On index selection
II. Simple indices which require no genetic parameters
or special expertise to construct

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Summary

Two simple indices (the base and Elston indices) are outlined and, using data for *Pinus radiata* and *P. caribaea* in Australia, are compared with the more sophisticated index developed by Smith and Hazel. The main advantages of the simple indices is that they do not require estimates of genetic parameters and are easy to construct. The base index is calculated as the sum of the products of economic weights and phenotypic values for each trait, while the Elston index is the product of the phenotypic value less the minimum observed value for each trait.

Where adverse genetic and phenotypic correlations occurred among traits (which was the case for *P. caribaea),* the simple indices led to substantially lower expected gains in some traits, and different groups of individuals were chosen as best by the simple indices compared with the Smith-Hazel index. However, where traits were positively associated (which was the case for *P. radiata)* the efficiencies of the simple indices approached that of the Smith-Hazel index, with all indices producing fairly similar expected gains and similar groups of individuals selected as best. It was concluded that where traits are positively associated the base and Elston indices can be reasonably reliable alternatives to the more sophisticated Smith-Hazel index.

Key words: Selection index, Smith-Hazel index, base index, Elston index, genetic gain.

Zusammenfassung

Es werden zwei einfache Indices, der Basis- und der Elston-Index, umrissen und indem diese in Australien für Daten von *Pinus radiata* und *Pinus caribaea* benutzt werden, mit dem anspruchsvolleren, von Smith und Hazel entwickelten, Index verglichen. Die Hauptvorteile der einfachen Indices sind, daß sie keine Schätzwerte für genetische Parameter erfordern und einfach zu konstruieren sind. Der Basis-Index wird aus der Summe der Produkte der ökonomischen Gebrauchswerte und der phänotypischen Werte für jedes Merkmal berechnet, während der Elston-Index das Produkt aus dem phänotypischen Wert, vermindert um den beobachteten Minimalwert für jedes Merkmal darstellt. Wo entgegengesetzte genetische und phänotypische Korrelationen zwischen Merkmalen auftraten, (wie das bei *Pinus caribaea* der Fall war) führten die einfachen Indices bei einigen Merkmalen zu wesentlich geringeren erwarteten Gewinnen, und durch die einfachen Indices wurden im Vergleich zum Smith-Hazel-Index verschiedene Gruppen von Individuen als die besten ausgewählt. Jedoch nähern sich die Nutzeffekte der einfachen Indices dem Index von Smith-Hazel an, wo Merkmale positiv korreliert waren, wie dies bei *Pinus radiata* der Fall war, und wo mit allen Indices ähnliche erwartete Gewinne hervorgebracht und ähnliche Individuen-Gruppen als beste selektiert wurden. Daraus wird gefolgert, daß dort, wo Merkmale positiv korreliert sind, der Basis- und der Elston-Index leidlich zuverlässige Alternativen zu dem anspruchsvolleren Hazel-Index sein können.

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Introduction

Index selection is one of three fundamental methods of selecting to improve more than one trait (the other techniques being independent culling levels and tandem selection). A number of different types of selection indices are available, but by far the best known is the index developed by Smith (1936) and later Hazel and Lush (1942) and Hazel (1943). The Smith-Hazel index (using Lin's 1978 terminology) has the very important advantage of being able to take account of inheritance and genetic and phenotypic correlations among traits in a way which should maximise the gain in total genetic merit. Construction of the Smith-Hazel index involves solving sets of linear equations which combine economic weightings for each trait along with genetic and phenotypic variances and covariances.

Hazel and Lush (1942) and Young (1961) have demonstrated that the Smith-Hazel index, calculated using reliable estimates of genetic parameters, is usually more efficient in terms of maximising genetic gain but never less efficient than independent culling levels, which in turn is more efficient than tandem selection. Young (1961) found the advantage of the Smith-Hazel index was largest when traits included in the index had adverse genetic associations. However, Williams (1962) pointed out that the efficiency of the Smith-Hazel index may be substantially reduced where the index is constructed using unreliable estimates of heritability and genetic correlations.

Part I of these articles on index selection (Cotterill and Jackson 1985) identifies lack of reliable estimates (or indeed no estimates) of heritability and genetic correlations, together with lack of special expertise and computing programs required to construct Smith-Hazel indices, as two major problems restricting widespread application of index selection in tree breeding. The object of this present article is to outline and compare two simple indices (identified as the base and Elston indices; using Lin's 1978 terminology) which do not require genetic parameters or special expertise to contruct. While the base and Elston indices are not the only alternatives to the Smith-Hazel index (Andrus and McGilliard 1975), they do appear to be the simplest of the indices reported in the literature. The base index has been employed previously in plant (Elgin *et al.* 1970; Eagles and Frey 1974) and tree breeding (Zed 1978) but the Elston index does not appear to have been used previously in plant, tree or animal breeding. Data for *Pinus radiata* and *P. caribaea* var. *hondurensis* are used to explore consequences of selection on base and Elston indices compared with the Smith-Hazel index.

Progeny Data

The data is from two open-pollinated progeny tests representing either: one, 2000 offspring of 28 families of *P. radiata* planted in 1969 at Mount Gambier, southern Australia; or two, 1500 offspring of 34 families of *P. cari-*

baea var. *hondurensis* planted in 1972 at Cardwell, northern Australia (details given by COTTERILL and JACKSON 1985). All trees in both progeny tests were measured at $4^{1}/_{2}$ years (after planting) for height (in metres), diameter (in cm; over-bark at 1.3 m), stem straightness (five-point subjective score; 5 = straight and vertical stem, 1 = crooked stem) and branch diameter (four or five-point score; 4 or 5 = thin branches, 1 = thick branches).

Genetic and phenotypic parameter values used to construct selection indices are presented in *Table 1*. The parameter estimates for *P. radiata* are means of estimates from COTTERILL and ZED (1980) for two progeny tests (identified as tests 5031 and 5042) in the Mount Gambier region, while the estimates for *P. caribaea* are means of estimates for two progeny tests in the Cardwell region (C. A. DEAN and R. L. EISEMANN, personal communication). The *P. radiata* and *P. caribaea* open-pollinated 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 calculated from large sets of data and, according to guidelines set by ROBERTSON (1959) and HARRIS (1964), should be reasonably reliable.

All indices compared in this study combine height, diameter, stem straightness and branch diameter. The SMITH-HAZEL and base indices combine these traits using linear equations while the ELSTON index uses a curvilinear selection function.

Constructing Smith-Hazel, Base and Elston Indices

1. SMITH-HAZEL *Index*

The SMITH-HAZEL index is usually written —

$$I = b_1 P_1 + b_2 P_2 + \ldots + b_n P_n \tag{1}$$

where P_j is the phenotypic value of the jth trait and b_j is the index coefficient for that same trait. The aim is to calculate the b coefficients so that selection on the index I will maximise gain in total genetic merit of the breeding population. Total genetic merit or breeding objective H is defined for each tree as the sum of the breeding values for individual traits, weighted by economic weights —

$$H = a_1 G_1 + a_2 G_2 + \ldots + a_n G_n \tag{2}$$

where G_j is the breeding value for the jth trait and a_j is its economic weight.

If truncation selection is carried out on the index I, the genetic change in the breeding objective ($\triangle H$) can be estimated as —

$$\Delta H = \beta_{IH}\, \sigma_I i \tag{3}$$

where β_{IH} is the regression of the index on the breeding objective, σ_I the phenotypic standard deviation of the index, and i the standardised selection differential. Since i is a constant, maximising $\triangle H$ is equivalent to maximising $\beta_{IH}\, \sigma_I$; where the latter term may be written as —

$$\beta_{IH}\, \sigma_I = \text{cov (IH)}\, \sigma_I^{-1} \tag{4}$$

cov (IH) being the covariance between I and H. Equation 4 can be rewritten in terms of the a and b coefficients for the jth and kth traits, and P_{jk} and G_{jk} which are the phenotypic and additive genetic variances (when j = k) and covariances (when j $\neq$ k) between the jth and kth traits —

$$\beta_{IH}\, \sigma_I = \sum_j \sum_k a_j b_k G_{jk}\, (\sum_j \sum_k b_j b_k P_{jk})^{-\frac{1}{2}} \tag{5}$$

To maximise $\beta_{IH}\, \sigma_I$ it is necessary to differentiate with respect to b_j and equate the result to zero; which yields the following linear equations —

$$\sum_k b_k P_{jk} = \sum_k a_k G_{jk} \tag{6}$$

or expressed in matrix notation —

$$\underline{b}\, \underline{P} = \underline{a}\, \underline{G}. \tag{7}$$

The index coefficients can therefore be calculated as —

$$\underline{b} = \underline{P}^{-1}\, \underline{a}\, \underline{G} \tag{8}$$

where $\underline{G}$ represents the matrix of the additive genetic variances of each trait and the additive genetic covariances between traits, $\underline{P}$ the matrix of phenotypic variances and covariances, $\underline{a}$ the column vector of economic weights, and $\underline{b}$ is of course the column vector of index coefficients. The above derivation of Equation 8 is given in more detail in TURNER and YOUNG (1969).

A number of computer programs are available for solving Equation 8, including a FORTRAN IV program (called RESI) described by COTTERILL and JACKSON (1981). Although RESI is well documented the program nevertheless requires some expertise to run and, of course, reasonably sophisticated

Table 1. — Maximum and minimum phenotypic values (Max-Min), estimates of phenotypic standard deviations (σ), heritabilities (h^2), and genetic and phenotypic correlations for *P. radiata* in southern Australia and *P. caribaea* var. *hondurensis* in northern Australia.

Trait	Max-Min	σ	h^2	Correlations			
				Ht.	Dia.	Stem str.	Branch dia.
P. radiata							
Height 4½ yr (m)	12.6-5.4	0.95	0.35		0.75[A]	0.35	0.0
Diameter 4½ yr (cm)	21.1-4.8	2.2	0.15	0.7[B]		0.4	0.0
Straightness (1-5 score)	5.0-1.0	1.0	0.2	0.3	0.2		0.45
Branch dia. (1-5 score)	4.0-1.0	0.9	0.2	0.0	-0.25	0.25	
P. caribaea							
Height 4½ yr (m)	10.7-2.3	1.4	0.25		0.8[A]	-0.1	-0.55
Diameter 4½ yr (cm)	16.7-3.0	2.2	0.4	0.8[B]		-0.1	-0.8
Straightness (1-5 score)	5.0-1.0	0.65	0.3	0.2	0.15		0.35
Banch dia. (1-4 score)	5.0-1.0	0.5	0.25	-0.4	-0.45	0.0	

[A] Genetic correlations in upper triangle.

[B] Phenotypic correlations in lower triangle.

computing facilities. The program requires as input parameters estimates of economic weights, heritabilities, phenotypic variances, and genetic and phenotypic correlations.

2. *Base Index*

The base index as proposed by WILLIAMS (1962) is the sum of the products of economic weights and phenotypic values for each trait —

$$I_b = a_1 P_1 + a_2 P_2 + \cdots + a_n P_n. \tag{9}$$

Economic weight being defined here (after the classical definition of HAZEL 1943) as the amount by which profit may be expected to increase for each unit of improvement in each trait. The a_j in Equation 9 therefore take into account the different scales on which each trait is measured. The base index is simply a derivation of the expression for net economic worth of an individual tree (Equation 4; COTTERILL and JACKSON 1985) and therefore the index has considerable intuitive appeal (ZED 1978).

The advantage of the base index is that it is easy to apply, while its main disadvantage, compared with the SMITH-HAZEL index, is that it does not take into account the inheritance of traits or their phenotypic or genetic associations. For this reason the base index should never be as efficient as the SMITH-HAZEL index constructed from reliable estimates of genetic parameters (WILLIAMS 1962). However, WILLIAMS (1962) and HARRIS (1964) calculate that where the available estimates of heritability and genetic correlations are unreliable (perhaps because they are based on too little data) the theoretical efficiency of the SMITH-HAZEL index may be reduced to a level approaching the efficiency of the base index. The base index does not require estimates of genetic parameters and is therefore free of errors due to inaccuracy in these parameters.

Selection experiments of ELGIN et al. (1970) and EAGLES and FREY (1974) support the theoretical conclusions of WILLIAMS (1962) and HARRIS (1964). ELGIN et al. (1970) found that after five generations of selection for five traits in lucerne *(Medicago sativa* L.) the base index produced approximately the same improvement in total phenotypic merit as the SMITH-HAZEL index; and both indices were better than independent culling which in turn was better than tandem selection. In each of the five generations, however, the heritabilities and genetic correlations used to construct the SMITH-HAZEL indices were estimated from very small sets of data and had high standard errors. (The authors do not report the actual magnitude or direction of the genetic and phenotypic correlations of the magnitude of heritabilities estimated for the five traits.) EAGLES and FREY (1974) found that after one generation of selection on two positively and highly correlated traits in oats *(Avena sativa* L.) the SMITH-HAZEL index, base index and independent culling levels produced almost equal genetic gains. Selection on only two traits having a high positive genetic correlation is not a rigorous test of the efficiency of alternative methods of selection (YOUNG 1961), and in this sense the findings of EAGLES and FREY (1974) are not surprising.

3. ELSTON *Index*

ELSTON (1963) proposed an index which is the product of the phenotypic value P_j less the minimum observed value m_j for each trait —

$$I_e = (P_1 - m_1)(P_2 - m_2) \cdots (P_n - m_n) \tag{10}$$

where m_j = minimum P_j. Note that before applying Equation 10 it is necessary for each trait to be measured on a scale that assigns increasing values for more favourable expressions of the trait. If there is a trait for which a smaller phenotypic value is desirable the direction of the scale should be changed by taking reciprocals of the observed values (ELSTON 1963). ELSTON also recommends that if the distribution of the P_j for a particular trait has a very different shape to the distributions for other traits, then the measurements of that trait should be transformed to lessen the difference.

Subtracting m_j in Equation 10 serves mainly to adjust (or "locate") the scale of measurement of each trait to begin at zero. Where the distributions of each trait are equally located, and similarly shaped, the ELSTON index can be shown to give approximately the same weight to a standard deviation change in any trait as it gives to a standard deviation change in any other trait (ELSTON 1963; BAKER 1974). This defines what ELSTON (1963), COTTERILL and JACKSON (1985) and others refer to as assigning "equal emphasis" to traits. ELSTON (1963) also points out that subtracting m_j in Equation 10 ensures that any individual having a phenotypic value for the jth trait which equals (or approaches) m_j will have an index value equal to (or approaching) zero and be automatically culled regardless of that individual's phenotypic values for other traits. In this sense the ELSTON index has some of the characteristics of independent culling levels so far as ranking and selection are concerned.

Of course, it is possible to assign m_j some value which is greater than the minimum P_j and in this way the ELSTON index may be made to approach more closely independent culling levels. For instance, setting $m_j >$ minimum P_j for one trait in the index would ensure that any individual having a phenotypic value below this culling level m_j would receive a negative index value and be culled regardless of its phenotypic values for other traits. However, assigning $m_j >$ minimum P_j for one trait would also locate the distribution of that trait differently and upset the equal emphasis nature of index. Where the m_j exceeded minimum P_j for more than one trait some mathematical constraint would be required to prevent multiplication of two negative values to give a positive index value.

ELSTON suggests that Equation 10 may be taken one step further by using logarithmic transformation —

$$I_\ell = \log(\hat{P}_1 - \hat{m}_1)\log(\hat{P}_2 - \hat{m}_2)\cdots\log(\hat{P}_n - \hat{m}_n) \tag{11}$$

where $\hat{P}_j = P_j - m_j$ and $\hat{m}_j$ is the lower bound to $\hat{P}_j$. This index is generally recommended by ELSTON (1963) where the distributions of traits are not similarly shaped, but under these circumstances it would appear more straightforward to alter the distribution of the offending trait(s) by prior transformation of data and then simply apply Equation 10. In this article we have studied the ELSTON index only as it is defined by Equation 10.

The main advantages of the ELSTON index are its simplicity and the fact that it sidesteps the problem of estimating relative economic weight. (However, the ELSTON index does entail some assumptions about economic weights, such as the assumption of equal emphasis). The non-linear nature of the ELSTON index may appeal to breeders under circumstances where the economic value of per-unit changes in traits is known to increase with increasing phenotypic values of the other traits in the index. The disadvantage of

Table 2. — Expected genetic gains for *P. radiata* and *P. caribaea* following selection on SMITH-HAZEL, base and ELSTON indices. The SMITH-HAZEL and base indices were constructed using economic weights determined by 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. The individual heritability (h^2_I) and index equation are given for each index.

Indices	Expected gain				h^2_I	Index equations[A]
	Ht. (m)	Dia. (cm)	Stem str. (point)	Branch dia. (point)		
P. radiata -						
SMITH-HAZEL index	0.74	0.92	0.44	0.23	0.30	$I = 5.2P_1 + 0.2P_2 + 2.2P_3 + 2.6P_4$
Base index	0.49	0.92	0.42	0.12	0.21	$I_b = 10.0P_1 + 4.4P_2 + 9.5P_3 + 10.6P_4$
ELSTON index	0.50	0.90	0.41	0.16	0.20	$I_e = (P_1 - 5.4)(P_2 - 4.8)(P_3 - 1.0)(P_4 - 1.0)$
P. caribaea -						
SMITH-HAZEL index	0.59	1.31	0.29	-0.10	0.21	$I = 0.8P_1 + 2.1P_2 + 5.8P_3 + 3.7P_4$
Base index	0.03	0.0	0.40	0.10	0.10	$I_b = 10.0P_1 + 6.4P_2 + 21.5P_3 + 28.0P_4$
ELSTON index	0.0	-0.10	0.33	0.22	0.09	$I_e = (P_1 - 2.3)(P_2 - 3.0)(P_3 - 1.0)(P_4 - 1.0)$

[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).

the ELSTON index is that, like the base index, it takes no account of the inheritance of traits or their genetic or phenotypic correlations.

Consequences of Using Base and Elston Indices

The efficiencies of the base and ELSTON indices have been quantified in terms of expected genetic gain in individual traits of *P. radiata* and *P. caribaea* (*Table 2*) and rankings of individual trees (*Table 3*) following mass selection (ignoring family information) on these simple indices compared with selection on reasonably reliable SMITH-HAZEL indices. The SMITH-HAZEL indices were constructed using genetic and phenotypic parameters given in *Table 1*, together with economic weights determined by the method of equal emphasis (actual weights given in *Table 3;* COTTERILL and JACKSON 1985). Other weights determined by more complex approaches are also presented in COTTERILL and JACKSON (1985) but it was considered unlikely that breeders having only sufficient information and expertise to apply the base or ELSTON indices would choose other than the most simple approach for estimating economic weights. The base indices in *Tables 2* and *3* were constructed using these same equal emphasis weights, while the ELSTON indices were constructed using minimum values (m_j) from *Table 1*.

Table 3. — Correlations between rankings based on SMITH-HAZEL index compared with base or ELSTON index values of 2000 trees in a progeny test of *P. radiata* and 1500 trees in a progeny test of *P. caribaea*. The SMITH-HAZEL and base indices were constructed using economic weights determined by equal emphasis. In brackets is the number of common trees ranked in the top 20 individuals by different indices.

	Base index	ELSTON index
P. radiata		
SMITH-HAZEL index	0.96 (16)	0.94 (14)
P. caribaea		
SMITH-HAZEL index	0.82 (2)	0.79 (0)

The genetic gain ($\triangle G_j$) expected in the jth trait as a consequence of mass selection on any of the above indices has been calculated as —

$$\triangle G_j = \text{cov} \ (G_j I) \ (i/\sigma_I) \qquad (12)$$

where cov ($G_j I$) is the covariance between the index I and the breeding value G_j of the jth trait. For the SMITH-HAZEL and base indices cov ($G_j I$) and σ_I were estimated indirectly as —

$$\text{cov} \ (G_j I) = \underline{G} \ \underline{b} \qquad (13)$$

$$\sigma_I^2 = \underline{b}^\tau \ \underline{P} \ \underline{b} \qquad (14)$$

where $\underline{b}^\tau$ is the transpose of $\underline{b}$. There seems to be no theory available for estimating cov ($G_j I$) and σ_I^2 indirectly for the non-linear ELSTON index. Consequently, these parameters were estimated directly for the ELSTON index by analyses of variance and covariance of phentotypic values and actual index values calculated for trees in the *P. radiata* progeny test at Mount Gambier and the *P. caribaea* progeny test at Cardwell. As a check on direct versus indirect procedures, the cov ($G_j I$) and σ_I^2 for the SMITH-HAZEL and base indices were calculated both directly and indirectly and the corresponding estimates proved to be approximately equal.

The expected gains $\triangle G_j$ presented in *Table 2* are calculated for mass selection at a rate of one tree in every 100 (i.e. i ≈ 2.67) in the progeny tests, disregarding the family origin of each tree. In analyses not reported here expected genetic gains were also calculated where the best individuals were chosen from each family (i.e. within-family selection) and the trends were identical to those presented in *Table 2*. *Table 2* also presents estimates of individual heritability (h^2_I) for each index, calculated directly from the analyses of variance of the actual index values of individual trees in the *P. radiata* and *P. caribaea* progeny tests (i.e. h^2_I = additive variance/phenotypic variance; see Equation 4, COTTERILL and ZED 1980).

It is apparent from *Table 2* that for *P. radiata* the base and ELSTON indices produced very similar expected gains in all the traits studied. The gains from these simple indices

for diameter and stem straightness were also similar to the gains produced by the Smith-Hazel index, but the latter (more sophisticated) index achieved greater gains in branch diameter and, in particular, height. The expected gain in height was 0.74 m for the Smith-Hazel index compared to around 0.5 m for the simple indices *(Table 2)*. For *P. caribaea* the base and Elston indices both led to fairly substantial gains in stem straightness (0.4 point under the base index and 0.33 point under the Elston index; *Table 2)* and some improvement in branch diameter. However, none of the simple indices produced any response in growth; in fact the Elston index actually led to a 0.1 cm decline in diameter *(Table 2)*. The Smith-Hazel index was much superior for *P. caribaea*, producing good expected gains of 0.59 m in height, 1.31 cm in diameter and 0.29 point in stem straightness; although there was a slight deterioration in branch diameter. The general superiority of the Smith-Hazel index for *P. radiata* and, in particular, *P. caribaea* is reflected in the higher individual heritabilities of this index compared with the base and Elston indices *(Tables 2)*.

In conclusion, the strong negative genetic and phenotypic correlations among growth and form traits of *P. caribaea (Table 1)* provide the most stringent test of the relative efficiencies of the different indices, and under these circumstances the Smith-Hazel index proved substantially superior. For instance, in the case of *P. radiata* (where traits had positive or at least zero genetic correlations) the base and Elston indices were reasonably heritable and led to fairly acceptable expected responses in individual traits. However, for *P. caribaea* (where growth and form traits had adverse genetic correlations) the base and Elston indices had fairly low individual heritabilities and led to zero or slightly negative responses in growth traits, which would be unacceptable to most breeders. The Smith-Hazel index also led to a deterioration in one trait (branch diameter) of *P. caribaea* but an important practical advantage of the more sophisticated Smith-Hazel index is that it can be applied with restrictions (the Kempthorne restriction) which may prevent deterioration of adversely correlated traits such as branch diameter while maximum gains continue to be achieved in the other traits included in the index (discussed by Cotterill and Jackson 1981; 1985). Another type of restriction (the Binet restriction) may be used with the Smith-Hazel index to maximise gain in mature traits as a consequence of index selection on juvenile traits (Cotterill and Jackson 1985). None of these restrictions can be implemented with the base or Elston indices.

The three index equations for *P. radiata* in *Table 2* have been solved using phenotypic values for each of the 2000 trees in the progeny test at Mount Gambier, while the three indices for *P. caribaea* have been solved using phenotypic values for the 1500 trees in the progeny test at Cardwell. The distributions of each trait were checked before solving the Elston indices and all distributions were found to be approximately normal (similarly shaped). *Table 3* presents Spearman's rank correlations which quantify the degree of agreement between rankings of the 2000 or 1500 trees as evaluated according to base or Elston indices compared with the Smith-Hazel indices. (A rank correlation of 1.0 would indicate complete agreement in the rankings of trees while a correlation of zero indicates complete disagreement.) *Table 3* also gives the number of common trees which were ranked in the top 20 individuals by different indices.

For *P. radiata* there was close agreement between rankings of individual trees according to the base or Elston indices and the rankings according to the Smith-Hazel index. Rank correlations ranged from 0.94 to 0.96, and between 14 and 16 individuals were common among the top 20 trees selected by corresponding indices *(Table 3)*. For *P. caribaea* the correlations between the base or Elston indices and the Smith-Hazel index were predictably lower (rank correlations ranging from 0.79 and 0.82), and no more than two trees were common among the respective top 20's.

It is interesting to note that the *P. caribaea* progeny test in northern Australia had been visually searched for plus trees before this study and four trees were identified as candidates for future seed orchards. The Smith-Hazel index ranked three of these selections in the top six individuals. The fourth seed orchard selection was ranked lower at 21 (because the tree was only average for height and form traits, although outstanding for diameter.) The Smith-Hazel index also identified other superior trees which had very favourable combinations of traits and appeared suitable for seed orchards but were overlooked in visual searching. The base and Elston indices did not rank any of the four seed orchard selections in the top 100 trees. These simple indices were placing far too much emphasis on form traits and often selecting trees which were below average for growth.

Conclusions

From this study we cannot recommend the base or Elston indices as methods of selection which are as efficient as the Smith-Hazel index constructed using reliable estimates of genetic parameters. However, under circumstances of positive genetic and phenotypic correlations among traits the base and Elston indices appear to be reasonably efficient, and could be usefully employed by breeders who do not have accurate estimates of genetic parameters or the expertise to construct reliable Smith-Hazel indices. At least the base and Elston indices provide the breeder with an objective rule for evaluating several traits simultaneously and, if used correctly, should prevent good trees being overlooked (a problem with visual searching). Before using any type of index selection, breeders would be well advised to check the consequences in terms of genetic gains expected from selection or, if this is prevented by inadequate information on genetic parameters, in terms of the phenotypes of the individual trees actually selected.

The best criterion for choosing among the simple indices reported here may be their intuitive appeal. For instance, if the breeder believes that total genetic value is reasonably reflected by the sum of the observed values of traits weighted by economic weights, then the base index would perhaps be favoured. Alternatively, if the breeder believes that total genetic value increases curvilinearly with increasing phenotypic values of traits, then the Elston index may be perferred.

Independent culling levels is, of course, another method of objectively selecting for several traits simultaneously and also appears to be reasonably efficient where positive associations exist among traits. However, independent culling has less intuitive and theoretical appeal than even the simple selection indices, because the former does not allow excellence in one trait to compensate, in any degree, for weakness in another.

Breeders should make every effort to get reliable genetic parameter estimates and acquire the expertise to construct Smith-Hazel indices. Where traits are known or at

least thought to be adversely correlated, this genetic information and expertise is vital because both the base and ELSTON indices can clearly lead to unacceptable responses from selection. The ability of the SMITH-HAZEL index to take account of phenotypic and genetic correlations, and to be applied with restrictions which limit changes in traits (as a protection against effects of uncertain or non-linear economic weight functions), make it a powerful tool for assuring satisfactory genetic gain when traits are adversely associated.

Acknowledgements

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Male Sterility in Alnus glutinosa (L.) Gaertn.

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Summary

The discovery of "non-structural" male sterile plants in Alnus glutinosa is reported. Plants bearing mutant male sterile flowers, possessing no apparent morphological differences to normal flowers, produce inviable pollen grains. Pollen viability was determined by germination tests in a medium which permitted 60—80% germination of control pollen if the pollen grains had been previously hydrated.

Key words: Tree, pollen, sterility, method.

Zusammenfassung

Es wird über die Auffindung „nicht-strukturell" männlich-steriler Bäume bei Alnus glutinosa berichtet. Männlich-sterile Bäume unterscheiden sich in ihren Blüten morphologisch nicht von normalen Bäumen, erzeugen aber nicht-viablen Pollen. Das in Keimprüfungen zur Untersuchung der Pollenviabilität verwendete Medium erlaubte die Keimung von 60—80% von Kontrollpollen, wenn die Pollenkörner zuvor Wasser aufgenommen hatten.

1. Introduction

The species of the genus Alnus, as well as all Betulaceae, are commonly classified as monoecious. In some families there are species which were classified on morphological grounds as monoecious or hermaphrodites, until careful pollination studies revealed that their sexual systems possess other components. Forest trees of great economic importance in the genera Cedrela, Swietenia, Toona, Entan-drophragma and Trichilia of the family Meliaceae are illustrative examples (STYLES 1972).

During artificial pollination work carried out with other objectives (LINARES BENSIMON 1984), in March, 1982, the author found three individuals of Alnus glutinosa whose male flowers, although normal in appearance, yielded no pollen.

Later observations of anthers of these three trees revealed that even though most anthers dehisced, in all cases the pollen remained adhered to the internal wall of the anthers, forming conglomerates. Apparently these trees were male sterile and in March 1984, experimental tests of pollen viability were carried out. The results are the object of this paper.

2. Material and Methods

The three individuals of Alnus glutinosa chosen for this study are located in two plots of the progeny test conducted by the Forest Experimental Station in the state of Hessen (Fed. Rep. of Germany), Compartment Nr 216b of the forest office of Gahrenberg.

These trees were planted in 1969 (WEISGERBER 1974) and, according to the records of this Station, the material originated by crossing the clones R10 and R4 growing in a seed orchard. For this study, the trees are labeled 209-4, 209-7 and 161-4 (plot number-location in the plot). Other trees known to produce abundant pollen were used as controls. A stereomicroscope and a photomicroscope were used to