vary widely in yield, that the environmental component in seed yield variation is large and the yield from hybrid crosses, is reduced over that from intraspecific crosses. Cone size can be used to predict numbers of seed and seed size but not seed quality.

Management of seed orchards requires large amounts of quite detailed knowledge on individual clones over several years so that roguing or environmental modification can be undertaken successfully.

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On index selection I. Methods of determining economic weight

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Summary

Three methods (called partial regression, desired gain and equal emphasis) are outlined for estimating economic weights for use in selection on the index developed by Smith and Hazel. Under the method of partial regression economic weights are determined as the coefficients in a partial regression of phenotypic values for each trait (dependent variates) on estimates of the net economic worth of individual trees (independent variate). Partial regression is argued to be theoretically the most correct approach for estimating economic weight. Under the method of desired gain breeders are required to specify the relative responses they would like to achieve in each trait. Economic weights are then determined to give expected genetic responses from index selection which are proportional to the gains desired. Under the method of equal emphasis economic weights are determined to give equal importance to a one standard deviation change in each trait.

Each method produced different sets of weights when applied to data for *Pinus radiata* and *P. caribaea* in Australia, and the consequences of these different weights are examined in terms of expected genetic gains and the phenotypic values of individuals retained following index selection. Such checks on the consequences of index selection are always recommended. Beyond this, the method of partial regression is generally recommended where good information is available on the economic worth of trees. Where there is poor economic information but reliable information is available on genetic parameters the method of desired gain would be favoured. Equal emphasis is appropriate only where traits have approximately equal economic importance per standard deviation change.

Key words: Selection index, Smith-Hazel index, economic weight, economic worth, genetic gain.

Zusammenfassung

Um ökonomische Gebrauchswerte bei der Indexselektion nach Smith und Hazel zu schätzen, werden drei Methoden (sog. Partialregression, erwünschte Gewinne und gleiche Schwerpunkte) umrissen. Bei dem Partialregressionsverfahren werden ökonomische Gebrauchswerte als Koeffizienten einer Partialregression phänotypischer Werte für jedes Merkmal (als abhängige Variable) für Schätzungen des ökonomischen Nettowertes für Einzelbäume (als unabhän-

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gige Variable) ermittelt. Die Partialregression erweist sich als theoretisch korrekteste Annäherung an den Gebrauchs-Schätzwert. Bei der Methode der erwünschten Gewinne sind die Züchter genötigt, die relativen Reaktionen zu spezifizieren, die sie bei jedem Merkmal erreichen wollen. Ökonomische Gebrauchswerte werden bestimmt, um erwartete genetische Reaktionen durch Indexselektion zu erzielen, die den gewünschten Gewinnen entsprechen. Mit der Methode der gleichen Schwerpunkte werden ökonomische Gebrauchswerte bestimmt, um jeder Veränderung der Standardabweichung in jedem Merkmal die gleiche Bedeutung beizumessen.

Jede Methode lieferte verschiedene Gruppen von Gebrauchswerten, wenn sie auf Daten von *Pinus radiata* und *Pinus caribaea* in Australien angewandt wurde. Die Konsequenzen dieser verschiedenen Gebrauchswerte werden als Ausdruck erwarteter genetischer Gewinne und als phänotypische Werte von Individuen untersucht, die nach Indexselektion zurückbehalten wurden. Eine solche Untersuchung der Konsequenzen der Indexselektion empfiehlt sich immer. Darüber hinaus empfiehlt sich die Methode der Partialregression generell dort, wo gute Informationen über den ökonomischen Wert der Bäume verfügbar sind. Wenn nur schwache ökonomische, aber zuverlässige Informationen über genetische Parameter verfügbar sind, ist die Methode des erwünschten Gewinnes vorzuziehen. Gleiche Schwerpunkte sind nur anzuwenden, wo Merkmale annähernd gleiche ökonomische Bedeutung in der Änderung der Standardabweichung zeigen.

Introduction

SMITH (1936) and later HAZEL (1943) developed index selection as a technique for efficiently evaluating several traits simultaneously. The SMITH-HAZEL index (using LIN's 1978 terminology) employs multiple regression to combine phenotypic values for multiple traits into a single index value; individuals having the highest index values are selected as best. Construction of the SMITH-HAZEL index involves solving sets of linear equations which include economic weightings for each trait as well as genetic and phenotypic variances and covariances (i.e. heritabilities and genetic and phenotypic correlations).

Over recent years there has been considerable interest in SMITH-HAZEL indices in tree breeding (ARBEZ and MILLIER 1972; ARBEZ *et al.* 1974; BARADAT 1976; BURDON 1979; SHELBOURNE and LOW 1980; COTTERILL and JACKSON 1981; BURDON 1982; CHRISTOPHE and BIROT 1983 DEAN *et al.* 1983), but widespread use of selection indices is undoubtedly limited by three problems: one, uncertainty regarding how economic weights should be determined; two, lack of reliable estimates of heritability and genetic correlations; three, lack of expertise and computing facilities needed for solving the sets of equations required to construct SMITH-HAZEL indices.

This article addresses problem "one". The objective of the paper is to outline three methods of determining economic weights (identified as the methods of partial regression, desired gain and equal emphasis) and to discuss the advantages and disadvantages of each method. Data for *Pinus radiata* D. DON and *P. caribaea* var. *hondurensis* in Australia are employed to examine consequences of index selection using economic weights determined by each method. Part II of these articles on index selection (COTTERILL 1985) addresses the above problems "two" and "three" of index selection.

Progeny Data

The data are from open-pollinated progeny tests representing either: one, 2000 offspring of 28 families of *P. radiata* planted in 1969 at Mount Gambier, southern Australia (lat. 37.5S, long. 140.5E); or two, 1500 offspring of 34 families of *P. caribaea* var. *hondurensis* planted in 1972 at Cardwell, northern Australia (lat. 18.1S, long. 146.0E). The field designs of both progeny tests were randomised blocks with either 6-tree row *(P. radiata)* or single-tree plots *(P. caribaea).* All trees in both progeny tests were assessed at $4^1/_2$ years (after planting) for height, diameter (overbark at 1.3 m), stem straightness (five-point subjective score; 5 = straight stem, 1 = crooked stem) and branch diameter (five-point score for *P. radiata* and four-point score for *P. caribaea;* 5 or 4 = thin branches, 1 = thick branches).

Economic data used to determine economic weights by partial regression were obtained for 308 trees felled (at random) at $11^1/_2$ years in the *P. radiata* progeny test. The method of partial regression, as described later, requires estimates of the net economic worth or profit (W) of trees. In this study W was calculated as the amount of money paid for logs recovered from each tree, less the costs of recovering those logs. The payment was actually a government "royalty" paid by saw mills for logs obtained from government owned plantations.

Each of the 308 trees felled were cut into 4.9 m logs and each log was graded as either "pulp qualiy" or one of five more economically valuable "case log" classifications. To be classified as "pulp" the log had to be at least 7.5 cm diameter (small-end). To be classified as "case" the log had to be at least 12 cm diameter and have good straightness Pulp logs were valued at a fixed price per cubic metre, while case logs were valued at a price per cubic meter which increased with increasing small-end diameter. Logs of less than 4.9 m length or 7.5 cm diameter were regarded as unsaleable and assigned zero economic value.

Genetic and phenotypic parameters used to construct selection indices are presented in *Table 1.* The parameter estimates for *P. radiata* are means of estimates presented by COTTERILL and ZED (1980) for two sites (5031 and 5042) in the Mount Gambier region, while the estimates for *P. caribaea* are means of estimates presented by DEAN and EISEMANN (1985) for two sites in the Cardwell region. The *P. radiata* and *P. caribaea* progeny data used in the present study provided part of the overall data base for the parameter estimates in *Table 1.* The genetic parameters given in *Table 1* are means of estimates from large sets of data and, according to guidelines set by ROBERTSON (1959) and HARRIS (1964), should be reasonably reliable.

Determining Economic Weights

The concept of economic weights was developed by HAZEL (1943) as part of the SMITH-HAZEL index and is most easily explained in the context of this index. The SMITH-HAZEL index is usually written — (1)

$$I = b_1P_1 + b_2P_2 + \dots + b_nP_n \quad (1)$$

where the P's are phenotypic values for each trait and the b's are index coefficients. The b's are calculated to maximise genetic gain in a variable H which is the total genetic merit or breeding objective and is defined as — (2)

$$H = a_1G_1 + a_2G_2 + \dots + a_nG_n \quad (2)$$

the a's being economic weights and the G's are the breeding values for each trait. Under a linear model, maximising genetic gain in H is equivalent to maximising the correlation r_{IH} between the index I and breeding objective H.

Table 1. — **Estimates of phenotypic means (μ), phenotypic standard deviations (σ), heritabilities (h^2), and genetic and phenotypic correlations for *P. radiata* at Mount Gambier and *P. caribaea* var. *hondurensis* at Cardwell.**

Trait	μ	σ	h^2	Correlations			
				Ht.	Dia.	Stem str.	Branch dia.
P. radiata							
Height 4½ yr (m)	9.8	0.95	0.35		0.75[A]	0.35	0.0
Diameter 4½ yr (cm)	14.4	2.2	0.15	0.7[B]		0.4	0.0
Straightness (1-5 score)	3.0	1.0	0.2	0.3	0.2		0.45
Branch dia. (1-5 score)	2.1	0.9	0.2	0.0	-0.25	0.25	
P. caribaea							
Height 4½ yr (m)	6.5	1.4	0.25		0.8[A]	-0.1	-0.55
Diameter 4½ yr (cm)	10.2	2.2	0.4	0.8[B]		-0.1	-0.8
Straightness (1-5 score)	2.0	0.65	0.3	0.2	0.15		0.35
Banch dia. (1-4 score)	2.7	0.5	0.25	-0.4	-0.45	0.0	

[A] Genetic correlations in upper triangle.

[B] Phenotypic correlations in lower triangle.

H is an unobservable variable in the sense that the breeding values of the individual trees being selected (the G's) are unknown. The SMITH-HAZEL index can therefore be considered as indirect selection for an unobservable variable H by truncation selection on an observable variable I, which is calculated to have maximum correlation with H. The well known matrix equation for solving sets of equations to calculate the b's in Equation 1 and maximise r_{IH} is — (3)

$$\underline{b} = \underline{P}^{-1}\underline{G}\ \underline{a} \qquad (3)$$

where $\underline{G}$ and $\underline{P}$ are the genetic and phenotypic variance-covariance matrices, and $\underline{a}$ is the column vector of economic weights (see textbooks such as TURNER and YOUNG 1969).

The Equation 2 which defines breeding objective H is mostly assumed linear, but there is no reason why hisher-powers or products of traits cannot be included in the definition of breeding objective if these higher powers are likely to increase the precision of the selection function (SMITH 1936). For instance, WILTON *et al.* (1968) developed a quadratic version of the SMITH-HAZEL index which includes squares and products of traits. Non-linearity in the definition of breeding objective may sometimes be more simply dealt with by logarithmic transformation (or some other transformation) to alter the scales of traits (LIN 1978).

The following are the best known methods of determining economic weights for index selection. It will become apparent that economic weights determined by any method are, like estimates of heritability or genetic correlation, applicable to only the particular population, environment and point in time for which they are estimated. (In other words, economic weights should be recalculated by the breeder for each new population, environment or time in which selection is to take place). The actual economic weights presented here are certainly not relevant to other breeding regions.

1 Method of Partial Regression

T h e o r y : Economic weights (a) are determined by partial regression of phenotypic values (P) on estimates of the net profit or net worth (W) of individual trees — (4)

$$W = \hat{c} + \hat{a}_1P_1 + \hat{a}_2P_2 + \ldots + \hat{a}_nP_n. \qquad (4)$$

The $\hat{c}$ is a constant and the regression coefficients (or economic weights), $\hat{a}_j$, estimate the amount by which net profit W changes when the phenotypic value P_j of the jth trait is increased by one unit of measurement; the other P's remaining constant. DUNLOP and YOUNG (1960) and ANDRUS and MCGILLIARD (1975) used the method of partial regression to estimate economic weights for index selection in animal breeding. To our knowledge the method has not been used in tree breeding, although BRIDGWATER and STONECYPHER (1979) employed simple regression techniques to estimate economic weights for *P. taeda* in the USA.

The main advantage of partial regression is that it is the method implied by the SMITH-HAZEL definition of breeding objective H (Equation 2). Standard errors of the economic weights can also be calculated. The main problem is that the reliability of partial regression estimates of economic weight depend directly on the accuracy of values of W used to solve Equation 4.

A conceptual difficulty with the method of partial regression is that, except for uncorrelated traits, estimates of economic weight will vary according to what traits are included in the regression of P_j on W. Note that the same set of traits, in the same order, should be included in both the regression of P_j on W (Equation 4) and the associated regression of G_j on H (Equation 2).

The set of traits used in the regressions of P_j on W and G_j on H are important because together these regressions determine the breeding objective (i.e. the regression of P_j on W determines what weights are given to the set of traits used in Equation 2 to define the breeding objective H). GJEDREM (1972) argues that it is preferable to use all known traits in the regression of G_j on H (and hence P_j on W), including traits of trivial economic importance. However, SMITH (1983) pointed out that, in practice, only traits for which reliable genetic information is available can be used in the regression of G_j on H; and these are usually only traits of non-trivial economic importance. Genetic information, such as heritabilities and genetic correlations, is seldom collected for minor economic traits. In the present study we have simplified matters by using only four major economic traits in Equations 2 and 4, and these same traits are also used in the indices.

It is worth mentioning that the same set of traits need not be used in the regression of G_j on H and the index. (Textbooks commonly assume that the same set of traits are used in both instances.) JAMES (1981) suggested that breeders should view separately the tasks of defining breeding objective (i.e. choosing traits and economic weights to use in Equation 2) and determining selection criterion (i.e. choosing traits to use in the index, Equation 1). This somewhat subtle distinction between breeding objective and selection criterion overcomes complications of having to adjust economic weights of traits in the index to take account of the effects of genetic partial regression with traits included in the breeding objective but for some reason omitted from the index.

W o r k e d E x a m p l e : Economic and phenotypic data for the 308 trees felled in the *P. radiata* progeny test were used to determine the following partial regression of P_j on W — (5)

$$W = -0.465 + 0.213P_1 - 0.052P_2 + 0.013P_3 - 0.025P_4 \qquad (5)$$

where W represents the net profit to the grower for logs recovered from each tree at 11½ years (i.e. royalty payments less costs of recovery); P_1 the phenotypic value of the tree for height at 4½ years (measured in metres), P_2 diameter at 4½ years (cm), P_3 stem straightness at 4½ years (1—5 score), and P_4 branch diameter at 4½ years (1—5 score). Note that $4^1/_2$ year (and not $11^1/_2$ year) phenotypic values of growth and form traits have been used as dependent variates in Equation 5 because these $4^1/_2$ year measurements represent the traits which are combined in example indices constructed later in this article.

Equation 5 suggests that a one meter increase in height at $4^1/_2$ years for *P. radiata* at Mount Gambier would increase the net worth W of a tree at $11^1/_2$ years by 0.213 economic units; other traits remaining fixed. The constant −0.465 represents the economic worth of a tree when all the four traits in Equation 5 have zero phenotypic values. The negative sign of the constant reflects the fact that costs associated with recovering logs were taken into account in assessing W.

Table 2 presents economic weights taken from Equation 5 together with their standard errors and 95% confidence limits. Also given are transformed versions of the weights with the relative weighting for height set at 10.0 to allow comparison among sets of weights determined by different methods.

The method of partial regression placed by far the greatest economic weighting on height (a = 0.213; *Table 2*), which is not surprising since height (and to a lesser extent straightness) largely determine how many 4.9 m logs are recovered from each tree. The relatively large regression coefficient for height in Equation 5 would also include effects due to associations between height and other economic traits which may or may not be included in the regression. In particular, height has strong positive phenotypic correlations with diameter and straightness (see *Table 1*) and, since height is the first trait (P_1) in Equation 5, the partial regression between height and W would include the effects (on W) of correlated changes in diameter and straightness which occur as a consequence of a one unit change in height.

The other traits included in Equation 5 were assigned low economic weights with diameter and branch diameter actually receiving slightly negative weightings (*Table 2*). The unique contribution of diameter (over and above its correlated effect with height) to the regression should be greater in second and subsequent thinnings where most logs would be of sufficient size to be graded "case", and end diameter then becomes the sole factor determining the royality paid per cubic meter. In the present study most logs were too small to be graded as case quality.

The partial regression weights in *Table 2* all have relatively large standard errors and the resulting confidence limits show that fairly wide ranges of regression coefficients could be fitted to the data. These large standard errors include errors in measuring or assigning scores to each of the traits, as well as errors in the assessment of the worth W of trees.

A major limitation of the partial regression weights determined from Equation 5 is that the worth W of trees was estimated for first thinnings only (i.e. at $11^1/_2$ years after planting). Estimates of W should ideally be obtained for the lifetime production of trees from planting to final harvest (at around 30 to 40 years for *P. radiata* at Mount Gambier) but we could find no older trees which had been adequately measured for height, diameter, stem straightness and branch diameter when they were around $4^1/_2$ years of age. The $4^1/_2$-year measurement is critical because juvenile traits recorded at about this age are the criteria for making (provisional) new-generation selections in the breeding program at Mount Gambier, and consequently are the appropriate dependent variates P_j for regressing on W in Equation 4. We intend to record further estimates of the worth of mature trees as they are removed in subsequent thinnings of the same *P. radiata* progeny test at Mount Gambier. Note that estimates of W for later thinnings should be discounted to a "present value" at say the time of first thinning to allow for the fact that the returns have taken longer to be realised and have therefore incurred greater costs (James 1978; 1981). Reliable stand-production models could be usefully employed to forecast from early measurements the net worth of expected production of individual trees over the rotation cycle of a plantation (Bridgwater and Stonecypher 1979); and thereby overcome the above delays in obtaining reliable estimates of "lifetime W".

Genetic and phenotypic associations between juvenile and mature traits, where these associations are known, may also be taken into account in index selection by using either a specialised index of the type developed by Baradat (1976), or the more general Binet restriction discussed by Cotterill and Jackson (1981). The Binet restriction in the Smith-Hazel index allows mature traits to be included in the definition of breeding objective (Equation 2) and therefore allows gains to be maximised for these traits, even though the traits are not routinely measured in progeny testing (because they take too long to be expressed) and hence are not included in the selection index (Equation 1).

Another potential limitation of the partial regression weights determined from Equation 5 is the degree to which royalty payments reflect the true economic importance of characteristics of the tree in the milling and marketing processes. The royalty payments took relatively little account of form traits, particularly branch diameter, but perhaps these traits are of only minimal importance in saw milling and even of less importance in pulping. Studies are currently in progress in the Mount Gambier region to quantify more accurately the influence which particular features of the tree (height, diameter, straightness, branching) have on output of sawn timber from local mills (Dr. D. B. Boomsma, Woods and Forests Department of South Australia, personal communication).

The above problems encountered in attempting to accurately estimate W highlight this previously mentioned limitation of the method of partial regression. The estimates of W we have used in this study are obviously not precise. Nevertheless they are sufficient for the purposes of demonstrating methodology and examining consequences of index selection using different weights.

2 *Method of Desired Gain*

Theory: Under this approach breeders are required to specify the relative amount of gain they would like to achieve in each trait included in the selection index. Using theory developed by Pešek and Baker (1969) economic weights may be determined to produce expected genetic gains from index selection that are proportional to the "desired gains" specified by breeders.

Desired gains specified by breeders might often be subjective, and the question arises about the benefit of choosing subjective desired gains against the alternative of short-cutting methodology and simply choosing subjectively the economic weights (a_j) themselves. We would argue that breeders should generally find the concept of desired gain more intelligible than the concept of economic weight, and therefore should be more competent to deduce realistic

Table 2. — Relative economic weights for *P. radiata* at Mount Gambier as determined by the methods of partial regression, desired gain and equal emphasis. Standard errors and 95% confidence limits (C.L.) are given for partial regression weights. All weights are expressed as actual values calculated, as well as values transformed so that height has a relative weighting of 10. The transformation is to facilitate comparison among methods.

Trait	Partial regression			Desired gain		Equal emphasis	
	Actual weights	C.L. 95%	Transf. weights	Actual weights	Transf. weights	Actual weigths	Transf. weights
Height 4½ yr	0.213 (±.108)	0.43 to zero	10.0	-2.20	-10.0	1.05	10.0
Dia. 4½ yr	-0.052 (±.048)	0.04 to -0.15	-2.4	11.73	53.3	0.46	4.4
Straightness	0.013 (±0.73)	0.16 to -0.13	0.6	-1.95	-8.9	1.00	9.5
Branch dia.	-0.025 (±.084)	0.14 to -0.19	-1.2	5.02	22.8	1.11	10.6

desired gains. PEŠEK and BAKER (1969) and CHRISTOPHE and BIROT (1983) suggest that while few breeders are prepared to assign relative economic weights to traits, most would be willing and confident to specify the relative amount of gain they would like to achieve in each trait included in the index.

Of course, it is preferable for desired gains to be estimated objectively. Reliable production and marketing models may be usefully employed to define a target type of tree required from breeding, and the relative desired gains then become the difference between the means of the present breeding population and the target for each trait (CHRISTOPHE and BIROT 1983). Individual traits would receive differing emphasis as their target values are approached at different rates over successive generations.

Where $\underline{d}$ represents the column vector of the relative desired gains for each trait in the selection index, PEŠEK and BAKER (1969) show that — (6)

$$\underline{b} = \underline{G}^{-1}\underline{d}. \qquad (6)$$

In this case the vector $\underline{b}$ coefficients are for a SMITH-HAZEL index which produces expected responses in each trait proportional to the desired responses. The appropriate matrix equation for estimating economic weights $\underline{a}$ given the regression coefficients $\underline{b}$ (i.e. solving backwards for $\underline{a}$) is — (7) and (8)

$$\underline{a} = \underline{G}^{-1}\underline{P}\ \underline{b}. \qquad (7)$$

Substituting Equation 6 -

$$\underline{a} = \underline{G}^{-1}\underline{P}\ \underline{G}^{-1}\ \underline{d} \qquad (8)$$

where $\underline{a}$ are the economic weights implied in choosing desired gains $\underline{d}$. In this study Equation 8 is solved only to compare weights determined by desired gain with weights determined by other methods; in practice it would be necessary only to solve Equation 6. Note that the expected genetic response (as distinct from the desired response) we refer to in this article is the genetic gain ($\triangle G_j$) which would be expected in the jth trait as a consequence of selection on the SMITH-HAZEL index, and may be calculated as — (9)

$$\Delta G_j = \text{cov}\ (G_j I)\ (i/\sigma_I) \qquad (9)$$

where cov ($G_j I$) is the covariance of the breeding value G_j of the jth trait and the index value I (in matrix notation cov ($G_j I$) = $\underline{G}\ \underline{b}$), σ_I is the phenotypic standard deviation of the index ($\sigma^2_I = \underline{b}^T\ \underline{P}\ \underline{b}$ where $\underline{b}^T$ is the transpose of $\underline{b}$), and i is the standardised selection differential.

Mathematically equivalent approaches to the above method of desired gain have been used by CHRISTOPHE and BIROT (1983) to determine economic weights for *Picea sitchensis* and *Pseudotsuga menziesii* in France, and by DEAN *et al.* (1983) for *P. radiata* in eastern Australia. Both articles calculate responses expected for each trait as a consequence of selection on indices constructed using different sets of economic weights. The breeder is then required to choose that set of economic weights which give the most desirable combination of expected gains for the particular selection program. CHRISTOPHE and BIROT (1983) prefer the term "weighting coefficients" to describe weights determined by desired gain.

The main problem with the method of desired gain is that economic weights so derived have errors of estimation that are correlated with the accuracy of genetic and phenotypic parameter estimates. HAZEL (1943) assumed that economic weights (or the breeding objective H) could be determined independently of the genetic parameters (or the index I). This assumption is required in his derivation of index coefficients b_j to maximise the correlation r_{IH}.

Worked Example: A set of responses, namely a 1 m response in height, 1.5 cm in diameter, ½ point in straightness and ¼ point in branch diameter, were specified as the relative gains desired from one generation of selection of *P. radiata* at Mount Gambier. These particular desired gains were chosen subjectively after some discussion among local geneticists.

The computer program RESI (originally described by COTTERILL and JACKSON 1981) has been upgraded by the junior author to solve Equations 6 and 8 and, using the above desired gains for *P. radiata* in Mount Gambier and appropriate genetic and phenotypic parameters from *Table 1*, the program determined economic weights according to desired gain (i.e. solving Equation 8) as $a_j = -2.20$ for height, 11.73 for diameter, −1.95 for straightness and 5.02 for branch diameter *(Table 2)*. Note that it is not possible to estimate standard errors for weights determined by desired gain.

The new version of RESI requires as input variables: heritabilities, phenotypic variances, phenotypic and genetic correlations, and either desired gains ($\underline{d}$) or conventional economic weights ($\underline{a}$). The program calculates index coefficients, expected responses in individual traits, and other parameters. The program is available on request from the senior author. Another desired gain version of RESI has been developed by Dr. R. L. EISEMANN (Forestry Department of Queensland, personal communication) while on study leave at the Forest Research Institute, New Zealand.

3 *Method of Equal Emphasis*

Theory: Economic weights are determined simply as the inverse of the phenotypic standard deviation (σ_j) of the jth trait — (10)

$$a_j = 1/\sigma_j. \qquad (10)$$

"Equal emphasis" or equal importance is given to each trait in the sense that a change of one standard deviation in any trait is calculated to be as important as a change of one standard deviation in another trait. The method of equal emphasis has been used by SHELBOURNE and LOW (1980) to determine economic weights for *P. radiata* in New Zealand. The philosophy of equal emphasis is built into the mathematical framework of a series of indices which are discussed in Part II of these articles on index selection.

The main problem with equal emphasis is that the underlying assumption of equal economic importance per standard deviation change in different traits is often wrong. The advantage of the method is its simplicity. Equal emphasis also offers some sort of base level protection against determining extremely erroneous economic weights for index selection.

The numerator of Equation 10 can obviously be altered to give different emphasis to different traits (i.e. $2/\sigma_1$ will give twice as much emphasis to trait 1), but this sort of approach usually amounts to choosing a fairly arbitrary set of weights. The Equation 10 as it is presented in this paper does not require breeders to specifiy relative weightings for traits; it merely requires the assumption of equal emphasis.

Worked Example: Phenotypic standard deviations given in *Table 1* have been used to calculate the following equal emphasis weights for *P. radiata* at Mount Gambier: $a_j = 1.05$ (i.e. 1/0.95) for height, 0.46 for diameter, 1.00 for stem straightness, and 1.11 for branch diameter.

Consequences of Different Economic Weights

Table 3 presents expected genetic gains for *P. radiata* and *P. caribaea* following simple mass selection on Smith-Hazel indices constructed using parameter estimates given in *Table 1,* together with either the economic weights for *P. radiata* in *Table 2* or weights determined for *P. caribaea* by desired gain and equal emphasis. The relative desired gains specified for *P. caribaea* were a 1 m response in height, 1.5 cm in diameter, ½ point in straightness, and no change in branch diameter. The zero desired gain for branch diameter reflects the fact that *P. caribaea* var. *hondurensis* already has fairly acceptable branch characteristics after one generation of selection at Cardwell. The equal emphasis weights for *P. caribaea* were determined from the phenotypic standard deviations presented in *Table 1.* Partial regression weights were not determined for *P. caribaea* because data were not obtained on the net worth of trees. Also presented in *Table 3* are the heritability and the correlation r_{IH} for each index.

The mass selection referred to above is of course selection for the best trees in the progeny tests (regardless of family origin). In analysis not reported here we calculated expected genetic gains for circumstances where the best individuals were chosen from each family (i.e. within-family selection) and the trends were found to be almost identical to those presented in *Table 3.*

The partial regression weights for *P. radiata* at Mount Gambier led to a Smith-Hazel index dominated by height (i.e. index coefficients were $b_1 = 4.1$ for height, compared with $b_j = -0.9$ for diameter, -0.1 for straightness, and -0.7 for branch diameter; *Table 3),* and consequently mass selection on the index (at an intensity of one tree in every 100) produced a large expected response of 0.91 m in height, a moderate 0.76 cm response in diameter, a low 0.14 point response in straightness, and an adverse response in branch diameter *(Table 3).* The desired gain weights for both *P. radiata* and *P. caribaea* led to much more balanced indices with no one trait dominating (i.e. no trait having a much larger index coefficient) and the expected responses were exactly proportional to the desired gains specified. It is interesting that the weights determined for height and diameter of *P. radiata* by partial regression and desired gain were reversed in sign. The explanation is probably that height and diameter are so highly correlated (both genetically and phenotypically; *Table 1)* they can almost be considered the same trait. The method of partial regression placed a high positive weighting on height and a negative weighting on diameter, and yet achieved a moderate correlated response in diameter. The method of desired gain produced 1.0 m : 1.5 cm relative responses in height: diameter by placing a fairly high negative weighting on height and a very high positive weighting on diameter.

In the case of *P. caribaea* the desired gain weights may have been expected to achieve greater absolute responses in height and diameter, but they did not because substantial selection pressure was obviously exerted on branch diameter (which has strong adverse genetic and phenotypic

Table 3. — Expected genetic gains for *P. radiata* and *P. caribaea* following selection on Smith-Hazel indices using economic weights determined by either partial regression, desired gain or equal emphasis. The expected gains are for individual selection at an intensity of one tree in every 100, and are determined in actual units of measurement for each trait. For each index the heritability (h^2_I) and correlation (r_{IH}) between index I and breeding objective H are given.

Economic weights				Expected gains				Index parameters		SMITH-HAZEL index equations[A]
Ht.	Dia.	Stem str.	Branch dia.	Ht. (m)	Dia. (cm)	Stem str. (point)	Branch dia. (point)	h^2_I	r_{IH}	
P. radiata										
Partial regression										
10.0	-2.4	0.6	-1.2	0.91	0.76	0.14	-0.11	0.36	0.64	$I = 4.1P_1-0.9P_2-0.1P_3-0.7P_4$
Desired gain										
-10.0	53.2	-8.9	22.8	0.67	1.01	0.34	0.17	0.25	0.44	$I = 1.8P_1+1.1P_2+0.3P_3+1.4P_4$
Equal emphasis										
10.0	4.4	9.5	10.6	0.74	0.92	0.44	0.23	0.30	0.54	$I = 5.2P_1+0.2P_2+2.2P_3+2.6P_4$
P. caribaea										
Desired gain										
10.0	4.8	11.2	34.8	0.56	0.84	0.28	0.00	0.21	0.45	$I = 2.0P_1+0.7P_2+3.5P_3+4.5P_4$
Equal emphasis										
10.0	6.4	21.5	28.0	0.59	1.31	0.29	-0.10	0.21	0.48	$I = 0.8P_1+2.1P_2+5.8P_3+3.7P_4$

[A] P_1 represents the phenotypic value for height at 4½ years (measured in metres), P_2 diameter at 4½ years (cm), P_3 stem straightness (1—5 score) and P_4 branch diameter (1—4 or 5 score).

correlations with height and diameter; *Table 1)* to prevent this trait from deteriorating (i.e. to achieve zero desired gain for branch diameter). Breeders should note this feature of desired gain that when negative correlations exist among traits the expected responses should be proportional to the desired gains specified, but the absolute values of these expected responses may be low. In an extreme case, equal desired gains specified for two traits which have similar inheritance and genetic and phenotypic correlations of −1, would lead to expected gains of approximately zero in each trait.

The equal emphasis weights produced expected responses for *P. radiata* that were fairly similar to the responses from desired gain weights *(Table 3)*. In the case of *P. caribaea* the equal emphasis weights produced a large expected response of 1.31 cm in diameter but at the expense of an adverse response in branch diameter *(Table 3)*. One way of dealing with the adverse responses in branch diameter caused by both the partial regression weights for *P. radiata* and equal emphasis weights for *P. caribaea* would be to impose the Kempthorne type restriction outlined by Cotterill and Jackson (1981). This restriction is intended to limit to zero the response expected in one (or more) traits included in the index (in this case the response in branch diameter), while maximum possible gains are achieved in other traits. Applying the Kempthorne restriction is in a sense similar to specifying zero desired gain for a particular trait (or traits), but of course in the case of the Kemthorne restriction the breeder does not also need to specify that responses in other traits be proportional to some set of desired gains.

It appears from *Table 3* that the Smith-Hazel index may sometimes be fairly robust to changes in economic weight at least under circumstances where traits are positively correlated (genetically and phenotypically). For instance, the methods of desired gain and equal emphasis determined very different weights for the highly and positively correlated traits height, diameter and stem straightness of *P. radiata*, but indices constructed using these weights led to reasonably similar expected gains. On the other hand, another different set of weights was determined for the same traits of *P. radiata* by partial regression and these weights led to expected gains which were quite different from the gains expected for desired gain and equal emphasis. Theory suggests that while the Smith-Hazel index may be robust to moderate changes in the economic weights assigned to individual traits (Pease *et al.* 1967; Vandepitte and Hazel 1977; Smith 1983), large changes (i.e. ± 200% or more) in weights can have a substantial effect on the efficiency of index selection (Smith 1983). It also seems that the Smith-Hazel index is much more sensitive to changes in economic weight when traits have adverse genetic correlations (Smith 1983). In analyses carried out for this study it was apparent that expected gains for the adversely correlated traits of *P. caribaea* were more sensitive to changes in relative economic weight than expected gains for the positively correlated traits of *P. radiata*.

We have mentioned previously that index selection can be considered as indirect selection for an unobservable variable (the breeding objective H) by truncation selection on an observable variable (the index I). Consequently the heritability of the index (h^2_I) and the correlation between I and H (r_{IH}) are important parameters in determining efficiency of the Smith-Hazel index. The heritability h^2_I of each index in *Table 3* was estimated in the same manner as the heritability of any one trait, by analyses of variance of actual index values calculated for individual trees in the *P. radiata* and *P. caribaea* progeny tests (i.e. additive variance/phenotypic variance; see Equation 4, Cotterill and Zed 1980). The correlation r_{IH} was determined as $r_{IH} = \sigma_I/\sigma_H$ where σ_H is the phenotypic standard deviation of H.

The index constructed using partial regression weights for *P. radiata* appears to be the most efficient of the indices in *Table 3*, having both a fairly high heritability (h^2_I = 0.36) and a strong correlation with the breeding objective (r_{IH} = 0.64). For *P. radiata* the index using equal emphasis weights was a little more efficient than the index using desired gain weights, while in the case of *P. caribaea* both indices were about equally efficient *(Table 3)*. The adverse correlations that exist among growth and form traits of *P. caribaea* evidently produced the lower heritabilities of indices constructed for that species.

Another way of studying consequences of methods of determining economic weight is to employ real data to demonstrate differences in the groups of trees selected as best by different indices. The three Smith-Hazel index equations for *P. radiata* in *Table 3* have been solved using phenotypic values for the 2000 trees in the progeny test at Mount Gambier, while the two indices for *P. caribaea* have been solved using the 1500 trees in the progeny test at Cardwell. *Table 4* presents Spearman's rank correlations which quantify the degree of agreement between rankings of the 2000 or 1500 trees, as evaluated according to each index. (A rank correlation of 1.0 would indicate complete agreement in the rankings of trees while a correlation of zero indicates complete disagreement). *Table 4* also gives the number of common trees which were ranked in the top 20 individuals by different indices.

In the case of *P. radiata* there was fairly close agreement between rankings of individual trees on index values determined for either desired gain or equal emphasis weights (rank correlation = 0.93; *Table 4)*. Eleven of the trees selected in the top 20 according to desired gain were also in the top 20 according to equal emphasis. There was, however, less agreement between rankings due to partial regression and desired gain (rank correlation = 0.73), and only two trees were common among the top 20 selected by each index *(Table 4)*. Comparison (in the field) of actual phenotypes of trees selected in the top 20 by either partial regression or desired gain revealed what is apparent from the expected gains given in *Table 3*. Partial regression ranked tall trees highly even though they sometimes had poor branch form, while desired gain selected no trees in the top 20 positions which had below average form.

Table 4. — Correlation between rankings based on Smith-Hazel index values of 2000 trees in a progeny test of *P. radiata* or 1500 trees in a progeny test of *P. caribaea*. The Smith-Hazel indices were constructed using economic weights determined by either partial regression, desired gain or equal emphasis. In brackets is the number of common trees ranked in the top 20 individuals by different indices.

	Desired gain	Equal emphasis
P. radiata		
Partial regression	0.73 (2)	0.75 (2)
Desired gain		0.93 (11)
P. caribaea		
Desired gain		0.96 (15)

There was similarly less agreement in rankings according to partial regression and equal emphasis (rank correlation = 0.75; *Table 4*). For *P. caribaea* there was very close agreement between rankings according to desired gain and equal emphasis (rank correlations = 0.96), with 15 trees common among the respective top 20's *(Table 4)*.

Ordinary product-moment correlations were also calculated between actual index values determined for individual trees using each of the different indices in *Table 3* and, although these correlations are not presented, their magnitude and sign were almost identical to the rank correlations in *Table 4*. The reason for preferring rank correlations in the present study is that the purpose of the selection index is to rank individuals so the best may be chosen for future breeding.

Conclusions

It is evident from this study that breeders should give careful consideration to the method they employ for determining economic weights, because different methods may produce very different sets of relative weights for traits and therefore different outcomes of index selection. Partial regression is theoretically the most correct approach to determining economic weights for SMITH-HAZEL indices and, in this study, partial regression weights appeared to produce the most efficient index. However, breeders would be unwise to employ partial regression unless reliable estimates of net worth W are available for a sample of trees in the breeding region. The estimates of W employed in the present study, although adequate for the purpose of demonstrating methodology, were clearly not sufficiently reliable to implement in a selection program.

Where W is not known but reliable estimates are available for genetic parameters, the method of desired gain offers an appealing alternative to partial regression. In circumstances where the desired gains themselves are determined subjectively the method may be criticised as being partly conjecture but this criticism is not valid where desired gains are determined in relation to some objectively defined target tree. Where traits have approximately equal importance per standard deviation the method of equal emphasis may prove very satisfactory. The method certainly has the advantage of simplicity. Of course, equal emphasis would be quite inappropriate where traits have very different economic importance.

Regardless of what method is used to determine economic weights, breeders must check the consequences of these weights in terms of expected responses in individual traits before going ahead and implementing index selection. This last point is particularly important since SMITH-HAZEL indices (and therefore economic weights) are often used rather trustingly with breeders having little or no knowledge of the selection pressure which is actually being exerted on the individual traits included in the index.

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