

## ADVANTAGES OF CLONAL FORESTRY FOR *PINUS RADIATA* — REAL OR IMAGINED ?

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### ABSTRACT

The advantages of using tested clones in *Pinus radiata* D. Don forests were compared with current open-pollinated and control-pollinated seed orchard strategies. Clonal forestry shares with control-pollinated orchard strategies advantages of shorter plant production times, control of pedigree, flexibility of deployment, multiplication of valuable crosses, and efficient capture of additive genetic gains. It may have additional advantages in increasing uniformity, allowing clone/site matching, controlling growth habit, and capturing non-additive genetic gains. However, a control-pollinated orchard strategy coupled with vegetative multiplication is currently proving to be more cost-efficient in establishing managed stands. Use of a clonal strategy requires evidence for greater economic gains.

**Keywords:** clonal forestry; controlled pollination; additive variance; general combining ability; specific combining ability; *Pinus radiata*.

### INTRODUCTION

During the last 20 years, rapid advances have been made in developing techniques of large-scale vegetative propagation of forest tree conifers and hardwoods. Numerous species can now be cheaply and efficiently multiplied using rooted stem cuttings. Micro-propagation (generally using embryo culture) provides another plant multiplication method that may soon enable mass production of several conifers (Smith 1986; Ritchie & Long 1986), including *Pinus radiata*. Not surprisingly, these developments have engendered considerable interest in the potential of clonal forestry – defined here as “the establishment of plantations using tested clones”.

The advantages of clonal forestry have been stated by many authors (e.g., Libby 1983; McKeand 1981), while others have begun to examine the effects of cloning on breeding and seed production programmes (Shaw & Hood 1985; Matheson & Lindgren 1985; Burdon 1986). Unfortunately, proponents of clonal forestry have not always recognised a distinction between the advantages of plant multiplication per se, and the additional advantages of using tested clones. The distinction becomes crucial when alternative methods of multiplication are available, allowing managers to choose both the genetic unit of multiplication and the amount of multiplication employed. For example, for *P. radiata* in New Zealand, multiplication of improved genotypes can

occur as seed from open-pollinated seed orchards (approximately half-sib families), as seed from control-pollinated seed orchards (pair-cross or polycross families), as cuttings from nursery propagation (families or single clones), and as micropropagules (families or single clones). It would be theoretically possible to meet the annual demand for *P. radiata* plants from any of these methods. Production costs and logistical constraints will differ, but genetic quality is likely to be the main factor affecting the ultimate choice of multiplication method.

Vegetative propagation can therefore be used for simple multiplication of improved seed stock, or for multiplication of individual performance-tested clones. A vegetative propagation technique must satisfy two criteria for successful implementation of clonal forestry:

- (1) The capacity to conserve the inherent superiority of candidate clones, without genetic change or further maturation, during a clonal testing phase, either through appropriate storage of clonal material or through rejuvenation of selected clones;
- (2) The capacity to multiply the selected clones to useful numbers at reasonable cost, and without dilution of gains in genetic quality by having to use a larger number of clones.

Early attempts to practise clonal forestry for *P. radiata* in New Zealand were based on a method of raising stem cuttings from hedged clonal archives (Thulin & Faulds 1968). These attempts ultimately failed on both criteria listed, since –

- (a) Deleterious maturation effects on rooting ability and growth rate of cuttings were a problem (even although these effects were delayed by the hedging process) and further maturation occurred when clones were repopulated (Sweet & Wells 1974);
- (b) The maintenance of clones in hedged archives was subject to attrition due to graft incompatibility and other propagation problems;
- (c) An impractically large number of hedges was required to produce useful numbers of stem cuttings.

This paper reviews some of the stated advantages of clonal forestry (using tested clones) for *P. radiata* in New Zealand in comparison with use of the products of open-pollinated and control-pollinated clonal seed orchards.

## **ADVANTAGES OF CLONAL FORESTRY**

Libby & Rauter (1984) listed as many as 18 advantages of clonal forestry (Table 1), which may be viewed as a synthesis of those put forward in the wide literature on cloning of forest trees. Since these authors do not clearly distinguish between cloning as a means of plant multiplication and the use of individual (and presumably tested) clones it is necessary to interpret their list for this distinction and as it may apply to the propagation of *P. radiata*.

### **Advantages Less Applicable to *P. radiata***

The somewhat daunting list of advantages in Table 1 can be reduced by removing those advantages that do not seem applicable to New Zealand *P. radiata* management.

TABLE 1—Advantages of clonal forestry (adapted from Libby &amp; Rauter 1984)

**A. Long-recognised advantages**

1. Ease of propagation\*: for species that are more easily propagated by cuttings than by seedlings.
2. Research\*: use of identified clones to reduce unwanted bias, or variability in experiments.
3. Capture of favourable information: effective selection for both additive and non-additive genetic components.
4. Cost-effective propagation of expensive genotypes: multiplication of expensive hybrids, control-cross families or genetically engineered plants.

**B. Increasingly appreciated advantages**

5. Unusual sites: propagation of ecotypes with specific adaptation to unusual sites.
6. Site-specific and broadly adapted clones: to enable clonal strategies of either deploying a best set of broadly adapted clones or carefully matched sets of best site-specific clones.
7. Prevent inbreds in plantations: by using pedigree clones, preventing planting of inbreds in production plantations.
8. Time from selection to production deployment: i.e., shorter time (for clones) between selection of superior trees and the availability of large quantities of planting stock, when compared to seedlings of clonal seed orchard progeny.
9. Knowledge: advantages of managing a well-understood set of clones.

**C. New advantages**

10. Genetic diversity: ability to control genetic diversity and design plantations that are significantly safer than seedling plantations from damage by pathogens or environmental agents (e.g., wind).
11. Species diversity\*: two elements of clonal forestry that contribute, through the ability to (a) match compatible clones in mixed-species plantations, and (b) to house clones of several different species in the same hedge orchard.
12. Reduction of reproductive activity: to choose "poor-flowering" clones to achieve reallocation of photosynthate from cone and pollen production to bole-wood growth.
13. Correlation breakers: to identify clones that "break" negative correlations between economically important traits and yield greater over-all gains from selection.
14. Maturation states other than juvenile: to choose a maturation state that confers advantages of improved resistance and tree form, when compared to the juvenile seedling state.
15. Donor management: simpler and cheaper management of hedged orchards than production seed orchards.
16. Deployability: specificity and flexibility of deployment of adapted clones to plantation sites.
17. Programmed planting sequences: maximising productivity by sequencing clones that make complementary demands on their environment.
18. Conservative philosophy: clonal forestry allows a more conservative approach to the genetic manipulation of forests than does classical tree improvement, since it may begin with a broader genetic base and, through constant evaluation, yield an increasingly reliable set of "production clones".

\* Advantages that do not appear to be applicable to *P. radiata* in New Zealand.

- The use of cloning for research purposes (Advantage 2, Table 1) can be accepted as important, with the proviso that research results gained from clones should then be applicable to the type of planting stock used in production plantations.
- Matched clones for use in mixed-species plantations (Advantage 11, Table 1) would be unlikely to be used with *P. radiata*, since the species is almost invariably grown in pure stands (although compatible species mixtures are recommended for use in "timberbelts").
- The major historical reason for using clones – for species that are more easily propagated by cuttings than by seedlings (Advantage 1, Table 1) – is not a crucial factor for establishing *P. radiata* plantations. Bare-rooted seedlings are currently cheaper to produce than either rooted cuttings (Menzies *et al.* 1985) or tissue culture plantlets (Smith *et al.* 1982).

### **Alternative Methods of Multiplication of *P. radiata***

Some review of alternative techniques of plant production is required to enable critical examination of the remaining advantages of clonal forestry as they relate to *P. radiata*.

#### *Open-pollinated seed orchards*

Conventional clonal seed orchards of *P. radiata* have been established from the mid-1950s to the present. These orchards have been successful in recent years in meeting total seed demand, and in greatly improving the genetic quality of production stands (Shelbourne *et al.* 1986). However, this conventional seed orchard approach has also been found to constrain the potential genetic quality of improved seed by:

- The need to maintain a minimum effective number of clones (at around 12 or more) to avoid inbreeding through crossing among trees of the same clone;
- Losses of trees due to graft incompatibility;
- Limits to flexibility, such that changes in preferred selection criteria can be implemented only by "roguing" after an orchard is fully established, or else by establishing new orchards;
- Pollen contamination from unimproved trees outside the orchard.

#### *Control-pollinated seed orchards*

Control-pollinated seed orchards have been developed as an alternative to the conventional open-pollinated orchards (Sweet & Krugman 1977). They consist of hedged trees of performance-tested parent clones, on which controlled pollination is carried out by injecting known pollens into cellulose bags containing the developing conelets. Compared with open-pollinated orchards, control-pollinated orchards have several advantages since:

- Pollen contamination can be eliminated;
- The minimum effective number of clones in the orchard can be reduced to as low as two without incurring inbreeding: this means that the number of pollen parents can be reduced to a minimum of one;
- Selection criteria can be altered to "tailor" seed mixes for use on specific sites or for specific quality criteria.

Crosses in control-pollinated orchards can be made either by using selection based on estimates of the general combining abilities (GCA) of the parent clones, or by repeating crosses that have already been tested for their general combining ability plus specific combining ability (SCA). Results of recent studies favour the use of parental GCA information (Carson 1986) which is the easier testing option.

The main disadvantages of control-pollinated orchards relate to the higher costs of seed production (about six times that for conventional orchards), and the smaller quantities of seed that can be produced.

#### *Vegetative propagation*

Recent work on *P. radiata* at the Forest Research Institute (Menzies *et al.* 1985) and elsewhere (Clarke & Slee 1985) has concentrated on rooting cuttings from younger trees (i.e., up to 5 years old). Several techniques are currently being evaluated for multiplying control-pollinated seed orchard stock. Used as a tool for "vegetative amplification" these techniques offer potentially high rates of multiplication without attrition of gains from maturation-related effects. However, the extension of in-bed multiplication methods to clonal forestry requires a successful method of preserving clones in an appropriate maturation state during the testing phase.

Micropropagation techniques offer an alternative method for multiplication of improved seed stock, based on a combination of embryo culture and mass culture of shoots arising from cotyledon tissue (D. R. Smith, pers. comm.). A pilot programme run by Tasman Forestry Ltd is currently mass-producing clones from selected control-pollinated families using this method. However, field tests of micropropagated material have indicated that growth rates may be less than for seedling stock of similar genetic quality (Smith 1986), and there are some additional problems in taking the method to a full production scale.

#### *State of current options for producing planting stock*

To summarise the state of current options for producing genetically improved *P. radiata* —

- Conventional open-pollinated seed orchards are producing seed that can be used as seedling stock, or can be vegetatively multiplied as juvenile cuttings;
- Control-pollinated seed orchards are producing more limited quantities of seed of polycross families, but which can be multiplied as juvenile cuttings;
- Clonal forestry, while not yet a practical commercial option, may become feasible in future. The most promising option is for the cold storage of tissue-cultured shoots during clonal testing, followed by multiplication of tissue cultures to create nursery stool beds suitable for mass production of cuttings (Smith 1984; Menzies *et al.* 1985).

In Table 2 are listed the estimates of 1987 "nursery gate" prices per thousand plants using the current propagation options (D. R. Smith, pers. comm.). For new cloning techniques to be competitive with existing rooted cutting techniques, they will need to be priced either at or under \$300 per thousand plants, or generate significant additional financial returns (Smith 1986).

TABLE 2—Prices for plants of *P. radiata* grown under alternative propagation options

Plant type	Price (NZ\$/1000 plants)
Seedlings from open-pollinated seed orchard seed	100
Seedlings from control-pollinated seed orchard seed	160
Cuttings from control-pollinated seed orchard seedlings	300
Micropropagated plants from embryo culture and mass culture of cotyledon tissue	500–700*

\* 1987 prices adjusted from 1983 estimates by Smith (1986). Prices dependent on process efficiency.

The question to be asked at this point in our planning is: "What advantages would clonal forestry offer when compared to available methods of plant production – particularly when compared with the vegetative multiplication of full-sib or polycross families produced by controlled pollination?"

### CLONAL FORESTRY v. CONTROL-POLLINATED ORCHARD STRATEGIES

*Clonal forestry will shorten the time taken to establish production plantations (Advantage 8, Table 1)*

One of the strongest arguments in favour of clonal forestry is based on the assertion that gains from genetic improvement can be more quickly translated into wood in the forest through cloning than through conventional methods. A clonal forestry strategy for *P. radiata* should be favoured by the existence of an aggressive breeding programme, in which gains from forward selection (of advanced-generation progeny) are clearly greater than gains from backward selection (of parents of tested progeny). However, it is unlikely that the mass-production of tested clones could be achieved as quickly as the vegetative multiplication of trees from crosses among good general combiners in a control-pollinated orchard. Thus, the advance represented by the control-pollinated orchard strategy has yielded a benefit previously (and loosely) ascribed to clonal forestry.

#### *Clonal forestry yields advantages in control of pedigree*

Pedigree control is achieved through use of control-pollinated seed orchards as well as through cloning. The use of this control, for example, to control the genetic diversity of production plantations by deploying sets of genetically dissimilar clones (Advantage 10, Table 1) becomes a matter of choice for the forest manager. In fact, the reasons advanced by Libby & Rauter (1984) are not compelling. Their conclusion (that "designed clonal plantations will be significantly safer against insects, disease or physical damage . . . than seedling plantations") cannot be readily accepted, since it is based on the incorrect assumption that genetic discontinuities (between clones) can be selected for without knowledge of the genetic basis for resistance to the damaging agents.

Similarly, there are no real "donor management" advantages for clonal forestry of *P. radiata* compared to a control-pollinated orchard approach (Advantage 15, Table 1). Small numbers of hedged clones in a control-pollinated orchard provide an easily

managed, cost-efficient alternative to clonal programmes based on numerous hedges or nursery stools. As already discussed, the main reasons for the failure of our early attempts at clonal forestry were problems of archive management and maintenance.

The elimination of inbreds in production plantations (Advantage 7, Table 1) can also be achieved using controlled pollination. It is desirable for *P. radiata*, since inbreeding depression can be severe for growth traits (M. Carson, unpubl. data). However, inbred seeds of *P. radiata* have low germination and inbred seedlings have low viability in the nursery. Both factors would reduce the likely impact of inbreeding on growth of production plantations.

The main advantage of pedigree control in control-pollinated seed orchards in New Zealand is the elimination of up to 50% pollen contamination experienced in conventional orchards – a clonal forestry strategy is not necessary to achieve this advantage.

#### *Clonal forestry offers greater flexibility in deployment of trees*

Several of the advantages of clonal forestry cited by Libby & Rauter (1984) relate to increased flexibility in allocating genotypes to specific planting sites (Advantages 5, 6, and 16, Table 1). They discussed clone/site matching in terms of adaptation only, but their argument is easily extended to cover the precise targeting of all selection criteria (including adaptation, growth rate, disease resistance, and tree form traits) in an appropriate mix that meets forest management requirements at a given site.

Progeny of conventional clonal seed orchards are genetically dissimilar, since they are the product of matings among typically 20 or more parents in all or most combinations. Even the offspring of a single cross will be genetically variable owing to segregation, while a controlled polycross progeny will have additional variability associated with the mix of differing pollen parents.

Clones allow great flexibility in deployment, since they are genetically uniform – their precise allocation to planting sites could yield large gains. These gains would arise from actively capitalising on "genotype-environment" or G×E interaction through selection of "site-specific" clones. Libby & Rauter (1984) gave the example of high-performance clones of hybrid poplar in Ontario, which "are carefully matched to plantations that have been site-mapped in considerable detail". However, New Zealand experience with growing *P. radiata* indicates that G×E interactions are generally important only (if at all) for growth rate, while the pattern of such interaction is both complex and obscure (S. D. Carson, unpubl. data). In addition, there would be tremendous logistical difficulties in screening clones as a prerequisite to their optimal deployment over New Zealand forest sites representing a wide range of soil types, and a latitudinal range of more than 10°.

The alternative to capitalising on G×E interaction with the "finely tuned" application of site-specific clones is to buffer against such interaction using mixtures of broadly adapted clones (Advantage 6, Table 1). But this advantage is also shared with conventional and control-pollinated seed orchard strategies, since orchard parents can be selected for good performance over large regions, or for any particular mix of selection traits. For very good reason, this emphasis on broadly adapted selections is

currently preferred for *P. radiata* improvement in New Zealand (Shelbourne *et al.* 1986). Although progeny of single pair-crosses could be deployed to more finely identified forest sites, we might expect to get diminishing returns at each descending step in the hierarchy of site types – to the extent that clone/site matching may simply not be worth the additional effort!

*There will be substantial economic gains from clonal forestry in utilising the experience gained with specific clones*

The advantages conferred by the accumulation of knowledge about particular clones (Advantages 9 and 17, Table 1) have been carefully qualified by Libby & Rauter 1984). Continuing use of widely established clones implies a slow "take-up" of new (and presumably better) clones produced by the breeding and testing programme – leading to losses in genetic gain per unit time. The sophisticated application of "programmed planting sequences" to produce clones that make complementary demands on their environment is acknowledged to require difficult and expensive experimentation. In fact, there is an analogy here with the site-specific clones discussed above – the gains from such fine-tuning must suffer from diminishing returns for greater effort, and the appropriate balance may not require control at the level of an individual clone.

Compared with horticultural practice, plantation management and tending practices for growing *P. radiata* in New Zealand currently lack the degree of control and sophistication to allow them to be applied on a stand-by-stand basis. We find it difficult even to track the allocation of conventional seed orchard seedlots through forest nurseries and into forest stands, let alone to prescribe different management as the crop matures! While one may recognise intuitively the advantages in having complete control of plant growth and growth habit at every forest site, the reality may not be worth pursuing. In any event, we will be better placed to weigh the benefits of clonal forestry after accomplishing the big leap to fine-tuning the management of pair-cross or polycross families produced by controlled pollination.

The claim of advantage for clonal forestry in allowing "a more conservative approach to the genetic manipulation of our forests than does classical tree improvement" (Advantage 18, Table 1) appears to be based more on philosophy than on economic gains. The authors contrast the selection of relatively few advanced-generation candidates as potential seed orchard parents with the hundreds of clones used as a basis for some clonal programmes. They claim that repeated evaluations (in clonal tests) of a production set of clones leads to their increasingly reliable performance in a clonal strategy that, in contrast with "aggressive schemes", "seems much more in tune with the conservative philosophy appropriate to a long-term crop such as forest trees". Libby & Rauter (1984) seem to be describing the contrast between the traditional mass selection and cloning methods used in the improvement of elms, poplars, and willows and the recurrent selection and breeding approach used principally in the improvement of pines. But clonal selection used alone (without concurrent breeding population improvement) is ultimately a "dead-end" strategy because it cannot tap the rich sources of genetic variation arising from recombination among desired genotypes. In recognition of this fact, breeders of agronomic varieties are now turning away from mass selection of clones and towards population improvement methods in their search for better varieties

(Gallais 1986). There would be no advantage to New Zealand in discarding the breeding population advance that has already been made with *P. radiata*. Clonal forestry would logically be adopted as a complement to the existing breeding programme rather than as a replacement for it.

#### *Clonal forestry will allow greater control of growth habit*

Libby & Rauter (1984) saw clonal forestry as offering additional control of tree morphology compared with what can be achieved using seedling trees. They cited the role of a more advanced maturation state in improving stem form and disease resistance of *P. radiata* cuttings (Advantage 14, Table 1). This is an exciting possibility that may well lead to large economic gains, since it may involve tapping not only all the non-additive gene effects but also variation that is not even genetic in nature. One promising example with *P. taeda* L. is the expression of maturation-related gains in resistance to the gall-forming fusiform rust (J. Frampton, pers. comm.). Aged cuttings and/or tissue culture plantlets may be used to establish stands in high-hazard regions where seedling trees can barely survive. A small maturation-related loss in growth rate would be readily accepted under these conditions. *Pinus radiata* in New Zealand is not attacked by as important a pathogen as fusiform rust, but the accidental importation of, for example, western gall rust could create a need for similar protection.

Rooted cuttings from *P. radiata* aged 4 years or older have been shown to have markedly superior stem form to that of seedling trees (Menzies *et al.* 1985). Unfortunately, there is also an associated loss of vigour with increased maturation. A compromise of improved stem form without growth loss may be possible with 3-year-old cutting donors, and current research is aimed at testing this hypothesis.

Maturation-related gains therefore represent a potential advantage of clonal forestry that could well be realised in future production plantations.

The concept of using clonal forestry to re-allocate biomass in trees so that they "make wood, and not love" (Libby 1983) is also intuitively attractive (Advantage 12, Table 1). However, the production of male and female strobili of *P. radiata* is known to be under strong additive genetic control (M. Carson, unpubl. data). Progress towards producing "non-flowering" trees could presumably be achieved through controlled-pollination of "poor-flowering" parents and subsequent multiplication of their seed as juvenile rooted cuttings. Clonal selection and multiplication might add some additional gain in "non-flowering", but it would probably make sense to exhaust the conventional options first.

Perhaps through an oversight, Libby & Rauter (1984) did not list increased uniformity as one of the advantages of clonal forestry. Uniformity in size (or growth) and stem form is likely to have a positive economic value independently of improvement in average performance for these traits. Improved predictability of distributions of tree and branch diameters, internode lengths, incidences of sweep, and gradients of wood density is likely to lead to reduced tending, harvesting, and wood-processing costs through more efficient use of manpower and machine resources. Although the true value of uniformity may be difficult to quantify for *P. radiata*, sufficient evidence exists for other plant crops to suggest that this value will be large.

Selection of similar phenotypes in *P. radiata* tree-improvement work has already led to an increase in the uniformity of controlled-cross progeny for strongly inherited traits like internode length (M. Carson, unpubl. data). Clonal forestry offers the promise of much greater uniformity for targeted log and wood quality traits, without the "scatter" that would inevitably occur from segregation among seedling progenies. There is little doubt that a clonal forestry strategy will allow greater control of growth habit than is offered by more conventional strategies. However, more research is required to quantify the advantages of this greater control. In the interim, experience gained from using progeny of control-pollinated orchards should assist us in further evaluating the clonal option.

*Clonal forestry will yield greater genetic gains from capture of both additive and non-additive genetic variance (Advantage 3, Table 1)*

Additional generic gain for a clonal forestry option based on a conventional tree-improvement programme can derive from:

- More efficient capture of additive variance, associated with greater precision of estimating the performance of cloned individuals, and/or
- Capture of non-additive genetic variance.

A more efficient capture of additive variance from clonal testing compared to family testing will depend on the trade-off between the effective heritability for clones *v.* families and the selection intensity that can be applied to each category. Clonal tests are more efficient than family tests of similar size, and their relative efficiency is greatest for traits with high heritability, and least for traits with low heritability. Their increased efficiency is due to a reduction in the experimental error component of variance relative to families since there is no segregational variance within clones, as there is within families. But the increased efficiency of clonal tests is gained by testing replicates of individual clones, and clonal replication reduces the total number of genotypes that can be compared in a test of a given size. For high-heritability traits (like wood density of *P. radiata*) clonal replication is not really necessary, as family and individual-tree data provide efficient estimates. For low-heritability traits (like leader malformation of *P. radiata*) clonal replication will need to be relatively large, which will inevitably require larger tests in order to maintain an adequate selection intensity. Populations of families may be managed to capture additive variance as efficiently as populations of clones; the correct choice of test site and trial design is likely to yield greater additive genetic gains than the choice of genetic unit for testing.

Clonal forestry does offer great theoretical advantages in capturing all the gains associated with selection for non-additive gene effects, which would otherwise be lost using either the conventional seed orchard approach, or the controlled-pollination option using GCA information. Although a proportion of the non-additive genetic variance (in the form of SCA) can be obtained in selection and propagation of tested full-sib families, the SCA may need to be as large as or larger than GCA for this to become worthwhile (Carson 1986). Non-additive variance may not be large enough even to justify the clonal forestry option. In a recent assessment of a 4.5-year-old *P. radiata* progeny trial at two New Zealand sites I found that estimates of SCA (comprising

variance due to dominance and epistasis) were much smaller than GCA estimates for traits measuring tree form, disease resistance, and wood density (Carson 1986). Other studies with *P. radiata* (e.g., R. D. Burdon, unpubl. data) have also shown that SCA is much smaller than GCA for form and disease traits, and is only of moderate importance for growth rate. Clearly, knowledge of the relative size of the non-additive and additive variances for important traits may be crucial in determining the potential for a clonal forestry option. For the *P. radiata* example, this advantage of a clonal option must be considered "not proven".

#### *Correlation breakers (Advantage 13, Table 1)*

The negative genetic correlations between growth rate and wood density, and between the long-internode habit and growth rate of *P. radiata* are important constraints in the tree improvement programme. Libby & Rauter (1984) noted these constraints and advocated clonal testing as a means of identifying unusual "correlation breakers" which are above-average in both of a pair of negatively correlated traits. The strength of this argument depends on a high relative importance of non-additive genetic variance, since family information may be equally efficient in capturing additive genetic variance (as already discussed). For clonal selection to be more effective, non-additive genes for two negatively correlated traits must interact to produce clones improved in both traits. Wood density and the long-internode habit of *P. radiata* are both highly heritable traits which are conditioned almost entirely by additive genetic variance (Carson 1986) while growth rate is mainly under additive genetic control. There seems therefore to be limited scope for an advantage of clones over families in testing for genotypes that break the negative correlations among these traits.

#### *Clonal forestry will allow us to better utilise valuable but expensive genotypes (Advantage 4, Table 1)*

It seems likely that the use of population improvement techniques in pine species like *P. radiata* will continue to produce small sets of more-or-less equally desirable genotypes, rather than the "valuable but expensive" genotypes discussed by Libby & Rauter (1984). Although unique valuable genotypes are the rule in numerous horticultural and agricultural plant varieties, important examples in forest trees are more difficult to find. Between-species hybrids using *P. radiata* may become an attractive possibility from development of genetic engineering technology, but their particular advantage may be less than would be indicated by existing examples in agriculture and horticulture. Within *P. radiata*, the production of pedigreed control-cross families has not proved too costly for production plantation use, and so the potential for reducing costs further through clonal forestry may be limited.

## **CONCLUSIONS**

This discussion of the perceived advantages of clonal forestry has raised questions as to the potential relevance of these advantages to *P. radiata* grown in New Zealand. Multiplication of progeny from control-pollinated seed orchards will allow us to utilise many of the advantages usually attributed to clonal forestry, while having the additional advantages of:

- Relatively cheap and efficient screening – since crosses can be based on parental GCA performance as determined from a more limited number and size of progeny trials than would be necessary for clonal testing;
- Easier archive management – since relatively small numbers of parent clones need to be maintained in archives;
- Lower nursery costs – since management of seedlings and juvenile cuttings is already inexpensive and well-understood without the need to develop operational methods for achieving high rates of multiplication or maintenance of clonal identity.

Managed stands of polycross or full-sib family origin will provide evidence on the advantages of increased flexibility in allocating genotypes to sites and management regimes, and of gaining increased uniformity. If this evidence is provided, then the extension to clonal forestry and pure stands should logically follow. Similarly, if greater genetic gains can be clearly demonstrated for the clonal option, then operational methods for capturing those gains should be fully evaluated. In the meantime, forest managers and planners should make best use of the promising genetic material now coming available from conventional and control-pollinated orchards, and consider clonal forestry as a possible strategy for making future gains.

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