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A STRATEGY FOR EFFICIENT SELECTION AND EVALUATION OF "DESIGNER BREEDS"

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EXECUTIVE SUMMARY

Profitability in New Zealand radiata pine forestry could be improved by utilising "designer breeds", that is, breeds selected for their genetic potential to maximise profitability on specific sites or for the production of specific end products. A tool to aid the efficient selection of parents is required in order to achieve maximum potential and utilisation. Development of a matrix of breeding values across parents in the New Zealand breeding population separately for each breeding goal is proposed. This would also facilitate integration of genetic changes into planning and prediction models like STANDPAK, and aid in optimisation of economic weights used to select superior parents. Inclusion of separate ratings for each of the major selection criterion is proposed as an addition to the breed ratings assigned by the New Zealand Seed Certification System.

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A STRATEGY FOR EFFICIENT SELECTION AND EVALUATION OF "DESIGNER BREEDS"

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INTRODUCTION

Control-pollinated orchards make it possible to select and mate small numbers of parents selected for specific traits. The resulting seed can be used directly as a production seedlot, or may even be deployed as stands comprised of specific single crosses. With increasing use of planting stock derived from control-pollinated seed orchards, it is now possible to produce "designer breeds", that is, seedlots with the genetic potential to maximise profitability on specific sites or (in combination with choice of silvicultural regime) for specific end uses.

Designer breeds are produced by emphasising different sets of selection criteria when selecting parents to produce planting stock for plantations (Carson, M. 1991). A mix of parents can be selected to produce seedlots that emphasise specific traits in order to maximise genetic gain measured in economic terms. For example, a very high genetic quality for straightness would be very important on an ex-farm site where the high fertility results in many crooked stems, but not very important on sandy soils where the trees are naturally much straighter. Also, high wood density could be emphasised for the production of structural timber, but is not as critical for pulpwood production. A strategy for facilitating the process of selecting parents on the basis of different selection criteria is proposed here.

The choice of customised selection criteria would be aided if planning models were available which reflected the effects of the possible genetic changes on economic worth and log quality. In addition, as the deployment of either single-family blocks or blocks containing few parents increases, it is important that forest managers have a better understanding of the impact of genetic manipulation. It is proposed here that planning models be modified for tree form traits in an analogous manner to which genetic changes in growth rate have already been modelled by modifying stand growth models (Carson and Garcia 1995).

Genetic improvements in different selection traits (for example, growth and branch habit) are not closely linked. Improvement in one trait does not necessarily mean the

same level of improvement will be achieved in another trait for alternative seed orchard candidates. For example, the best parents for growth rate are not all the best parents for Dothistroma resistance. Parents with offspring high in Dothistroma resistance but low in growth potential can be selected, as well as parents high in resistance and high in growth potential.

The relative genetic worth of parents in the New Zealand radiata pine breeding programme for each of the economically important traits is best expressed as an overall ranking which applies to all New Zealand sites (Carson, S. 1991). Genotype by environment interaction is not large enough in New Zealand for any of the common selection criteria to warrant selection aimed at specific regional breeds adapted to local site and climatic conditions. However, even though the ranking of parents is expected to be similar for all New Zealand sites for a given trait, the mean performances and the magnitude of differences among parents often varies dramatically among specific sites. These factors must be taken into account when the effects of genetic change are considered.

Planning models utilise different modules to take into account the effect of different factors on the final characteristics of the stand. For example, growth models predict stand volume, while a branch model is used to predict knot size. Predictions from all modules are brought together to construct an overall prediction of the volume and quality of different log types and product mixes. If genetic changes in traits affecting log and wood quality can be accounted for in this process, the overall performance of improved seedlots selected for different breeding goals can be predicted not just for growth, but also for quality traits. In order to do this, the genetic value of a seedlot for different traits must be input into the appropriate module of STANDPAK.

A strategy for producing tools to aid in selection and evaluation of designer breeds is proposed which takes these modelling and genetic considerations into account through integrating genetic changes into planning models (Table 1).

SELECTING DESIGNER BREEDS

History of selection and testing of seed orchard parents

Radiata pine plus trees have been selected in New Zealand since the 1950s. Each group of plus trees, that is, each 'series', was selected within a certain time period for a specific set of selection criteria and in a particular manner. For example, the '850 series' was selected in the early 1950's by very intensively searching forest plantations all over

New Zealand for outstanding trees for increased growth and good stem form and light, uniform branching habit. In contrast, the '268 series' was selected in 1968 by partitioning a stand in northern Kaingaroa Forest into 1 ha blocks and selecting the best tree in each block with somewhat greater emphasis on multinodality. Another series, the '870 series', was selected primarily for extremely long internodes, combined with acceptable growth and form.

Radiata pine plus trees have been progeny tested almost exclusively in comparison with others selected at the same time, that is, with those in the same series. Progeny testing of the select trees usually began shortly after selection of a new series. Progeny of select trees in a series were almost exclusively planted and assessed for important traits on several sites as a group, so parents in a series were well tested and ranked against one another, but parents in different series were not until recently. The best parents were selected for use in seed orchards using a genetic selection index combining their values for different selection traits. A set of selection criteria was used that reflected breeders perceptions of the relative importance of the selection traits for a general or special-purpose breeds.

Table 1. Steps proposed for producing tools to aid selection and evaluation of designer breeds.

DEVELOPMENT

OUTCOME

- 1. Calculate matrix of New Zealand-wide breeding values (which will often be based on subjective scores) including all parents and all of the commonly used selection criteria.
- Much more efficient selection of "designer breeds", that is, those with custom designed selection criteria.
- 2. Link breeding values to economically meaningful variables by measuring progeny trials and genetic gain trials. In this process, a) regional differences in mean performance and b) the magnitude of genetic differences within regions will be quantified.
- More accurate nomination of the desired mix of growth and log and wood quality traits to meet optimum management and end-product requirements, that is, the criteria for designer breeds
- 3. Modify modelling systems to allow input of seedlot ratings separately for a number of different traits, such as, growth rate, straightness, and internode frequency.

Use of planning models for more accurate prediction of performance of designer breeds, and prediction which allows comparison of alternate sets of economic weights placed on the various selection criteria for sue on specific sites and specific silvicultural regimes.

Production of designer breeds

Vegetatively-propagated genetic copies (ramets) of selected parents were established in open-pollinated orchards from the mid-1950's until 1985. These orchards allowed little flexibility for use of more than one set of selection criteria and required that all ramets of select clones be planted in an orchard during the same time period. Large numbers of parents were required in the orchards in order to avoid cross-pollination leading to relatedness in their offspring. In addition, a long lead time until seed production was required even on the better sites, because of the lack of pollen on the orchard trees in the first four to five years. This was exacerbated by the impact of poor orchard siting, which depressed cone and seed production.

Some flexibility for selection for different objectives can be obtained in open-pollinated orchards by only collecting seed from specific sets of parent clones. However, selection is then effective only on the female side of the pedigree, and the pollen cloud is still contributed by all of the orchard parents. In addition, a proportion of pollen even in a mature orchard (estimated to be as high as 50% in one case) originates from unselected trees planted outside of the orchard. This severely limits both the overall gain and the range of designer breeds that can be produced from an open-pollinated orchard through different emphasis on alternate selection criteria.

The advent of control-pollinated orchards has greatly increased flexibility for producing seedlots selected for a wide variety of objectives (Carson *et al.* 1992). Pollen is being collected elsewhere and targeted to female cones on specific parents; it is no longer necessary to have an intimate mixture of unrelated ramets, as in open-pollinated orchards. Further, it is no longer necessary to have a large number of different parents in an orchard in order to avoid relatedness. Finally, complete control of the pollen parent means that only a small number of specifically chosen fathers need be utilised. As a result, parents in different plus-tree selection series which were selected and propagated at very different times and in very different places are being mated in control-pollinated orchards.

Proposal: development of a matrix of breeding values

With the increased genetic gains available from increased flexibility, both a better overall ranking of all parents in the breeding programme and sound estimates of comparative breeding values across selection series become essential. Further, previous rankings of parents based on multiple traits are not particularly useful for selecting parents for designer breeds, where emphasis is on customising the mix and relative

weighting of selection traits. With very few exceptions, ranking for multiple traits represents a compromise in ranking for the various selection criteria. Parents do not rank the same for all traits. For example, the best parent for growth rate is not necessarily the best for straightness or for any other selection criterion and vice versa. Thus, parental ranking for each seperate trait is required in order to efficiently choose parents whose progeny show high genetic gains for that trait.

The NZ Radiata Pine Breeding Cooperative has supported the process of using existing data to calculate national tables of breeding values for all important selection criteria and for all parents in the breeding population (as illustrated in Table 2). Numbers in the body of Table 2 represent the gain contributed by each parent to a control-pollinated seedlot when compared to the mean of all parents, expressed in the units of the originally measured trait. For the most commonly used selection traits such breeding values will be appropriate for

Table 2. Hypothetical matrix of parental breeding values across series separately for each selection criteria.

	Breeding Value				
Parent	Diameter (mm)	Dothistroma (%)	Straightness ¹	Internode Frequency ¹	Needle Retention ¹
268.A	20	13	9	7	4
268.B	19	5	3	6	3.5
875.C	19	12	. 8	8	2
850.D	18	0	8	9	2.5
268.E	18	-3 .	7	4	3.5
880.F	1 7	14	9	6	4
•	•	•	•	•	•
•	•	•	•	•	•
•	•	•	•	•	•
268.G	0	0	9	2	1.5
880.H	0	5	2	7	2.5
•	•		•	•	•
•	•	•	•	•	•
•	•	•	•	•	•
850.I	-18	5	5	6	1.5
850.J	-19	7	2	4	3
875.K	-19	-2	6	2	3.5
268.L	-20	-12	8	3	3

^{1.} subjective scores.

selecting parents to produce seedlots for use anywhere in New Zealand. A recent study has shown that genotype by environment interaction in New Zealand is not sufficiently large to warrant the selection of regionalised breeds (Carson, S. 1991), and that combining data from a number of reliable progeny tests strengthens the validity of the national ranking of parents by their breeding value.

The genetic gain arising from use of a seedlot can be estimated from Table 2 as the weighted average of the value for different parents, the weighting reflecting the parental contribution to the seedlot. Optimally designed seedlots could be developed by calculating the genetic changes expected with different parental compositions of candidate seedlots. The data in Table 2 are hyppothetical, but illustrate the nature of the trade-offs among selection criteria. Actual breeding values in such a table will be very useful for selecting parents for designer breeds.

PREDICTING YIELD AND QUALITY OF "DESIGNER BREEDS"

Economic value of genetic changes

The existance of a matrix of parental breeding values for each selection criterion will facilitate prediction of performance of improved seedlots through the use of planning models like STANDPAK. Parental breeding values (as illustrated in Table 2) represent the relative genetic worth of their offspring as determined from field progeny trials. Many of the selection variables are subjectively assessed, but they have proven to be very effective for identifying relative differences since they are very quick and inexpensive to measure. Cost effective measurement traits are essential in order to measure the typically 8,000 to 12,000 trees per progeny test site. Balanced trials with good experimental design and a large number of replications are utilised in order to identify the best parents. However, the real economic value of changing one unit of, for example, the subjective straightness score, or one unit of the internode frequency score is not well quantified by parental breeding values such as those illustrated in Table 2.

STANDPAK consists of numerous models, structured within several modules which, given input of current stand measurements, predict the status of the stand and its log and timber products for any age and over a wide range of management and utilisation options. For example, growth models predict stand growth and volume, while the log making module predicts the effect of sweep and branch size on log quality (Figure 1). Future volume, log quality, product out-turn, and financial return can all be predicted from a range of input variables at the forest stand level (West 1993, Whiteside 1990).

STANDPAK is widely used for evaluating different management options, scheduling of pruning and thinning operations, and predicting wood yields by log quality classes.

Most of the growth models used in STANDPAK have already been modified to reflect genetic improvement in stand yield (Carson and Garcia 1995). In the modified growth models, the rate of change of the height, stocking and basal area functions is modified by genetic gain multipliers. The values of the multipliers depends on a seedlot's genetic potential for increased growth. Currently, the New Zealand Seed Certification Service assigns to commercial seedlots a 'GF rating', which is based on a seedlot's genetic worth for a combination of growth and stem form. The Seed Certification ratings are based on parental breeding values and the contribution of each parent to the seedlot (Vincent 1987). At the moment, the magnitude of the genetic gain multipliers can be modified by inputting a seedlot's GF rating into the growth models. In the modified growth models, genetic gain multipliers for GF ratings between 2 and 22 have been developed by fitting the multiplier parameter to existing data from genetic gain trials.

Proposal: modify planning models to reflect genetic changes influencing log quality

In order to more accurately predict the quality and value of a stand, research is being directed toward quantifying the economic effect of altering genetic quality of a seedlot

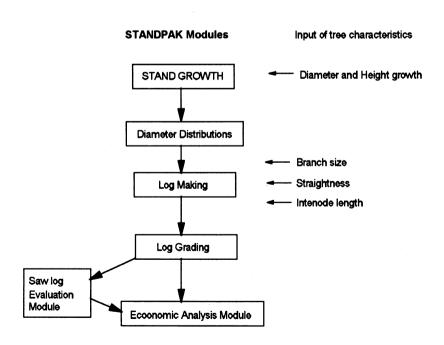


Figure 1. Schematic of modules in STANDPAK.

for straightness, internode frequency and other genetic selection traits. The proposal is to specify the genetic value of each trait based on breeding values and to use this as input to the appropriate module of STANDPAK (Figure 1) or other planning models in an analogous way to inputting the GF rating to growth models as described above. The results of genetic changes in straightness, branch habit, and other log quality variables could be predicted by developing methodology to input genetic changes into the appropriate modules of STANDPAK. Functions relating these changes and breeding values are being developed (Turner, et. al 1995).

As described previously, parental breeding values, illustrated in Table 2 and Figure 2, are developed by combining genetic data from progeny field trials in all parts of the country. The ranking of parents embodied by the breeding values represents their expected relative performance on any site in New Zealand. Performance on specific sites will deviate from the ranking represented by the breeding values because of uncontrolled genetic and environmental variance, but the overall breeding value rankings represent the best prediction of the relative performance of the parents. The breeding values provide the most reliable estimates of relative genetic worth of progeny seedlots when planted in New Zealand plantations.

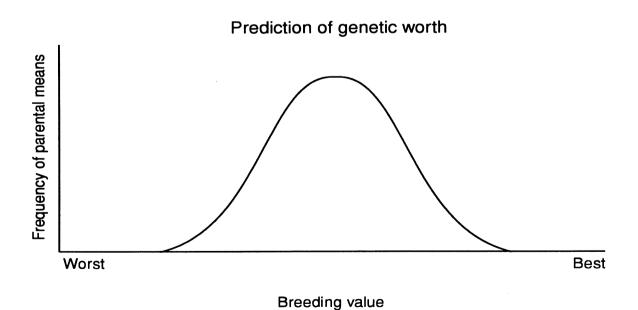


Figure 2. Hypothetical schematic of parental breeding values developed from subjective progeny test scores.

(Based on subjective scores. Valid for all plantations.)

However, while we expect that the predicted relative rankings of parents will be relatively stable, it is clear that the average performance of the same seedlots will differ on different New Zealand sites (Figure 3). For example, trees on average are all much straighter when grown on the Auckland sands than in the Central North Island no matter what their genetic make-up. Also, trees grown on sandy soils tend to have finer branches, and shorter internodes than those grown on most other sites. The large morphological differences in radiata pine grown on different sites provide one of the bases for using breeds with a varying mix of selection traits, such that selected genetic differences can add to the forest site's existing propensity to produce trees of a particular type.

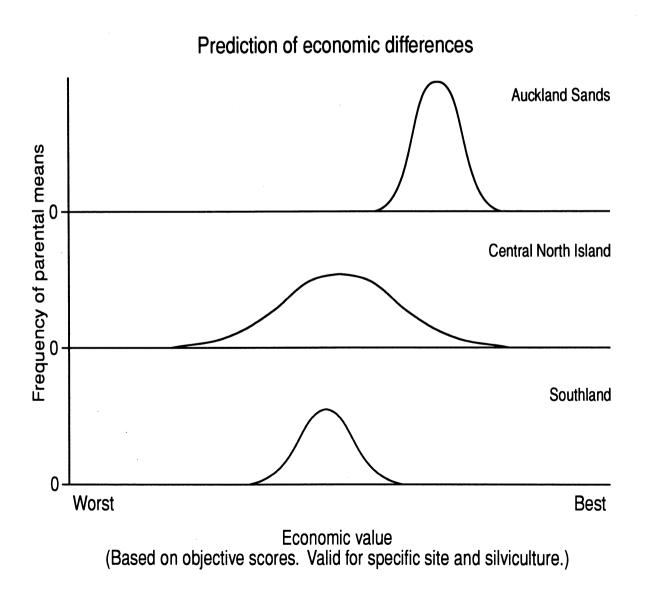


Figure 3. Hypothetical schematic of objective measure reflecting economic differences in parental performance for a single selection trait.

In addition to a seedlot with the same genetic composition showing different mean performance on different sites, the absolute difference among seedlots also differs from site-to-site (Figure 3). The magnitude of differences among genetically-improved parents (the genetic variance) differs by region. For example, the difference between the best and the worst parents for straightness will be much greater on Central North Island sites than on the Auckland sands. An actual measurement of internode length on offspring of the same parents in progeny trials planted on both the Auckland Sands and in the Central North Island illustrates these points by showing both a strong regional difference and a difference in variance among parents (Figure 4).

The variables measured in progeny trials for parental selection for log quality traits are subjectively scored, giving them their greatest utility when trees within the same stands are compared. The subjective scores, however, frequently have little utility for comparisons of economic worth across regions. For planning models, input values

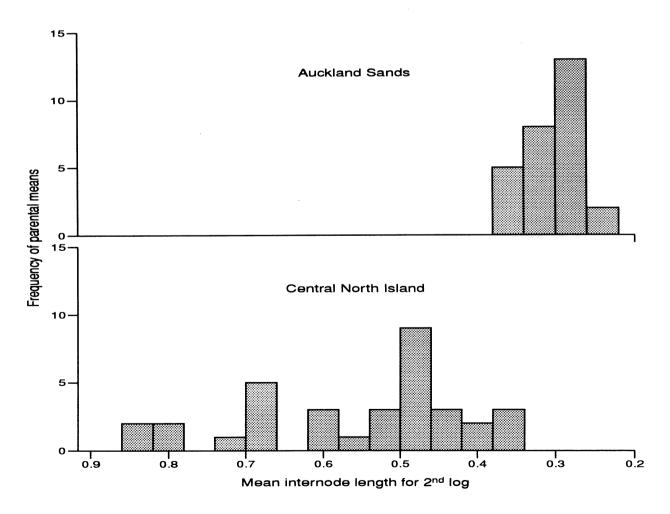


Figure 4. Distribution of mean parental values for internode length in a progeny trial planted on the Auckland Sands and in the Central North Island.

representing the genetic effect of altering log quality traits could be developed by (a) developing objective measures closely related to economic worth for these traits, (b) quantifying regional differences in the average performance of all improved trees and (c) estimating the variance of parental means within regions. For each selection trait, information about parental performance similar to that illustrated in Figure 3 would be gathered.

Regional differences in expression of mean performance and genetic variance for individual traits (that is, quantification of Figure 3) might be obtained by using the objective measurement techniques to measure the top, bottom, and middle of the breeding value scale in a number of progeny trials planted in different regions. This could be supplemented by assessing seedlots in large block genetic gain trials, particularly if these seedlots have been selected to emphasise variation in specific traits (as has been done so far for fast growth vs slower growth, long-internode vs multinodal, and high vs low density breeds).

Once national breeding values can be related to objective measures closely allied to economic worth as described above, we propose that the appropriate modules in planning models be modified in order to accept input on a seedlot's genetic quality for each of the traits which are being genetically manipulated. The information quantified as described above would be incorporated into the models so that regional differences in performance, both in mean and genetic variance, would be taken into account when predictions were made. Of course, specification of genetic quality for each selection criterion separately is required to provide accurate input to different modules of STANDPAK.

Determining optimal economic weights of selection traits

When it becomes possible to input breeding values for different selection criteria directly into the appropriate modules of STANDPAK, the volume and quality of stands resulting from designer breeds can more accurately be predicted and compared. By using values calculated for actual parents in the breeding population, real future seedlots can be simulated and compared. Two alternative seedlots could be compared for (say) volume production, log quality, product out-turn, financial return and other criteria. Seedlots could be compared for their performance if used in different regions. This approach will greatly facilitate determination of the appropriate economic weights for the various selection criteria for designer breeds.

FUTURE DIRECTION OF NEW ZEALAND SEED CERTIFICATION

The New Zealand Seed Certification Service has so far developed three separate rating scales (three separate breed ratings) for rating a seedlot's genetic worth. A seedlot will have different ratings for each breed, because each breed emphasises a different set of selection criteria (Table 3). The growth and form breed emphasises growth and stem straightness, plus malformation or acceptability, with growth weighted twice as much as stem form. Breed ratings for two special purpose breeds are available. The Dothistroma resistant breed ranks seedlots to achieve optimum volume growth on high risk Dothistroma sites. The long-internode breed rating provides a ranking for internode frequency. Certification for both special purpose breeds also includes the rating for the seedlot in question for the growth and form breed. A wood density breed (emphasising increased density and growth) and a pole breed (emphasising multiple branching and straightness) are available from the tree improvement programme but are not yet rated by the Seed Certification Service.

The New Zealand Seed Certification Service is progressing toward an enhancement of the rating system where, in addition to the breeding ratings now available, an additional vector of trait ratings is provided for seedlots with multiple parentage for potential inputs into STANDPAK. Such a vector could be presented on the certificate and be in a form something like "GR22 ST7 IF6 DR18" that is, with a growth (GR) rating, straightness (ST) rating, internode frequency (IF) rating, and Dothistroma resistance (DR) rating. Work is progressing toward providing separate trait ratings for a number of traits for each radiata pine seedlot registered.

Table 3. Radiata Pine Breeds

Breed	Seed Certification Code	Selection Criteria
Growth and form	GF	GROWTH, straightness, malformation
Dothistroma Resistant	DR	RESISTANCE, GROWTH
Long Internode	LI L	LONG INTERNODES, growth
High Density	-	increased density, growth
Pole Production	-	multiple branching, straightness

Breeding values over all series have already been calculated for Dothistroma resistance and for stem diameter. It is intended that the Seed Certification Service will soon offer a trait rating for growth based on the breeding values for diameter and perhaps height, and that this number will be input to the growth models, rather than the GF rating. A more precise prediction of growth rate should be achieved by associating growth rate multipliers with genetic worth for growth alone, rather than for GF rating, because in the GF rating, the rating of genetic potential for growth is confounded with the rating for stem form. Seedlot ratings for stem form traits will be provided in an analogous way to growth ratings when breeding values are available for these traits. When models predicting stem form can be modified to reflect the affect of genetic changes, the seedlot ratings for the individual traits, the trait ratings, would then be used as inputs into the appropriate modules in the planning models.

EXTENSION TO CLONAL FORESTRY

The promise of true clonal forestry, that is, the use of tested clones, would allow even greater flexibility in the choice of selection criteria. When the use of tested clones becomes a widely used practice and ranking information is available, a similar system for rating and evaluating their performance via planning models can be developed in a completely analogous way to that proposed here for family forestry.

CONCLUSIONS

The increasing shift toward the use of control-pollinated seed and vegetatively-multiplied cuttings for supplying planting stock for production forests provides a vehicle for forest owners not only to increase gain from tree breeding, but also to customise the emphasis placed on selection criteria, such as growth rate, straightness, branching habit and disease resistance, which contribute to achieving important breeding goals. Customised selection criteria might be desirable to maximise profitability on sites with particular characteristics (for example, high risk for disease) or in forest stands destined for specific end uses (for example, poles or pulp) (Carson, M. 1991).

It is recommended that a matrix of breeding values be developed across all parents in the New Zealand breeding population regardless of series, and with separate breeding values for each trait. This will better facilitate selection of designer breeds, that is, seedlots intended to maximise genetic gain on specific sites or for specific end uses. It is also recommended that genetic changes in stem form traits, especially straightness and branch habit, be incorporated into planning models as separate traits. The modules of planning models which specifically deal with these traits could be modified to reflect the extent of genetic changes which occur in different parts of the country, and predictions obtained for specific seedlots by inputting Seed Certification ratings for the separate traits into the appropriate module.

Complete implementation of these recommendations will require several years of research, and as such, represent long term goals. However, they provide a framework for focusing the incorporation of genetic changes into prediction models while taking into account the biology of genetic change. Implementation of the recommended system would enable more efficient selection and better prediction of performance of designer breeds, and provide a method for determining optimal economic weights for the various selection criteria, thus maximising the profit from genetic selection. The New Zealand Seed Certification Service, and planning models (including STANDPAK) would be the vehicles for technology transfer of this information.

GLOSSARY

- **economic weights:** the relative weight given to each selection criterion reflecting it's economic importance compared to the other selection traits.
- **breed ratings:** a number assigned by the New Zealand Seed Certification Service which reflects a particular seedlot's relative genetic worth for a specified set of selection criteria, each with a specified economic weight.
- **breeding goal:** the goal sought by selecting for a particular selection criterion, for example, increased volume at rotation age (see **selection criteria**).
- **breeding population:** the set of tree genotypes (called clones or parents) which is considered to represent the best performers intended for crossing and re-selection for the next generation.
- **breeding value:** a number which represents a parent's relative genetic worth either for a single trait or for a mix of traits, each with a specific economic worth.
- **designer breeds:** offspring of sets of parents selected for their genetic potential to perform optimally on specific sites or for the production of specific end products.
- clonal forestry: planting of tested clones in production forests.
- **genetic gain:** a change in performance of a stand of trees as a result of genetic selection and breeding.

- **genetic selection index:** a method of combining progeny trial information from different sites and for different traits which takes heritability, genetic variance, and relative economic weights of the various selection traits into account.
- **genetic worth:** the relative performance of a seedlot with a particular parentage or genetic identity.
- **GF rating:** a breed rating assigned by the New Zealand Seed Certification Service which reflects a seedlot's relative genetic worth for growth and stem form with growth given twice as much weight as stem form.
- **production population:** the set of tree genotypes (called clones or parents) which is considered to represent the very best performers intended for current seed orchard production.
- ramets: vegetatively-propagated genetic copies (ramets) of a tree.
- **selection criterion:** the actual trait upon which genetic selection is performed, for example, diameter at age 8 (see **breeding goal**).
- **trait rating:** a number assigned by the New Zealand Seed Certification Service which reflects a particular seedlot's relative genetic worth for one specified selection criterion.

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