreversibility)	***	**	***			
Virus infection	?	**	?	*?	*?	***

***denotes extremely important ...... *denotes of minor importance. ? denotes situation uncertain.

biological constraints that dominate the choice of breeding procedures and even the organisation of breeding. The constraints relate to: maturation, seed production, grafting, rooting and growth of cuttings, *in vitro* propagation, pollination biology, and crossability between species. Some of the constraints are inherent features of LLPs, some are not. In breeding LLPs, however, all such constraints can be troublesome.

Among LLPs, the constraints are extremely variable, so too are the breeding methods. Hence advances in propagation technology, e.g. *in vitro* propagation, or improvement of more conventional vegetative propagation, can dramatically change breeding methods.

Maturation creates many problems. A kiwifruit vine takes several years to manifest its sex, let alone its fruit and cropping characteristics. In forest trees a candidate genotype is often intractable for mass vegetative propagation by the time it is proven (Burdon, 1982). Control of maturation state could free resources for some very rewarding aspects of breeding.

Seed (or fruit) production, in its abundance and timing, is of variable significance. For fruits and nuts it is most important. In forest trees, however, seed production may assure mass propagation and genetic recombination, but probably compromises wood production.

The production of cuttings or grafts can be crucial for some crops, and yet be an unlikely prospect in others. Grafting demands subsequent compatibility as well as initial take. It also requires rootstocks that are at once suited to the scion cultivars, climate, soil and management regime.

Tissue culture may offer greatly extended use of cuttings, control of maturation state, genetic manipulation, or elimination of viruses.

Dioecy is unwelcome in fruit growing, and may be hard to overcome. Self-fertility in LLPs may lead to inbreeding depression. The only promising route to crop uniformity without vegetative propagation is to produce haploids — if they are viable and fertile.

Crossability between species has obvious advantages — provided one can mass-produce F1 hybrids.

The breeder must seek improvements in propagation technology without holding up the immediate breeding work. Often there are many possible avenues for improved propagation which will necessitate exploring a range of possible propagation technologies at major research effort.

Genetic parameters, technical requirements, and management considerations must also influence the choice of breeding methods. Where uniformity and seedlessness are needed, e.g. in citrus, a clonal system may be mandatory. Strong non-additive gene effects will favour either mass-production of controlled crosses, or a clonal option. In outbreeding forage grasses and many forest trees the currently available options make genetic segregation inevitable, but this within-crop variability can be a buffer against pest attacks and genotype-environment interaction.

SIGNIFICANCE OF VIRUSES

Viruses in LLPs can mimic somatic mutations. While the problem is now widely recognised, its extent is not yet clear. Viruses can cause an insidious decline in cultivar performance, and lead to graft incompatibility. However, culture methods often exist to rid vegetative material of debilitating viruses; most such viruses are not transmitted by seed; viruses show little tendency to overcome host resistance through mutation, and there is the prospect of cross-protecting plants with asymptomatic strains.

SELECTION CRITERIA

LLPs are not distinguished by a common set of breeding objectives, or selection criteria (Table 2). They do, however, pose some special problems in choice of selection criteria.

Genetic improvement and the management systems are

Table 2. Approximate relative importance of different categories of selection criteria in a range of long-lived perennials, with special reference to New Zealand conditions. (Note: this is intended to illustrate contrasts among species rather than to attempt definitive statements for each case)

Criteria	*Pinus radiata*	Apples	Kiwifruit	Perennial ryegrass	Lucerne	Wine grapes
Environmental tolerances	*	*	**	***	***	****
Disease/pest resistance	**	***	?	**	****	***
Ideotype	****	***	*?	****	***	
Production	****	**	**	**	*	**
Seasonality		**	****	***	**	**
Harvesting characteristics		**				*
Quality traits	****	****	****	**	**	****
Propagation characteristics	*		***	*	**	

**** denotes extremely important.
⋮
* denotes of minor importance.
? denotes situation uncertain.

often alternative routes to particular objectives, but the ideal is a synergism between the two. Among fruit trees, the advantages of 'column-habit' mutants in apples depend on streamlined propagation and establishment. In forage grasses management must be matched to biotic type. In forest trees genetic improvement effort may not mean improved product quality, but instead maintain product quality under management practices that greatly reduce growing costs, e.g. maintaining acceptable wood density with shorter rotations.

Even if the relationship between breeding and management practices is defined, the choice of selection criteria remains vexing, since the pursuit of any selection criterion will tend to reduce genetic gain in others. The question is especially vexing with LLPs, where the time frame exacerbates risks and where there is often little management or marketing experience. Technical criteria involve market risks, while pest resistance can involve major, and often unknown, biological risks. Learning by mistakes may therefore be very costly. The best genetic defences are to have the genetic variability available, plus the propagation technology for prompt utilisation of new selections.

SCREENING

Definitive screening often comes from progeny tests, but these are often very cumbersome for LLPs. Such tests can have the additional justifications of providing genetic parameter estimates, retaining pedigree, and providing candidates and family information for 'forward' selection. However, since the same mating and field design parameters are not efficient for all objectives compromises must always be made.

Projecting future performance in LLPs from juvenile phenotypes can be acutely difficult, unless juvenile-adult correlations are known to be good. Also difficult to predict is productivity of a crop as distinct from individual plant performance. Empirical screening of numerous candidates for their contributions (perhaps in interaction with others) to crop performance is likely to be prohibitive and, when achieved, give selections that are already obsolete for other selection criteria. The problems of screening in LLPs create a special temptation to seek simplistic indicators of certain selection goals, e.g. photosynthetic rate to indicate growth rate, but such indicators often fail both empirically and under theoretical scrutiny. However, frost and herbicide resistance are characteristics that may be readily identified by artificial screening.

For disease resistance, artificial screening is relatively attractive, but it may be important not to direct the screening at a single mechanism of resistance which by itself could lack durability against pathotype shifts.

The concept of the ideotype for defining complex selection criteria has particular attractions with LLPs — if ideotypes are defined correctly and if clonal propagation is available for ideotypes that are not readily subject to genetic fixation. Forage plant breeding has implicitly recognised the ideotype concept for various management regimes. Explicit recognition in 'column-habit' apples, is a recent case in fruit breeding. In forest trees we are moving towards ideotype definition (Karki, 1985; Shelbourne *et al.*, in prep.), but a more definitive application of ideotypes is required than for cereals where selection among segregants can easily be followed by empirical testing of candidate lines.

Genotype-environment interaction is very important in screening and to the structure of breeding programmes. I believe that the interactive behaviour of environments has often received inadequate attention relative to the interactive behaviour of genotypes. This is especially true where emphasis must be on population improvement — the situation in many LLPs. Apart from the need to define unavoidable environmental breeding units we should try identify environments that give good resolution of genetic differences and, better still, that identify broadly adapted genotypes.

Perennials, by being exposed to all seasons and to climatic fluctuations, tend to face comparatively complex environments. This is particularly so with forest trees, where limited manipulation of environment may be possible. It may thus be difficult to proceed beyond empirical screening, except by applying basic genecology.

SELECTION METHODOLOGY

Selection methodology has inbuilt problems with most LLPs. Different traits are expressed at different ages, and involve different amounts of effort per individual screened. For individual traits threshold levels of acceptability are often perceived. These factors favour sequential culling. Such culling, however, may prejudice the estimation of genetic parameters and thus prevent effective use of selection indices in later culling.

LONG-TERM AND SHORT-TERM CONSIDERATIONS

Conflicts usually arise between short-term and long-term considerations — maximising first-generation culling may prejudice future genetic gains. Breeders of annuals can turn over several generations before making a release, but with LLPs this is often prohibitive.

In fruit tree or vine breeding it is natural to seek new cultivars from each crossing generation with early and heavy culling for thresholds of acceptability. Such immediate culling may compromise success in a subsequent generation, but the logistics of retaining and managing a large number of segregants are daunting. An orchard of seedlings comprising a breeding population could demand at least as much work as a commercial orchard, without producing the requisite quality and uniformity of fruit. Any way of recouping costs of running such orchards would be attractive.

An underlying issue here is gene conservation. Living collections are often necessary if the genetic resources are to be usable. Moderate selection in such material seems essential for many LLPs, to give acceptable breeding material within reasonable time. Such selection can also allow larger populations to be kept for a given opportunity cost; this factor may far outweight any loss of genetic variability from the selection *per se*.

BREEDING STRATEGY

Just as important as individual aspects of breeding is overall strategy. Forest tree breeding is an instructive example. In methodology it has closer affinities with animal breeding than with breeding crops like cereals. Because of the large and long-term commitments entailed in decisions much theoretical work has been directed at choice of : selection methods, selection criteria, the timing and intensities of selection, generation intervals, mating designs and field layouts. This has evolved into the well-developed discipline of tree breeding strategy, (e.g. Matheson, 1983; Namkoong *et al.*, 1980; Namkoong, 1977; Burdon *et al.*, 1978; Libby, 1973).

A good strategy should accommodate uncertainties regarding genetic parameters, appropriate selection criteria, cost and price structures, and future propagation technology. The components of a strategy can be listed as:

- Organisation of populations — e.g. seed orchards, breeding populations (progeny trials and archives), gene resources
- Methodology — selection methods, mating designs, field designs, screening methods, propagation technology
- Research programme

Just as important as the components are how they are integrated, and their timing. The organisation of populations is especially important for achieving long-term flexibility. In forest trees, seed orchards are underpinned by breeding populations which, while less select, represent broader genetic bases. Breeding populations are likewise underpinned by gene resources. The usefulness of this organisation, however, depends on a means of rapid propagation if new selections become imperative. The value of a shortened generation interval will depend on efficient early screening. Improved methods of multiplication greatly enhance the value of early screening.

Blunders in tree breeding strategy have proved very costly. Using the wrong species or geographic race, too small a breeding population or an inappropriate mating design, can force a fresh start.

PSYCHOLOGICAL AND ORGANISATIONAL ISSUES

To continue with the same example, tree breeding may appear to give breeders ample time to avoid blunders, but it often proves otherwise. The time frame and work content, while unforgiving of blunders, can make it difficult to retain a perspective when attending to daily matters. Moreover, various research and breeding operations, e.g. establishment of progeny trials and seed orchards, must be conducted in parallel. Hence, decisions often entail guesses, and more important, there can be an insidious increase in the commitment to follow through experiments while routine propagation must continue. Such commitments can deter the breeder from acting promptly upon fresh information or new breeding objectives.

Writing a forward development plan is invaluable. It directly assists the breeders and allows outsiders to make a more effective input. Explicit critical path analysis and scenario studies may be under-used tools.

Breeding of LLPs such as forest trees can demand an especially sustained and intensive commitment. This requires strong central direction. Like much plant breeding, tree breeding is done within research organisations. However, tree breeding work can be an anomaly in a research organisation. A juxtaposition of research and breeding is admirable, with the breeding work providing much research information, but the pressure of breeding work can make it difficult to sustain a balanced research effort. University involvement can help.

The protocols for plant variety registration can be a problem for LLPs. This arises where propagation constraints and the need for genetic diversity within crops place emphasis on progressive population improvement. With forest trees, however, one might register individual clones, albeit as crop components rather than actual crops. Plant breeders' protection stimulates breeding work by private enterprise, but such work with LLPs has tended to focus on end products rather than the infrastructure of gene resources and breeding populations.

IMPACT OF NEW DEVELOPMENTS

Advances in genetic knowledge and techniques could revolutionise plant breeding, although comparatively few changes are likely to follow quickly.

It is a challenge to apply genetic theory and knowledge to enhance the efficiency and reduce the risks of breeding. We have made much progress in this direction with forest trees. Much work on grapes, however, is almost counter to current genetic theory.

The possible short cuts using genetic manipulation look especially attractive for LLPs, particularly for fruits where highly specific characteristics may be sought. Yet we must achieve co-adapted genomes, despite any manipulation, for the comparatively 'wild' environments in which many perennials are grown. Manipulation, along with new propagation technology, at once promises high gains and a line of defence against risks in plant breeding. However, I do not see it substituting for gene conservation but rather helping to capitalise upon it.

A CASE HISTORY — PINUS RADIATA IN NEW ZEALAND

Although fast-growing, *Pinus radiata* is still a LLP. It has a feasible generation time of 10 years or more and it requires at least five to eight years for satisfactory evaluation of progenies. Grafting is easy but plagued by delayed incompatibility. Seed production is relatively light and not especially precocious, with at least two years from pollination to cone ripening. Maturation makes it difficult to root cuttings, it is essentially irreversible, and is a major constraint.

Intensive breeding of *P. radiata* centred at first on multiclonal seed orchards, producing open-pollinated synthetic 'breeds'. For various reasons such orchards have been large, producing general-purpose stocks but each serving a broad geographic region. (However, some provision has been made for producing an alternative crop type, the so-called 'uninodal' crop type which, in contrast to the general-purpose 'multinodal', is characterised by long intervals between consecutive clusters of branches on the stem.) Such seed orchards now produce nearly 100% of the country's seed requirements, but they are very cumbersome and slow to deliver genetic gains. Technical problems with propagation still tie up major resources. The lead time from selection to full seed production, pollen contamination from outside the orchards, and unequal fecundity among parent clones, have all eroded potential genetic gains. Work on the promotion of flowering and seed production gave disappointing results, beyong confirming the importance of choice of orchard site.

We are now testing a new type of seed orchard, based on controlled pollination. This offers heterosis, if only through crossing parents with complementary merits. It will provide lines that are far more specialised and will allow continual upgrading or restructuring of synthetic varieties as new selections become available. The potential advantages of breed specialisation are becoming clearer, thanks to better information on genetic correlations between traits and on the relative importance of different selection criteria in different regions. How much planting stock can be produced directly by controlled crossing is not known, but we have the technology for mass vegetative multiplication of pilot-scale crosses between the latest selections. In retrospect, vegetative multiplication of juvenile material received belated attention.

While the use of genetically diverse crops seems prudent, we may progress to clonal forestry. Such clones would be grown in either mosaics or intimate mixtures.

Attention to long-term breeding requirements and the potential genetic vulnerability of the species was somewhat belated. After one major re-start we have two large pedigreed breeding populations representing the divergent multinodal and uninodal crop types. These will have effective sizes of 300 or more, and will give cumulative additive genetic gains which will be supplemented through intensive selection for the orchards. The breeding populations are supported by even broader based gene pools, derived mainly from recent collections in natural stands. The value of the gene pools against a new disease depends on pre-emptive cleaning-up by mild mass selection, and having the means for effective screening and rapid propagation of new selections.

The complexity of the breeding programme has prompted a formal Development Plan, which sets out the history, forward strategy of the breeding programme, and proposals (Shelbourne *et al.*, in prep.). Some other tree breeding organisations are doing the same (Cotterill, 1984; Rauter, 1984).

OPPORTUNITIES AND TEMPTATIONS - A PERSPECTIVE

Despite the problems there are often major advantages in breeding LLPs. Many LLPs, notably forest trees, have little or no history of true domestication. Hence the genetic bases are often essentially intact, leaving great scope for selection between and within populations.

Starting with wild material, breeders can often avoid mistakes that have plagued past breeding of crop plants (and fruits). Hopefully, the potential magnitude of the problems will make breeders duly cautious.

For disease resistance, undomesticated species will tend to have the natural pathosystems intact, with multiple resistance factors present. This will help avoid the boom-and-bust resistance of some intensively domesticated crops, a phenomenon that could be disastrous in forest trees where the resistance may need to last for the rotation and not just until a new cultivar is produced.

Few generalisations are possible for other areas of genetic improvement. The greatest gains in production from plant breeding are typically from boosting low harvest indices. Among LLPs, however, harvest index ranges from very high in forest trees to very low in nut crops. The importance and nature of quality-related selection goals must vary according to the range of products from LLPs.

Easy vegetative propagation, however, has great dangers. It favours concentration on the single best clones, which can lead to either spectacular epidemics, or crop decline through the spread of viruses. It also can provide a disincentive to seek for something better. It can thus stifle the work on genecology and population improvement that allows progress towards the full genetic potentials. Easy crossability between species is another mixed blessing, particularly when vegetative propagation is easy. The temptation has been to hybridise without due selection within the parental populations. The combinations of qualities sought by hybridisation may have been easily obtainable and fixable within a parental species. Without ready means of vegetative propagation hybrids often remain as curiosities in arboreta. In retrospect, poplar breeding could have been more efficient if begun with due regard to these principles (Mohrdiek, 1983); New Zealand and Australia had to make a fresh start after overseas breeding had been effectively nullified by new diseases.

Whatever the pitfalls, the scope for breeding LLPs is epitomised by Hayward Wright's achievements with kiwifruit despite minimal knowledge and material. Less spectacular, but still substantial in relation to input have been the changes in *Pinus radiata* in one generation. By the same token, there is a special need to remember that genetic intervention can work unwitting mischief as well as great good.

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SYMPOSIUM DISCUSSION

Dr N.G. Hogenboom, Institute of Horticultural Plant Breeding

What is the prospect of speeding up the programmes and having better possibilities for selection, by producing haploids?

Burdon

That depends very much on the species. With poplars it may well be possible. With conifers I think it presents extreme problems. Conifers carry a very heavy load of embryo lethals which seem to function as an effective self-incompatibility system.

If we can achieve uniformity by vegetative propagation, we have an alternative means of achieving the uniformity which haploidisation promises. We could use haploidisation as a means of very stringent screening, but that will introduce an extra stage in the screening process. We would have, in effect, to go through an extra generation.

T.P. Palmer, private breeder, N.Z.

The objection to single clones — I was not clear whether you were talking about using single clones as parents or as production populations. In poplars for instance, I believe there are a lot of single clone populations in production.

Burdon

Indeed and there has been an absolute disaster with poplars in New Zealand, probably largely as a result of using single clones. In 1973, when two leaf rusts came into New Zealand they completely overturned all the screening work that had been done by the Ministry of Works at Aokautere. There were 9 clones that were recommended for general use and all were unacceptably affected by the rusts. A crash programme of selection of resistant clones was embarked on and has had considerable success. So, poplars in fact represent a classic example of a clonal forestry failure.

Palmer

Do they grow single clones in Europe where they have been growing poplars for a long time?

Burdon

Yes. They certainly have had problems with diseases although in the areas where they grow poplars the diseases have not been so damaging as in New Zealand. I think one has got to remember that poplars are not grown on a really large scale — they tend to be grown in relatively small woodlots. When dealing with a species like *Pinus radiata* — grown over hundreds of thousands of hectares on an extreme range of sites and under a very big range of rainfall — I think we have to be much more conservative.

Dr A.D. Thomson, Botany Division, DSIR

Has consideration been given to the inclusion of indigenous species in the breeding programme? *Nothofagus* and native podocarps are excellent timbers.

Burdon

We have looked at the question and would not consider having a breeding programme. A breeding programme depends on commercial interest in growing a species and on being able to regenerate it artificially. These are two conditions which are certainly not yet met. We have however done some groundwork — we have looked at native species and geographic races. A tree breeding programme has to service a large planting programme. For instance there is only one forest tree species in New Zealand for which we have an intensive and elaborate breeding programme (*Pinus radiata*). There are smaller breeding programmes for some of the eucalypt species but these were established, to some extent, incidental to problems of getting satisfactory seed sources.

Mr G. Pringle, Division of Horticulture and Processing, DSIR

What is the chromosome complement of *Pinus radiata* and its relatives, and to what extent has this influenced the breeding programme?

Burdon

P. radiata, like almost all conifers, has a diploid number of 24 chromosomes. The conifers as a group are cytologically very stable and any departure from that normal complement, aneuploidy or polyploidy, is quite disastrous. We are not consciously addressing the question of diploidy; we just treat *P. radiata* as an outbreeder and assume that all the traits we are working with are inherited quantitatively. That may not be strictly true, but experience suggests that you can have some major gene effects without making the quantitative assumptions seriously invalid.