Table 3. — Estimates of genetic variables as determined from measurement of length, width and thickness of seeds from 23 species/varieties of *Acacia*.

Parameters		Estimate for character		
		Length (mm)	Width (mm)	Thickness (mm)
General mean	$\bar{x}$	8.30	6.93	2.63
Species variance	(σ^2_L)	3.3337	3.6760	0.7138
Error variance	(σ^2_E)	0.4867	0.3417	0.0816
Species coefficient of variation (%)	$\frac{\sqrt{\sigma^2_L}) \times 100}{\bar{x}}$	22.0	27.7	32.1
Error coefficient of variation (%)	$\frac{\sqrt{\sigma^2_E}) \times 100}{\bar{x}}$	8.4	8.4	10.9
%-contributions	$\frac{(\sigma^2_L)}{\sigma^2_P} \times 100$	86.9	90.9	89.7

variance $= \sigma^2_P = \sigma^2_L + \sigma^2_E$

from 8.342 mm to 12.112 mm ($\bar{x}$ = 6.931 mm). The expected 'genetic' value ($\bar{x}$ plus expected 'genetic' advance) from the best 5% of the phenotypes for the respective characters would be expected to exceed the general mean.

It may be concluded that seed characters like length, width and thickness, observed as independent characters and character association patterns change between pairs of traits. Significant variation existed for each trait. Each character showed higher species coefficient of variation, higher %-contributions and lower error coefficient of variation. The strong positive correlation between length and width indicated that improvement in one character may improve the other.

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Optimizing Breeding Zones: Genetic Flexibility or Maximum Value?

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Summary

When the performance of genotypes vary across an environmental gradient in a non-linear manner the matching of genotypes and sites is a complex problem. To overcome this breeding zones are usually allocated so that sets of genotypes are used across different parts of the range to maximise production across all anticipated planting sites. Two different approaches to determining the number and constitution of these populations and the demarcation of their planting zone boundaries are contrasted. Both approaches use non-linear models to define the relationship between relative performance of a genotype and an environmental gradient. The approaches differ however, in the criterion used for choosing the populations. One approach will lead to a guaranteed minimum yield at each site whilst the other approach maximises the expected yield over the total range of planting sites.

Key words: Genotype x environment interaction, breeding zones, non-linear modelling.

For tree species that are planted over a wide range of sites, the relative performance of genotypes may vary depending on environmental factors that vary with site location. In such cases, breeding values must be measured over a range of sites instead of only in some "average" site. In fact, the definition of an "average" assumes that a frequency distribution of anticipated planting sites exists and planting on "average" sites assumes that the distribution mean can be estimated. Consequently, to maximize the breeding value of a set of genotypes, breeding populations, or provenances, their integrated performance over sites must be evaluated for a range of sites.

In the simplest case, site variations may cause no change in the relative performance of genotypes in all important traits and the same trees would be selected for breeding

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**) USDA Forest Service, Southeastern Forest Experiment Station, Genetics Department, Box 7614, North Carolina State University Raleigh, NC 27695-7614, USA regardless of the site distribution [e.g., Juvenile height growth in coastal Douglas-fir in British Columbia, (Yeh and Heaman, 1987)]. If true for all traits of importance, then selection is simple and no subdivision of sites by breeding populations is necessary. However, in many cases, genotype and provenance rankings may change, at least in some traits, as a result of site differences. If these are linear changes in performance along an environmental gradient, then the breeder must switch among populations to maximize gain and for this, simple rules can be derived (Rehfeldt, 1984). Unfortunately, there is no inherent reason to believe in the generality of either uniform or linear performances (Gregorius and Namkoong, 1987) and the nonlinearity of any one trait that is a component of total breeding value would imply a nonlinear "interaction" of total genotypic value over sites (Namkoong, 1985). The problem then is how to select sets of genotypes or populations to maximize breeding value over the range of anticipated planting sites.

One solution to the optimization problem is to select populations that not only perform well on the average, but also are relatively stable in that good performance (Finlay and Wilkinson, 1963; Perkins and Jinks, 1968; Freeman and Perkins, 1971). If there are uniformly superior entries, then merely selecting the best population is, obviously, a simple and optimal solution. Otherwise, however, the analysis of such stability parameters offers little guide to how much advantage might be gained by splitting the sites into two or more groups and selecting for performance within site groups, nor can such analyses indicate which set of populations to use on which subdivision of sites.

A second approach is taken to determine rules for seed transfer that assumes a strong correlation between performance and distance of the planting site from the seed source. If such relationships exist for total breeding value with some composite measure of geographic and topographic distance, rules for limiting the source populations that should be used in a given planting can be derived. The breeding objective in this case is to maximize value at the planting site and the goal is to maximize performance on all sites. Such rules, however, cannot be readily used to derive an optimum pairing of a small set of populations to a subdivision of planting sites since each of many planting sites could require a different population.

A third approach, taken in the two accompanying papers, uses particular forms of nonlinear site responses along an environmental gradient to determine the optimum range of sites for given sets of populations and conversely, to determine the optimum set of populations for a given range of sites. In both papers, it is assumed that provenance and progeny tests can be used to estimate the response of populations to a range of sites. It is assumed that the population's response function or "norm of reaction" can be estimated as a function of a site variable and that it is transformable to a function with a single peak performance at some planting site that may not be the site of origin (e.g. Namkoong, 1969). Conversely, at any planting site, the best population may not be the local source as is often assumed (e.g., Rehfeldt, 1984).

In both the Raymond and Lindgren (R-L) analysis and in the Roberds and Namkoong (R-N) analyses, a single mode curve is assumed to adequately describe the response function; R-L using the Cauchy, and R-N using the Gaussian forms. With such functions, a switch is made at the site where the response function of one population drops below that for the alternate population, and the set of populations is chosen that optimizes a concept of yield. However, the perspectives taken by the two papers are not identical and, hence, neither are the prescriptions for optimal selections. Raymond and Lindgren are interested in examining the response functions of each population relative to alternate populations with the objective of identifying populations with good performance over some set of sites. From these analyses, rules for defining zones for using populations can be derived. The decision as to where to change from one population to another is based on a predetermined level of acceptable performance (e.g. 95% of the maximum possible yield). Zones are set by starting at an arbitrary planting site, choosing the maximum yielding population and using that population over the range of sites along the site variable where its yield is at least 95% of the maximum yielding population in those sites. At the boundaries along the site variable where its relative yield falls below the minimum, the breeder chooses another population which has at least 95% of the maximum at the switch site and has at least that minimum relative yield over as broad a range of other sites as possible. For populations that have symmetrical performance response functions as described in R-L, the chosen population would have a maximum yield at the middle of its response function. This would be used over a range of sites of similar magnitude as the first, but shifted from the first population chosen. There is, therefore, a minimum relative performance for all sites, and a rule for determining an optimum zonation for source populations. An alternative would be to estimate the average performance of a population across zones of differing sizes by integrating the function between defined limits. An optimal number of zones could then be determined by using an optimization procedure, such as that used by R-N. Questions of optimal zone size in relation to allocation of resources, size of breeding populations and, hence, potential selection intensities could then be addressed (D. Lindgren, personal communication).

In contrast, the objective of R-N is to maximize the expected yield of populations over the total range of planting sites. By optimum choice of populations to maximize total yield, the critical sites at which switches between populations are made is also determined. R-N first assumes that for reasons of economy, a finite number of populations is determined and if that number is two, then the two populations are chosen that in combination can subdivide the sites to yield more than any other combination of two populations. Similarly, for three, four, or any finite number of populations (n), specific choices of different sets of populations would be chosen that subdivide the sites to yield more than any other choice of n populations. In an earlier paper (Roberds and Namkoong, 1989), the R-N theories were described and solutions for response curves with the same maximum yield were derived. In the accompanying paper, R-N find solutions with those assumptions relaxed. However, in general, R-N requires that the expected value of yield over the range of sites is maximized and, hence, requires that a frequency distribution of sites is explicitly stated. In R-L, no such distribution is assumed.

While both R-L and R-N provide rules for choosing source populations and their zones of planting, the critical difference between R-L and R-N lies in the criterion of value that they use. For R-N, an expected value is maximized, while for R-L a safe minimum solution is derived. For any particular site, the R-L solution would guarantee a minimum relative yield, while R-N would not necessarily do so. If it is important to ensure minimum yield in every plantation, then R-L uses the better criterion of goodness. For the expected value of a regional breeding program, the R-N solution would be maximum while R-L would not necessarily be so. If average regional maximization is most important, then R-N uses the more appropriate criterion of goodness to maximize. For a predetermined number of source populations, R-N can provide an optimum solution while R-L cannot always guarantee that its minimum yield can be guarenteed. Therefore, the solution for the optimum number of source populations will not in general be the same. For a given number of populations, R-L can determine the minimum site yield that would result which might be less than desired, but they could derive minimum yield as a function of population number to guide policy. In contrast, R-N can determine the expected value of the set of populations for those population numbers, and can prescribe breeding zones as a function of population number. For R-N, the frequency distribution of sites is critical information, and even if the distribution is uniform and has strict limits, the optimization procedure will maximze the expected value. For R-L, the frequency distribution is irrelevant, since optimization is derived on a site-by-site basis.

We therefore believe that the breeder has a choice to make among several approaches to choosing source populations and demarcating their planting site zones. In the accompanying two papers, different views are offered and it is hoped that, by contrasting them, the relative merits of all approaches can be more widely discussed and that sharper debates on breeding philosophy and testing techniques will ensue.

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Genetic Flexibility – A Model for Determining the Range of Suitable Environments for a Seed Source

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Abstract

A mathematical model describing the relative performance of different seed sources over a range of environments has been developed and tested using data from Scots pine in Sweden and white ash in the USA. The components of the model have a direct biological interpretation in terms of the fundamental nature of the problem : i.e. the maximal performance of a seed source, where this maximum will occur and the range of suitable sites for such a seed source. Comparisons can thus be made between seed sources as to their site preferences and the relative flexibility of each seed source calculated. Decisions regarding the optimal deployment of seed may thus be simplified and such information used to refine the allocation of breeding zones.

The model requires that a one-dimensional environmental gradient be defined. Such gradients may relate to a single overriding environmental factor (e.g. winter cold) which can be described by geographical information such as latitude, altitude and distance from the sea. Definition of this gradient is a necessary prerequisite to application of this model. Methods for establishing such gradients are discussed.

Key words: Breeding zones, *Pinus sylvestris*, genotype by environment interaction.

Introduction

Interactions between genotypes and environments are a potential problem in forestry in that they can lead to the choice of a 'less-than-most-productive' seed source for a particular site (Matheson and Raymond, 1986). For species which exhibit clinal variation over a wide range of environments this problem is intensified, especially if variation patterns closely match environmental changes. The presence of genotype by environment (G × E) interactions serve to complicate decisions regarding establishment of breeding populations and design of breeding strategy. Once it has been established that such interactions exist, it is essential to determine whether they are of practical importance for a breeding program. Finding a significant GxE interaction does not necessarily imply that it will have a major impact on future breeding strategy (Matheson and Raymond, 1984, 1986).

If such interactions are found to be real and important, there are two approaches available; either to classify and

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