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NOTE

Incorporating economic weights into radiata pine breeding selection decisions

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Abstract: This article introduces the concept of "robust selection", which proposes tree selection based on the stochastic simulation of economic values to account for the inherent uncertainty of economic weights used in tree selection for breeding programs. The proposed method uses both median ranking and ranking variability as criteria for breeding selection. Using consensus genetic and economic parameters from the New Zealand Radiata Pine Breeding Company program, we compare three selection strategies: deterministic application of economic weights from a vertically integrated bioeconomic model, an equal-weight index often used in operations, and robust selection. All strategies aim to increase value for a breeding objective that includes four traits, i.e., volume, stem sweep, branch size, and wood stiffness (measured as modulus of elasticity), based on a selection index that considers five criteria, i.e., stem diameter at breast height (1.3 m), straightness, branching score, wood density, and modulus of elasticity. Two-thirds of the selected trees were unique for each of the selection strategies. Robust selection achieved the best realised gain for three of the four selection criteria and was the middle performer in the last selection criteria. Considering the high intrinsic uncertainty of economic weights, we suggest that the relevant criterion for the selection of individuals is the maximum median ranking, subject to an acceptable level of variation in that ranking, rather than their narrow performance under a single economic scenario. This will lead to tree selections that perform well under a wide range of economic circumstances.

Key words: breeding objectives, economic weights, simulation, economic evaluation, risk analysis.

Résumé : Cet article introduit le concept de « sélection robuste » qui propose une sélection fondée sur la simulation stochastique de la valeur économique pour tenir compte de l'incertitude inhérente du poids économique utilisé pour la sélection des arbres dans les programmes d'amélioration. La méthode qui est proposée utilise le classement médian et la variabilité du classement comme critères pour la sélection. À l'aide de paramètres génétiques et économiques du programme de la New Zealand Radiata Pine Breeding Company qui font consensus, nous avons comparé trois stratégies de sélection : l'application déterministique du poids économique provenant d'un modèle bioéconomique verticalement intégré, un indice de poids équivalent souvent utilisé dans les opérations et la sélection robuste. Toutes les stratégies visent à augmenter la valeur d'un objectif d'amélioration qui inclut le volume, la courbure du tronc, la dimension des branches et la rigidité du bois à partir d'un indice de sélection qui tient compte du diamètre du tronc, de sa rectitude, de la note de branchaison, de la densité du bois et du module d'élasticité. Les deux tiers des arbres sélectionnés avec chacune des stratégies étaient uniques. La sélection robuste a produit le meilleur gain pour trois des quatre critères de sélection et occupe la position intermédiaire pour l'autre critère. En tenant compte de l'importante incertitude intrinsèque du poids économique, nous suggérons que le critère pertinent pour la sélection des individus soit le classement médian maximum, qui est sujet à un degré acceptable de variation dans ce classement, plutôt que leur performance étroite dans le cadre d'un seul scénario économique. Cela va engendrer la sélection d'individus qui performent bien dans une vaste gamme de conditions économiques. [Traduit par la Rédaction]

Mots-clés : objectifs d'amélioration, poids économique, simulation, évaluation économique, analyse de risques.

Introduction

The selection of superior trees is central to breeding programs, aiming to identify individuals with maximum economic–genetic value for a combination of characteristics of economic importance. These trees are mated to produce the next generation and deployed in commercial forests. Optimal selection decisions depend not only on the economic relevance of each trait, but also on many estimates of their genetic parameters, including heritabilities and genetic correlations (Hazel 1943; Schneeberger et al. 1992; Van Vleck 1993).

The New Zealand forest industry has used selection indices since the mid-1970s (Burdon 1979) but initially focussed on collecting data to estimate genetic parameters, while relying on crude estimates of economic weights, e.g., 2 for growth and 1 for basic density (see Cotterill and Jackson (1985) for alternative methods). Although the incorporation of economic information into the selection of trees for breeding is supported both on theoretical and on logical grounds, it has not been implemented fully by tree breeders (see Apiolaza and Greaves (2001) for common reasons). Formal estimation of economic weights was first attempted for eucalypts in the early 1990s (Borralho et al. 1993), and modelling the economic importance of radiata pine (*Pinus radiata* D. Don) traits started in the late 1990s (e.g., Chambers and Borralho 1999; Apiolaza and Garrick 2001; Ivković et al. 2006*b*). In spite of a significant volume of research on this topic, both researchers and the industry still feel more comfortable (or less uncomfortable) dealing with genetic parameters than economic weights. Both genetic and economic parameters are subject to substantial uncertainty for the following reasons.

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1. The genetic architecture of the traits, i.e., their variability, genetic control, and association between traits, is subject to uncertainty, because they are estimates that are obtained from different samples of genotypes, growing in different sites and over a long period of time.
2. There are gaps in the available genetic information, particularly if a trait has only recently been identified as important, and filling those gaps may take decades, particularly for age–age correlations.
3. Economic values are subject to a high degree of uncertainty, as they will be realised several decades in the future. Even for relatively fast-growing tree species such as radiata pine, the lag between breeding decision making and realisation of value from harvested trees can be 50 years or more.
4. The forest growers, who are the ultimate customers of tree breeders, may have different views of the future, different silvicultural strategies, and different target products or markets.
5. A particular selection may be deployed for a number of years, and over the period that this population is harvested, the technology and market requirements may change.

Although the uncertainty associated with genetic parameters might be reduced through additional data and analysis, the uncertainty in economic parameters is unavoidable, because it is generated by the necessarily long time frames from selection to harvest of the improved crop and the different views of the future among forest growers who will use the improved seed. The long time frames make this a much larger issue for tree breeding than for animal breeding, where selection index theory was initially developed. Selection methodologies that account for this inherent uncertainty in tree breeding are required.

Bioeconomic models, which show the relationship between changes in the management of the resource and the subsequent quality and quantity of output from the forest, have been the most popular approach used to estimate economic weights in tree breeding. Ivković et al. (2006*b*) constructed separate bioeconomic models for a forest grower, a processor, and an integrated firm and obtained different values for the economic weights, mirroring the experience of animal breeders, as discussed by Goddard (1998). For a discussion of other methods of calculating economic weights in tree breeding, see Alzamora (2010).

This paper outlines an alternative approach to incorporating economic information into selection decisions. We use genetic and economic data for radiata pine in New Zealand to first calculate deterministic selection index coefficients. This was followed by the introduction of a simulation approach to the use of economic weights and a proposal for the selection of "robust" genotypes that are stable (in the sense of being highly ranked performers) under the likely variation in economic-weight values.

Materials and methods

Selection indices combine the predicted breeding values (s_i; often called the best linear unbiased prediction (BLUP)) of multiple traits for each individual to calculate the following index I on which to base the selection:

$$I = b_1 s_1 + b_2 s_2 + \ldots + b_n s_n = \boldsymbol{b}'\boldsymbol{s}$$

where $\boldsymbol{s}$ is a vector of breeding values for selection criteria (often assessed at 1/4 to 1/3 of rotation age), and $\boldsymbol{b}$ is the vector of index coefficients. When selecting on index values, breeders aim to maximise the following breeding-objective function H, a linear combination of the genetic values for each trait (a_i) weighted by their economic values v_i (value per unit of increase in the trait):

$$H = v_1 a_1 + v_2 a_2 + \ldots + v_n a_n = \boldsymbol{v}'\boldsymbol{a}$$

where $\boldsymbol{v}$ is the vector of economic values, and $\boldsymbol{a}$ is the vector of genetic values for the traits that we wish to improve (often at rotation age). Therefore, H represents the genetic–economic worth of an individual. The index coefficients ($\boldsymbol{b}$) that maximise the correlation between I and H are calculated as follows (Schneeberger et al. 1992):

$$\boldsymbol{b} = \mathbf{G}_{\mathrm{ss}}^{-1}\mathbf{G}_{\mathrm{so}}\boldsymbol{v} \tag{1}$$

where $\mathbf{G}_{\mathrm{ss}}$ and $\mathbf{G}_{\mathrm{so}}$ are the additive covariance matrix for selection criteria and the additive covariance matrix between selection criteria and objective traits, respectively, and the $\boldsymbol{b}$ coefficients combine genetic and economic information (heritabilities, genetic correlations, and economic weights). Equation 1 is an extension of Hazel's (1943) and van Vleck's (1993) work.

Selection indices link characteristics that breeders would like to improve (objective traits in H) with the characteristics that they assess (selection criteria in I). This distinction is very relevant for tree breeders, because they often use criteria that are expressed early in the life of the trees and easier to assess than objective traits. For example, radiata pine progeny trials are routinely assessed for diameter at breast height (1.3 m) at age eight, rather than for volume at rotation age.

These indices assume that $\mathbf{G}_{\mathrm{ss}}$, $\mathbf{G}_{\mathrm{so}}$, and $\boldsymbol{v}$ are known with certainty; however, we have already pointed out that genetic and, particularly, economic parameters are subject to much uncertainty. Because the sources of uncertainty of economic parameters are largely related to the long time frames and the different views of the future that may be held by those who plant improved seed, they are not able to be removed through further analysis. Therefore, selection decisions should recognise the inherent uncertainty in the estimation and application of economic weights. What is required is the best estimate of the economic value of the trait and an estimate of the uncertainty in these estimates.

We propose a method, which we call "robust selection", that uses (*i*) economic weights drawn from distributions centred around published values to calculate selection index coefficients and (*ii*) the selection of individuals that have both high rankings and a low ranking variability. Therefore, the selection process will involve n times of (*i*) drawing a set of economic weights, (*ii*) calculating coefficients using eq. 1, (*iii*) applying the index to all trees, and (*iv*) ranking the trees. Then, trees are evaluated on the basis of their median ranking across all draws of economic weights, subject to a ranking variability that is lower than a predetermined threshold.

Robust selection will be compared with the deterministic application of economic weights calculated by Ivković et al. (2006*a*), using the estimates for the integrated direct sawlog option presented in Table 1 and an equal-weight index often used by the New Zealand Radiata Pine Breeding Company (where all coefficients of $\boldsymbol{b}$ are equal to 1) for selecting trees for breeding from an elite population.

We assume that all genetic parameters in $\mathbf{G}_{\mathrm{ss}}$ and $\mathbf{G}_{\mathrm{so}}$ are known without error to focus the comparison only on varying economic weights. Robust selection was implemented using the R statistical system (R Core Team 2014), and both the code and the breeding values used in the test are available in the Supplementary material[1].

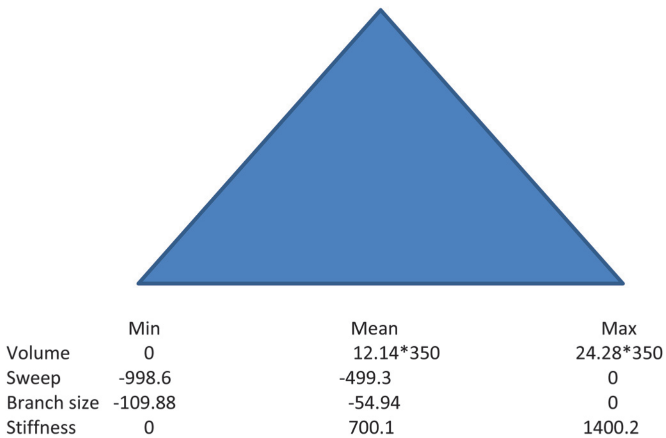
[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0363: cjfr-2014-0363suppl.zip contains the R code and the data set.

Table 1. Economic weights for New Zealand radiata pine based on the three different viewpoints.

		Objective traits			
Viewpoint	Regime	Volume	SWE	BRS	MOE
Grower	Direct sawlog	12.42	−40.88	−9.2	387.6
	Minimum tending	9.031	−53.85	−63.06	497.4
Sawmiller	Direct sawlog	−0.0065	−2.958	−0.416	8.25
	Minimum tending	0.0346	−6.5	−2	14.25
Integrated	Direct sawlog	12.14	−499.3	−54.94	700.1
	Minimum tending	17.97	−1087	−186.5	1242

Note: SWE, stem sweep; BRS, branch size; MOE, modulus of elasticity.

Fig. 1. The assumed distributions for economic weights.



To illustrate the proposed method, we have assumed a minimum value of zero and a maximum value of twice the mean value for each trait with a positive mean value. For a trait with a negative mean value, the maximum value was assumed to be zero, and the minimum value was assumed to be twice the mean value. A triangular distribution was used for each trait (see Fig. 1).

Although this assumed level of variation is somewhat arbitrary, it is supported by the variation in economic weights from bioeconomic models (e.g., see Table 1). It seems intuitively reasonable to assume for wood-quality traits that the trait has no economic value at the minimum point on the distribution. To ensure a symmetrical distribution, the maximum point on the distribution is a value that is double the mean estimate.

The economic weights shown in Table 1 were used in the analysis, except that for volume, their units were changed from $m^3 \cdot tree^{-1}$ to $m^3 \cdot ha^{-1}$ by using a scaling factor of 350 $trees \cdot ha^{-1}$ to expand volume from tree level to hectare level, matching Ivković et al. (2010).

Genetic parameters

"Consensus" or "accepted" genetic parameters for selection criteria and objective traits for the New Zealand Radiata Pine Breeding Company program are presented in Tables 2–4. This information is exactly as presented by Ivković et al. (2010); however, Table 4 contains updated phenotypic variances for objective traits, as they were incorrectly reported in 2010 (S. Kumar, personal communication).

Breeding values

We will test the performance of the different selection indices by applying them to a preliminary set of 481 candidates of a 2007 elite population. This population was a selection of approximately 10 individuals from 50 families, which were from the 268 progeny trial, compartment 1350, Kaingaroa Forest (P. Jefferson, personal communication) For each tree, there are predicted breeding values (univariate BLUP, expressed as deviation from the overall population mean) for stem diameter at breast height, stem straightness, branching habit, wood basic density, and modulus of elasticity (estimated using time-of-flight acoustic tools). The data set is presented in the Supplementary material[1]; however, the genetic identities have been changed.

Table 2. Additive genetic correlation among selection criteria.

	DBH08	STR08	BR08	DEN08	MOE08
DBH08	1	0.05	0.29	−0.25	−0.35
STR08		1	0.15	0.05	0.05
BR08			1	−0.05	−0.10
DEN08				1	0.48
MOE08					1

Note: For all selection criteria, trees were accessed at age 8. DBH, diameter at breast height; STR, straightness; BR, branching score; DEN, wood density; MOE, modulus of elasticity.

Table 3. Additive genetic correlations between selection criteria and objective traits.

	Objective traits			
Selection criteria	VOL25	SWE25	BIX25	MOE25
DBH08	0.70	0.10	0.45	−0.30
STR08	0.14	−0.70	0.05	−0.10
BR908	0.15	0.05	−0.70	−0.11
DEN08	−0.19	0.09	−0.11	0.45
MOE08	−0.20	−0.25	−0.14	0.70

Note: For selection criteria, trees were accessed at age 8. Objective traits were accessed at age 25. Trait BR9 was the assessment of branching on a 9 point scale. VOL, volume; SWE, stem sweep; BIX, branch index; MOE, modulus of elasticity; DBH, diameter at breast height; STR, straightness; BR, branching score; DEN, wood density; MOE, modulus of elasticity.

Table 4. Heritability and variance components for selection criteria and objective traits.

	h^2	σ_p^2	$\sigma_a^2 = \sigma_p^2 h^2$
Selection criteria			
DBH08	0.18	1100	198
STR08	0.25	3.8	0.95
BR08	0.35	4.7	1.65
DEN08	0.65	552	358.8
MOE08	0.55	2.08	1.14
Objective traits			
VOL25	0.25	0.3	0.08
SWE25	0.14	0.49	0.07
BIX25	0.15	95	14.25
MOE25	0.40	1.7	0.68

Note: h^2 is the heritability of the trait, σ_p^2 is the phenotypic variability, and $\sigma_a^2 = \sigma_p^2 h^2$ is the additive genetic variance. DBH, diameter at breast height; STR, straightness; BR, branching score; DEN, wood density; MOE, modulus of elasticity; VOL, volume; SWE, stem sweep; BIX, branch index.

Results

We will show the results using three alternatives for incorporating economic weights into selection decisions. Selection index coefficients were calculated using deterministic economic weights for a direct sawlog vertically integrated regime and equal index weights using data from Tables 1 to 4. The indices were applied to the breeding values for all genotypes, which were then ranked in decreasing order of index value. This is the standard implementa-

Fig. 2. Selection index values for all 482 individuals, ranked in decreasing order.

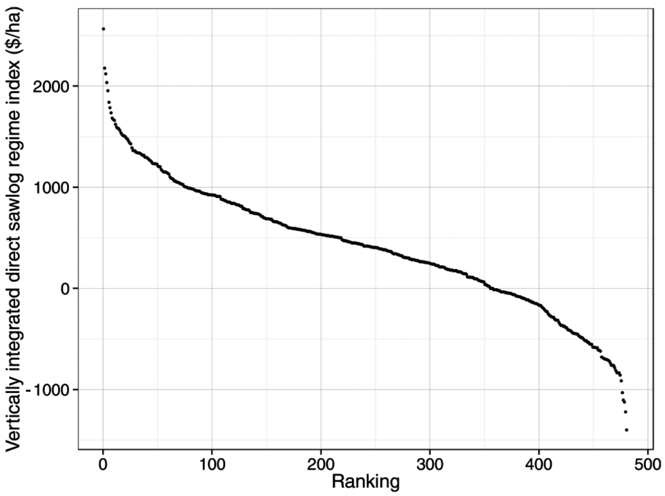
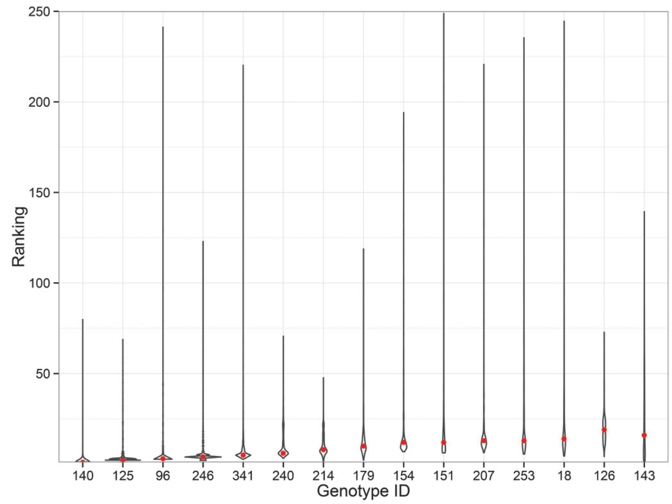


Fig. 3. Violin plots of the distribution of ranking positions for the top 10 selections, based on maximising the selection index value under 1000 scenarios of economic weights.



tion of economic weights in a breeding program. Figure 2 shows a simple ranking based on index value, with some obvious candidates for selection, some obvious candidates for rejection, and a majority of genotypes with near average performance, where the economic penalty for choosing the next lowest ranked candidate is relatively small.

In the case of robust selection, the assumed triangular distribution of economic weights was used to calculate the median ranking and the range of rankings for these selections (Fig. 3). It should be noted that the ranking distributions are highly skewed — we are selecting from those individuals at the superior end of the curve; therefore, most of their index values are high. Figure 3 shows that some of the selections made by maximising the selection index value are ranked highly throughout the range of economic circumstances represented by the probability distributions described above (e.g., trees 140, 214, and 126), while others are ranked much more poorly in some economic circumstances (e.g., trees 96, 341, 151, 207, 253, and 18).

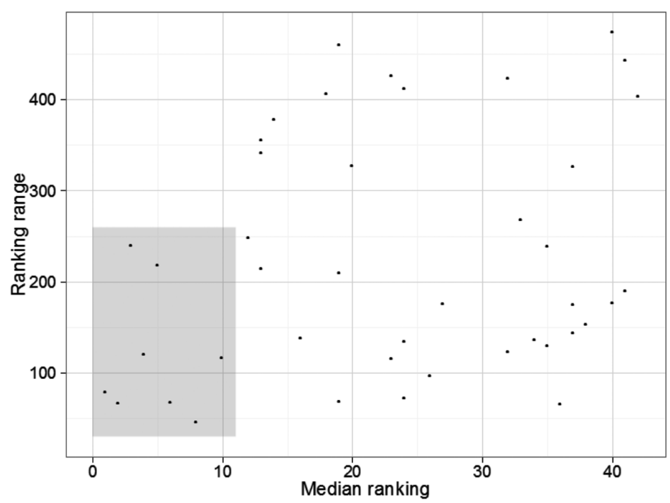
Robust selection targets genotypes that avoid the wide range of rankings displayed by some of the selections chosen by simply maximising the selection index value. It does this by selecting the individuals with the largest median ranking, while making that selection subject to an acceptable threshold of ranking variability.

The second selection reduces the variability considerably. If we look at the top 42 trees in terms of their mean index value (Fig. 4), we can see again that there are a few top performers with high rankings and low ranking variability (those within the shaded rectangle); however, below that point, there is a clear trade-off between median ranking and ranking variability.

Comparing conventional selection using economic weights with robust selection and equal-weight selection (another method often employed by tree breeders) shows that assumptions of future economic circumstances certainly make a difference in terms of the trees selected under each strategy (Fig. 5). Only 4 of the top 15 trees were common to all strategies, whereas 5–7 trees were common to two strategies. At least 40% of the selections are unique for each of the strategies.

Table 5 shows the genetic gain achieved under the three strategies described above — robust selection provides the best gain for three of the four traits and is the middle performer in the last trait. When compared with the deterministic economic weights for a direct sawlog regime, robust selection performs better for all traits except volume. Equal weight selection is not recommended, as the selection of values for weights is entirely arbitrary, ignoring

Fig. 4. Top 42 individuals, based on the selection index value.



all economic information and genetic information generated by progeny trials.

Discussion

Robust selection uses two decision criteria that are absent from the standard implementation of economic weights. The implementation of the method focuses on ranking, rather than on the selection index value. It is fundamental to the method to select individuals with a low ranking variability. These are the individuals that perform most reliably under the full range of economic circumstances. Tree breeders always wish to select the individuals that rank the highest. In robust selection, we propose selecting those that have the maximum median ranking, subject to a predetermined ranking variability. Figure 6 shows that both the very high and very low ranked individuals tend to have a low ranking variability.

To implement robust selection, a probability distribution of economic weights is required. Although these distributions have been assumed in the example shown above, they could be provided from the results of sensitivity analysis conducted using a bioeconomic model. A sensitivity analysis of this type would include historic variation in log prices and other data inputs. In addition, we have assumed that there were no correlations be-

Fig. 5. Trees selected under the different strategies (equal weight, deterministic, and robust).

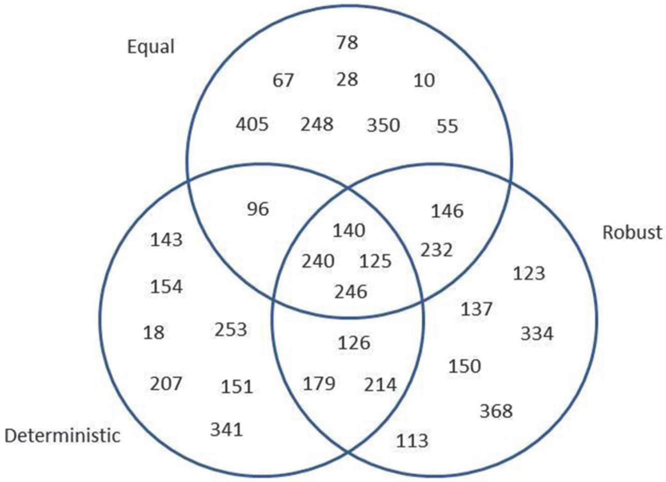
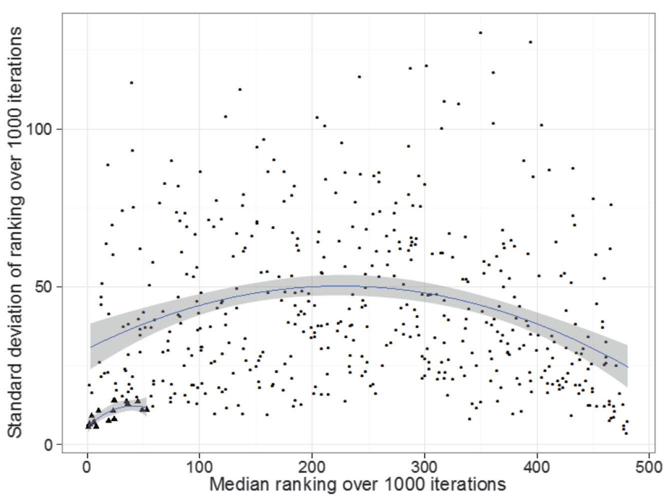


Table 5. Breeding value gain under the three candidate strategies.

Strategies	Objective traits Diameter	Straightness	Branch size	Stiffness
Deterministic	21.03	−0.08	1.23	0.81
Equal weights	9.69	−0.34	0.80	0.71
Robust selection	15.47	0.20	1.25	0.88

Fig. 6. RPBC elite population rankings, where triangles represent trees chosen by robust selection.



tween the economic weights. However, if these correlations did exist and were known, they could be accommodated by using the standard tools of risk analysis.

A useful selection tool should (*i*) provide appropriate weightings to reflect the relative importance of a number of different traits, (*ii*) recognize the inherent uncertainty in economic information, generated by the long time frames in tree breeding, in both the breeding and deployment cycles, and the different objectives of stakeholders (very relevant for breeding programs involving multiple firms), and (*iii*) lead to an agreement among members on economic weights for breeding selection. The process of implementing economic weights should include further analysis to investigate the impact of different choices of the probability distribution and mean value of economic weights.

As has been noted by Hoogstra and Schanz (2008), there is a tendency among decision makers in forestry and in other business areas to ignore uncertainty. This indicates a potential for a much wider application of the methods outlined in this paper. For example, the uncertainties in the economic values also exist for the genetic parameters. We have assumed a perfect knowledge of genetic parameters to emphasize the effect of uncertainty present in economic information; however, the same approach could be expanded to incorporate knowledge of the uncertainty of these parameters as well. The methods outlined in this paper could also be used to evaluate silvicultural and other investment options in forestry where there is uncertainty about future values of input data.

Conclusion

There has been an extensive research investment in New Zealand to enhance the selection of improved trees to increase the competitive advantage of radiata pine and enhance the species suitability and market acceptance in a range of end uses. Breeding theory requires that the optimal selection of multiple traits uses economic weights to specify the value of each trait. The focus of implementation of economic weights to date has been to choose the individuals that maximise the index value. Where the economic weights and other inputs into the calculation of the index are known with certainty, this method will provide the highest ranked candidates.

Nevertheless, where input values are not certain, we contend that the relevant criterion for the selection of individuals is the maximum median ranking, subject to an acceptable level of variation in that ranking. This will provide the selections that are most likely to be ranked high, under the full range of expected future economic values. We have shown that there are a number of reasons why there is inherent uncertainty in any estimate of economic weights. We have also provided a method to implement selection for breeding that will minimise the impact of this uncertainty on the value of the final crop. This approach is consistent with investment theory, which proposes that we should not only consider the expected value of the return from an investment but also the variability of that return, as a measure of risk.

The investment in tree improvement is significant, and the methods that we are proposing will provide a more defensible selection for the use of this investment by the industry in the future and will lead to a more complete adoption of a rigorous method of choosing among investment alternatives, taking into account the information uncertainty.

Acknowledgements

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