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Population selection to maximize value in an environmental gradient *

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Summary. A theory for determining optimum planting and breeding zones is described. The theory is based on a model consisting of Gaussian response functions for traits that vary in a gradient for a single environmental variable. Environments are assumed to be normally distributed with known mean and variance. Methods are presented for determining parameters of response functions that maximize the expected value for such a trait when two, three and four populations are selected for breeding or as sources of propagules. Expected value is maximized only when the populations selected have response functions symmetrically arrayed about the mean of the environmental variable. Maximum expected value was shown to increase with increasing number of selected populations at a rate that depends upon the ratio of homostasis to environmental variability. The methods presented are illustrated with data on performance of Scots pine provenances in Sweden.

Key words: Response function – Genotype-environment interaction – Seed transfer zones – Breeding zones – Scots pine

Introduction

Where genotypes are bred for use over a range of environments or economic states, maximizing value by matching genotypes to environments or economic conditions is a significant problem. An implicit assumption in this situation is that the value of a breeding population is not constant over the full environmental or economic range. Among clones, lines, families, or whole populations over the entire range of a species, the existence of a single, uniformly best entity is rare. A suitable approach for breeding programs under these conditions is to identify a target population of environments (TPE) for each breeding population (Comstock 1977). Two fundamental factors heavily influence this breeding problem. First, the combination of optimal levels of all trait expressions is difficult or impossible to breed into a single population. Second, environmental adaptabilities in all traits do not extend sufficiently over environments to produce uniformly homeostatic responses. Breeding populations, therefore, generally have had and will continue to have non-uniform value response functions.

Since forest tree species are almost always bred for a variety of environments or economic conditions, tree breeders must devise a breeding strategy for maximizing the value of propagules under variable conditions. For highly intensive forestry, the goal might be to produce continued yield improvements with individual clones for particular sites representing a restricted TPE. For less intensive forestry, improvements will probably be made on a population basis where propagules from secondary populations or provenances are collectively used. Each such population will be associated with a particular TPE for which it can be used in forestation.

The value of the breeding or selection program depends on how well the resulting populations fit the range of economic effects as well as ecological conditions of the planting sites. Here we confine attention to selection for high yield over the range of an environmental variable (x), and permit x to represent a single variable, such as elevation, or a composite of several site factors. There are then several ways to address the problem of maximizing the value of a breeder's set of populations. One way is to select the best one population for an "average" site or to

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select the population which produces maximum average yield over all sites. This approach would maximize yield if there were a uniformly best population or environmental response form that could be developed by breeding. If, however, as suggested above, a uniformly best type does not exist, then other strategies must be considered.

A second approach is to find a population for each planting site and to shift the source population composition with each shift in planting site. Such is the intent of designating seed transfer zones (Rehfeldt 1979) or of defining best sources for a large array of planting sites (Raymond and Lindgren 1986, 1988). This approach would maximize value if an infinite or very large array of different populations could be found, or if separate breeding populations could be established, one for each planting site. Since these options could never be economically feasible, a smaller number of populations must be chosen as either provenance sources or as breeding populations. The problem, therefore, is to determine how many and which populations to select, and how to draw appropriate zone boundaries.

Measurement of value

The value of a trait over a range of environments depends upon the expression of the trait in each environment as well as on the frequency at which each environment occurs. Where there is a continuous gradient in an environmental factor, the value of the trait can be expressed as a continuous function of the environmental variable. These functions, known as response functions or norms of reaction, are of particular importance in the study of genotype-environment interactions (Knight 1973). The expected value of such a response function (the mean computed by weighting the trait expression for each environment by the frequency at which that environment occurs) is an intuitively appealing measure of trait values.

The Gaussian function is particularly useful for describing trait response of populations to varying environments. For the response of the i^th^ population to a single environmental variable, x, this function is defined as:

$$f_i(x) = [k_i/\sqrt{2\pi\eta_i}]\, e^{-(x-\mu_i)^2/2\eta_i} \qquad (1)$$

where k_i is a parameter that scales yield from zero to one in units of the character of interest, μ_i represents that environment at which response is maximal, and η_i measures uniformity or homeostasis of response over the environmental range. When $k_i = 1$, $f_i(x)$ becomes the normal probability density function. A similar use for the Gaussian function occurs in ecology where it serves as the utilization function in niche theory (Christiansen and Fenchel 1977).

The Gaussian function has a number of properties that make it useful as a response function. Its parameters have a biological interpretation and its properties are well known. It has a single modal maximum and is symmetrical about that modal point. It tends to zero for extreme values of the environment, but is positive for $k_i > 0$. An additional desirable feature is that its parameters can be easily estimated by taking the logarithm of the function and estimating the coefficients of the resulting quadratic function by the method of least squares (Wright 1968).

The other factor required for the expected value of the response function is the probability density of the distribution of planting environments. To determine this function, we assume that sites chosen for growing a species will be infrequent in portions of the environmental gradient where the species is poorly adapted, and that they will be most frequent in that part of the environmental gradient where the species is best adapted. For example, along an elevational gradient, species such as Ponderosa pine (*Pinus ponderosa*) are rarely planted at either the highest or lowest elevations, but are the species of choice in the middle elevations. Thus, it is assumed that the proportion of sites available for growing the species is greatest at a value of x that is near the center of the zone of adaptability of the species, and that this proportion declines as values of x depart from this point. Such a proportion will be close to zero near the limits of adaptability of the species, at values of x for which the performance of another species is generally much better, and for sites that are mostly better suited for alternative land uses. On the basis of these assumptions, we use a normal distribution to represent the distribution of environments. Hence, we consider $x \sim N(\mu_e, \sigma_e^2)$ where μ_e and σ_e^2 are both known. Then, if the probability density function for x is represented by $g(x)$,

$$g(x) = [1/\sigma_e\sqrt{2\pi}]\, e^{-(x-\mu_e)^2/2\sigma_e^2} \qquad (2)$$

where μ_e represents the environmental mean and σ_e^2 the environmental variance.

If population response functions differ, the expected value will be influenced by the choice of populations and their response functions, and by the zones in which these populations are planted. As a result, for a given environmental distribution, it is possible to maximize value by choice of a set of populations with a particular profile of response functions and planting zones.

Maximizing expected value

Costs limit the number of seed sources within a species that are used to produce propagules. Likewise, tree breeding programs are restricted to only a few breeding populations for a species. Therefore, a general objective is to maximize value for a trait by choice of a restricted number of populations and zones where they should be grown. Here we report the results of a theory in which parameters of response functions for a finite set of populations are derived and zones are defined in an environmental gradient for use of these populations. We assume that each of the chosen populations will be used only on that segment of the environmental gradient (x) where its response is greater than or equal to the response of each of the other chosen populations. As a result, response functions are truncated at values of x for which functions for adjacent populations are equal.

For any such subset of populations, value of a trait across the range of the environmental variable x can be expressed as:

$$\mathrm{v}(x)=\begin{cases} \mathrm{f}_1(x) & \text{for} \quad -\infty < x \leq \mathrm{t}_1 \\ \mathrm{f}_2(x) & \text{for} \quad \mathrm{t}_1 \leq x \leq \mathrm{t}_2 \\ \vdots & \\ \mathrm{f}_i(x) & \text{for} \quad \mathrm{t}_{i-1} \leq x \leq \mathrm{t}_i \\ \vdots & \\ \mathrm{f}_n(x) & \text{for} \quad \mathrm{t}_{n-1} \leq x < \infty \end{cases} \tag{3}$$

where n represents the number of populations, the $\mathrm{f}_i(x)$ are the response functions defined by (1), and the t_i are truncation points for the $\mathrm{f}_i(x)$. The expected value of $\mathrm{v}(x)$ then is found to be

$$\mathrm{V}=\sum_{i=1}^{n} \int_{\mathrm{t}_{i-1}}^{\mathrm{t}_i} \mathrm{f}_i(x)\,\mathrm{g}(x)\,\mathrm{d}x \tag{4}$$

where $\mathrm{t}_0=-\infty$, $\mathrm{t}_n=\infty$, and $\mathrm{g}(x)$ is the normal probability density function (p.d.f.) defined in (2).

A necessary condition to maximize V by appropriate choices of the response functions $\mathrm{f}_i(x)$ and the t_i, is that the partial derivatives of V with respect to the t_i and the parameters of the $\mathrm{f}_i(x)$ are all equal to zero. This very general case remains to be developed and solved. For cases where the response functions are similar in size and shape but differ with respect to x values which yield maximum response, however, simplifications are possible that make solutions tractable. For such cases, we can assume that the scale and homeostasis parameters (k_i and η_i) are constant for the collection of populations and are represented by k and η. For convenience, we also adopt the convention that $\mu_i \leq \mu_{i+1}$ for all i, where μ_i is the environment at which response for the i^th^ population is maximum. Because response functions for all populations have the same form and differ only in values for the mode parameter, the interior truncation points are found to be $\mathrm{t}_i=(\mu_i+\mu_{i+1})/2$ for $1<i<n$. Thus V is a function only of the mode parameters, μ_i, for the $\mathrm{f}_i(x)$, since μ_e, σ_e^2, k and η are fixed. Selection of populations and their growing zones to maximize expected value is then reduced to maximizing V with respect to the μ_i. Values of the μ_i that maximize V are obtained by solving the system of equations defined by:

$$\dot{\mathrm{V}}=\begin{bmatrix} \partial \mathrm{V}/\partial\mu_1 \\ \partial \mathrm{V}/\partial\mu_2 \\ \vdots \\ \partial \mathrm{V}/\partial\mu_i \\ \vdots \\ \partial \mathrm{V}/\partial\mu_n \end{bmatrix}=\begin{bmatrix} 0 \\ 0 \\ \\ 0 \\ \\ 0 \end{bmatrix}. \tag{5}$$

The partial derivates in V can be shown to be

$$\partial \mathrm{V}/\partial\mu_i=\int_{\mathrm{t}_{i-1}}^{\mathrm{t}_i} [(x-\mu_i)/\eta]\,\mathrm{f}_i(x)\,\mathrm{g}(x)\,\mathrm{d}x. \tag{6}$$

Setting $\partial\mathrm{V}/\partial\mu_i=0$ for each i and solving for μ_i yields

$$\mu_i^*=\int_{\mathrm{t}_{i-1}}^{\mathrm{t}_i} x\,\mathrm{f}_i(x)\,\mathrm{g}(x)\,\mathrm{d}x \Big/ \int_{\mathrm{t}_{i-1}}^{\mathrm{t}_i} \mathrm{f}_i(x)\,\mathrm{g}(x)\,\mathrm{d}x. \tag{7}$$

These μ_i^* are the mode parameters that maximize value as defined in (4), and populations with response functions having these parameters maximize yield.

Optimum choice of populations

Results for two and three populations were first reported by Roberds and Namkoong (1986). In this paper, we more explicitly discuss those results and compare them with results for four populations. For each of these cases $n=2, 3, 4$, solutions for mode values have been shown to be unique and symmetrically distributed about the environmental mean μ_e. We thus report only those values for which $\mu_i^* \geq \mu_e$. Proofs for these results will follow in a subsequent paper.

Values for the optimum mode parameters are dependent on the number of populations as well as values for η and σ_e^2. The ratio η/σ_e^2 gives a measure of the degree of homeostasis in relation to the level of environmental variability. It is a useful, standardized index and is hereafter called the homeostatic index and denoted by hs.

Two populations

The upper optimum mode value for two populations is given by

$$\mu_2^*=\int_{\mu_e}^{\infty} x\,\mathrm{f}_2(x)\,\mathrm{g}(x) \Big/ \int_{\mu_e}^{\infty} \mathrm{f}_2(x)\,\mathrm{g}(x)\,\mathrm{d}x. \tag{8}$$

For this case, the environmental mean is seen to be the appropriate truncation point defining planting zones for two populations. Upper and lower bounds for these optimum mode parameters are defined by the limits,

$$\lim_{\eta\to\infty}\mu_2=\mu_e+\sigma_e\sqrt{2/\pi} \quad \text{and} \quad \lim_{\eta\to 0}\mu_2=\mu_e. \tag{9}$$

Thus, when two populations are chosen, large mode differences are optimal for species with large hs. There is, however, a limit to how extremely differentiated optimal populations can be. Even if hs is very large and the populations have essentially uniform performance levels over all environments, it is clear from (9) that they cannot depart by more than approximately $0.8\,\sigma_e$ from μ_e. As hs levels approach zero, the optimum choice of populations have mode parameters close to μ_e. Furthermore, at low values of hs, differences between modes of optimum populations and μ_e change greatly with changes in hs (Fig. 1). However, above hs = 3, where the optimum difference from μ_e is approximately $0.76\sigma_e$ units, there is little change in these differences with increasing hs.

Since most species have populations with a breadth of adaptibility, hs is rarely close to zero and some inter-population differentation is expected to be optimal. It is evident, however, that a choice of two populations with maximal performance in opposing extreme environments is not optimal. It is clear from (9) that there are limits within which optimal populations can be chosen.

The expected value for optimum choices of populations is also a function of hs. For a given σ_e^2 and k, the maximum expected value declines with increasing values for hs (Fig. 2). This decline is a result of decreasing maximum performance with increasing hs. For small values of hs, Namkoong (1976) noted that two optimally arrayed populations have substantially greater value than a single optimal population. The extent of the difference is evident from the expected value curves presented in Fig. 2. At hs = 0.1, there is a 67% benefit for using two populations (Roberds and Namkoong 1986), but for hs > 3 the advantage is much reduced. Above hs = 25 the benefit falls below 1% and there is little reason for choosing two populations over one.

Three populations

Optimum mode parameters for the middle and upper populations in sets of three populations are given by the expressions,

$$\mu_2^* = \mu_e \quad \text{and}$$

$$\mu_3^* = \int_{(\mu_2^*+\mu_3^*)/2}^{\infty} x\,\mathrm{f}_3(x)\,\mathrm{g}(x)\,\mathrm{d}x \Bigg/ \int_{(\mu_2^*+\mu_3^*)/2}^{\infty} \mathrm{f}_3(x)\,\mathrm{g}(x)\,\mathrm{d}x\,. \qquad (10)$$

Upper mode parameters for this case are greater than the corresponding parameters for two populations (Fig. 1). The same trends in optimal differentiation exist for three populations as for two populations. For small hs values, μ_3^* is close to $\mu_2^* = \mu_e$, but for large hs, it never exceeds $1.224\ \sigma_e$ units from μ_e. As with two populations, the change in μ_3^* as hs increases is small for hs > 3.

Expected values are greater for three populations than for two (Fig. 2), but the differences are not as large as those found between one and two populations and the benefit is substantial only for hs < 10. For hs = 0.1, the advantage is 26% but drops to less than 1% for hs ≥ 10 (Roberds and Namkoong 1986).

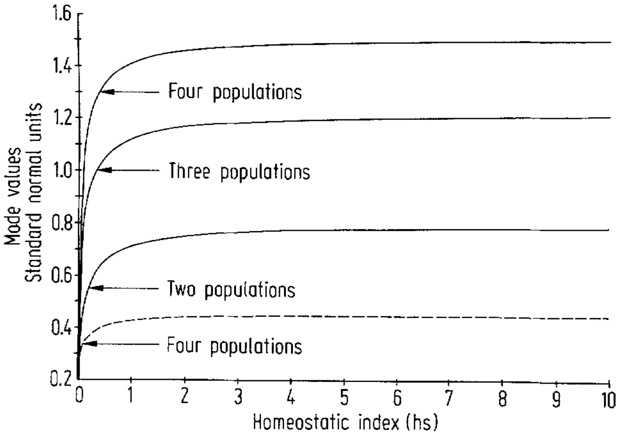

Fig. 1. Optimum values for upper mode parameters for two, three, and four populations. *Solid curves* are for exterior populations. The *dashed curve* represents the upper interior population for the four-population case

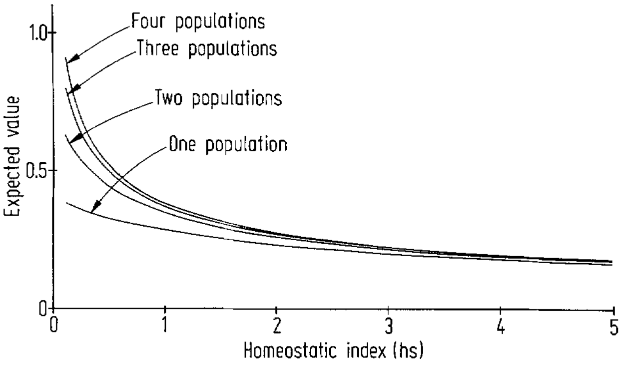

Fig. 2. Maximum expected values for one, two, three and four populations. Expected values are given in k/σ_e units

Four populations

Values for the upper optimum modes for four populations are given by

$$\mu_3^* = \int_{\mu_e}^{(\mu_3^*+\mu_4^*)/2} x\,\mathrm{f}_3(x)\,\mathrm{g}(x)\,\mathrm{d}x \Bigg/ \int_{\mu_e}^{(\mu_3^*+\mu_4^*)/2} \mathrm{f}_3(x)\,\mathrm{g}(x)\,\mathrm{d}x$$

and

$$\mu_4^* = \int_{(\mu_3^*+\mu_4^*)/2}^{\infty} x\,\mathrm{f}_4(x)\,\mathrm{g}(x)\,\mathrm{d}x \Bigg/ \int_{(\mu_3^*+\mu_4^*)/2}^{\infty} \mathrm{f}_4(x)\,\mathrm{g}(x)\,\mathrm{d}x\,. \qquad (11)$$

Values for μ_4^* are greater than values for the upper mode for three populations (Fig. 1) and reach a value of approximately 1.51 σ_e units above μ_e as hs becomes very large. Similar to results for two and three populations, μ_4^* moves close to μ_e as hs becomes small. Values for μ_3^* fall between μ_e and μ_2^* for two populations (Fig. 1) and reach a value of approximately 0.45 σ_e units above μ_e for large hs.

Expected values for four populations are greater than those for three populations (Fig. 2), but the advantage is greater than 1% only when $hs < 3$. Differences are still substantial for small values of hs – the advantage is greater than 14% for $hs \leq 0.1$.

Scots pine populations in Sweden

Data collected from Scots pine (*Pinus sylvestris* L.) populations in Sweden can be used to illustrate application of the optimization theory described. The Cauchy response function was fitted to data from six provenances by Raymond and Lindgren (1988). Total production per hectare for each provenance was measured at five or more locations. Provenance performance in each environment was expressed as a percentage of the performance for the most productive provenance in that environment. The environmental variable consisted of a site-severity-index, which is a measure of relative severity of the environment and is a function of the latitude and altitude. Details about the test locations, severity index, and description of the provenances can be found in Raymond and Lindgren (1986).

The Cauchy function is of the form

$$y = \mathrm{a}/[1 + ((x - \mathrm{b})/\mathrm{c})^2] \tag{12}$$

where y is the response variable, x is the environmental variable, a is a parameter representing maximal performance, b is a parameter reflecting the value of x at which maximal performance occurs, and c is a parameter describing the width of the function (Raymond and Lindgren 1988). From estimates of these parameters, values for the η and k parameters of the Gaussian response function defined in (1) were determined. The latter values were considered common to the response functions for every Scots pine provenance in Sweden. Parameters μ_i and k are related to parameters a and b of the Cauchy function as follows: $\mu_i = \mathrm{b}$, $\mathrm{k} = \mathrm{a}\sqrt{2\pi\eta}$. The relationship $\eta = 0.75\ \mathrm{c}^2$ was found to hold approximately for the data from the six provenances. Estimates of c were averaged over the six provenances to provide a basis for determining η. The average value for c is 5.35 giving a value of 21.47 for the η parameter. Two of the underlying assumptions for our optimization theory are: (1) there is at least one population with maximum response for each value of the environmental variable; and (2) the level of maximum response is the same for all populations. Given these two assumptions and use of the percent of maximum performance at an environment as the scale for the response variable, the a parameter was set equal to 100. The resulting value for k was then found to be 1161.38.

Little information was available about the distribution of planting environments for Scots pine in Sweden. In fact, there may be a uniform distribution of planting sites due to the Swedish National Forestry policy for forest regeneration. Even then, we suspect that there may actually be a de facto frequency distribution. For purposes of this paper, we therefore had to rely on intuitive judgement to set appropriate values for the distribution parameters. A value of 3.0 appears to be reasonable for the mean site index value for Scots pine planting sites in Sweden (C.A. Raymond, personal communication). Since there was little information for selecting a reasonable value for the variance parameter, we chose to use two values in our analysis. A value of $\sigma_e^2 = 16.66$ represents the appropriate parameter value if 95% of the planting sites have severity index values ranging between -5.0 and 11.0 when planting sites are assumed to be normally distributed about $\mu_e = 3.0$. Similarly, $\sigma_e^2 = 23.65$ if 90% of the planting sites are found within that same range of severity indices. Homeostatic index values are $hs = 1.29$ for $\sigma_e^2 = 16.66$ and $hs = 0.91$ for $\sigma_e^2 = 23.65$.

Optimal choices of provenances and planting zones determined on the basis of these assumptions and estimates are given in Table 1 for choices of two, three, and four provenances as sources of seed. As an example, if hs can be assumed to be 0.91 and optimal planting zones and choice of provenances are desired for four sources of seed, the appropriate choices are: (1) the provenance that produces maximal performance at about severity index -3.84 as a source of seed for sites with index values below -1.45; (2) the provenance with maximal response at approximately 0.93 for sites with values between -1.45 and 3.1; (3) the provenance with maximal response around 5.07 for sites with indices between 3.0 and 7.46; and (4) the provenance with maximal response at approximately 9.84 for sites with index values above 7.45. These choices are illustrated in Fig. 3.

A measure of the efficiency in value production can be obtained for these optimal seed source choices by comparing their expected values to the potential maximum value that could be achieved if every environment was planted with seed from the provenance that produces maximal value in that environment. The latter is impossible in forestry practice because costs limit the number of seed sources. For the yield variable in the Scots pine example in Sweden, the potential maximum value is 100. Comparison of expected values resulting from optimal zonation with this potential maximum value (Table 1) reveals that if a 6% reduction in value from the potential maximum is acceptable, four provenances give adequate performance. If a 10% reduction in value is acceptable, three seed sources are adequate. Use of only two seed sources would result in a yield loss of more than 10%, which would probably be considered excessive.

Discussion

The optimization theory described provides a method for determining a finite number of optimal seed zones and seed sources both for the transfer of seed and for breeding. A value function is used which reflects differential population performance over a range of environments. It is based upon trait response to a single environmental gradient, regardless of whether the gradient is for a single environmental variable, such as latitude, altitude, temperature, soil moisture or nutrient level, or for an index of two or more environmental components, such as the severity index developed to classify Scots pine sites in northern Sweden (Eriksson et al. 1980). That environmental variable is used to delineate planting zones. Response over the range of environments is characterized in terms of nonlinear growth functions (Gaussian), and zones are derived such that in its zone each selected population performs better than the other populations in the selected set.

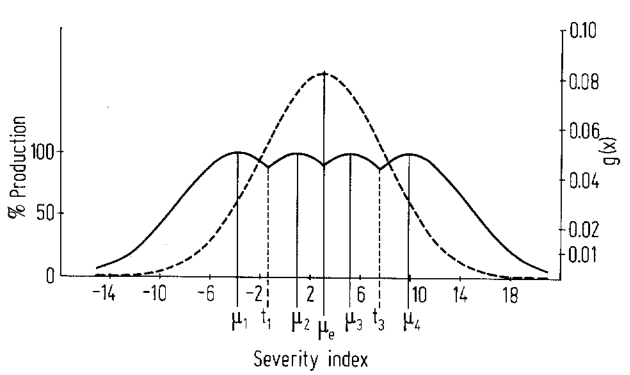

Fig. 3. Illustration of optimal choices for four Scots pine provenances and their planting zones in Sweden. *Solid curves* represent provenance response functions ($f_i(x)$) and the *dashed curve* represents the probability density function ($g(x)$) for environments with $\mu_e = 3.0$ and $\sigma_e^2 = 23.65$

The theory does not require that local sources be optimal. A unique feature of the theory is that it includes the distribution of environments as a factor in the assessment of value. Environments that are infrequent are given little weight and those that are common receive the greatest weight in determining value. In this respect, the method for choosing seed zones and sources of seed resulting from the theory differs from all other techniques that have been suggested. While results of our theory are specific to Gaussian functions, the methods described for selecting populations and their planting zones are expected to be widely applicable.

A number of methods have been suggested for establishing seed transfer or breeding zones, but the optimality of most of them is open to question. Among the proposed methods, the contour plot technique of Clausen (1984) is useful for selecting seed sources at specific test sites and predicting their performance at those locations. Its use,

Table 1. Optimum Scots pine populations for two environmental distributions. Distribution A has $\mu_e = 3.0$ and hs = 1.29 and distribution B has $\mu_e = 3.0$ and hs = 0.91

Popul. no.	Environmental Distribution					
	A			B		
	Popul. mode	Planting zone	Expected value	Popul. mode	Planting zone	Expected value
Two populations						
1	0.02	≤3.00		−0.45	≤3.00	
2	5.98	>3.00		6.45	>3.00	
			88.74			85.17
Three populations						
1	−1.68	≤0.66		−2.45	≤0.27	
2	3.0	0.67−5.34		3.00	0.27−5.73	
3	7.68	>5.34		8.45	>5.73	
			93.59			91.33
Four populations						
1	−2.85	≤−0.81		−3.84	<−1.45	
2	1.23	−0.80−3.0		0.93	−1.44−3.0	
3	4.77	3.01−6.81		5.07	3.01−7.45	
4	8.85	>6.81		9.84	>7.45	
			95.85			94.30

however, has been confined to evaluating performance at each test location separately. Performance across environments is not measured and the distribution of environments is not considered. Rehfeldt (1979) uses multiple regression techniques and mean differences associated with least significant differences (lsd) at a fixed level of probability to specify seed transfer zones. An assumption for this method is that local sources are optimal. Application of this technique, therefore, is questionable where local races are not optimal – a situation which is known to exist for some species in some environments (Namkoong 1969). Again, the distribution of environments is not considered in defining zones. Raymond and Lindgren (1986, 1988) use reponse functions to determine zones of acceptable performance for individual provenances. Their method is based on nonlinear response functions (Cauchy) and is not restricted to cases where local sources are optimal. These zones of acceptable response, however, are set irrespective of performance of other provenances and without consideration of the distribution of environments, but may reflect a closer approximation to Swedish forestry policy than to assume a normal distribution.

The theory presented here and the results derived are directly applicable to breeding. At the beginning of breeding programs, base populations for breeding and breeding zones can be chosen by the methods described. During subsequent breeding, breeders may wish to focus on the parameters of the response functions, singly or simultaneously, as targets for change through breeding. As breeding changes the response functions, breeding zones may need to be redrawn to maximize value. If the primary focus of breeding is to increase yield by selecting for a large k value alone, breeding zones will not be appreciably affected and will not need to be changed as progress is made. If the shape of the response function is a target for change, breeding zones must be reassessed as progress is made and appropriate changes in zone boundaries made if progress from selection is to be maximized.

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