



A model integrating seed source adaptation and seed use

D. LINDGREN¹ and C.C. YING²

¹*Department of Forest Genetics and Plant Physiology, Swedish University of Agricultural Sciences, SE 901 83 UMEÅ, Sweden;* ²*Research Branch, B.C. Ministry of Forests, Victoria, British Columbia, V8W 9C2, Canada*

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Abstract. A conceptual model that considers the performance (adaptability) of a seed source (=an origin) and the location or range of its deployment is developed employing the Cauchy function. The model assumes that there exists an optimal site type for each provenance origin (genetic material), and that loss in performance is a function of the “distance” (a measure of increasing maladaptation) from the optimal site. The model requires the estimate of three parameters: a site requirement value that measures site type in one dimension; a measure of optimal performance; and a flexibility measure of the width of seed source adaptability. The Cauchy function has a known integral, thus the average adaptability over a range (a possible seed use zone) can be mathematically evaluated. The model was also extended to seed orchard crops representing progeny of parents of variable origins. Scots pine information in Sweden was used to demonstrate possible applications of the model.

1. Introduction

Efficient deployment of superior provenance seeds from natural stands or genetically improved seeds from seed orchards is an important silvicultural decision. A commercial seed source – from a natural stand or seed orchard – has a range of environments within which it is possible to realise a high and reliable yield, but beyond that its use will result in lower expected yield due to maladaptation. To aid this decision, seed zone and seed transfer guidelines have been developed in all major forest regions. Delineation of zones is often made according to geographic features and administrative convenience, but is being gradually improved by incorporating ecological information and provenance testing results (Lester et al. 1990). This approach represents largely a qualitative, not a quantitative process.

A quantitative approach using regression coefficients to scale latitudinal transfer was first suggested by Morgenstern and Loche (1969). Camp-

bell (1974, 1983, 1991) and Rehfeldt (1988, 1990) have conceptually and methodologically advanced this quantitative process employing predictive function models to scale seed transfer. A function model is constructed using regression technique. Roberds and Namkoong (1989) and Raymond and Lindgren (1990) have proposed different response models derived from mathematical functions to guide the selection of seed sources. Operational application of Campbell and Rehfeldt's models is pertinent to natural seed sources because of the underlying assumption of local adaptation in their models. The essence of their approach lies in minimising biological risk (maladaptation). The basis of Roberds/Namkoong's and Raymond/Lindgren's response functions, on the other hand, aims at maximising high yield. These approaches, conceptually at least, treat seed source as a separate entity from seed zone.

Here we develop and evaluate a model, which allows the quantitative evaluation of the loss in deployment of genetic materials in relation to the range of adaptability in the material and the range over which it is deployed. We believe a model of this nature is a useful tool in aiding decision making on deployment of genetic materials.

2. Theoretical framework

We assume a seed source achieves its optimal performance at one site type (not necessarily the site type where it is growing), at other site types its use will result in loss of productivity due to maladaptation. Loss increases with increasing ecological difference of the site from the optimum for the seed source. The site type can be quantified by a single value. A seed source can be quantified by the site type value where its performance is optimal. Conceptually then, the forest is a range of sites, which can be characterised by a continuum of values. Expressed in different way, performance of a seed source, compared to that of the optimal one for a site, decreases with the increasing difference from the optimal site type value. Therefore, performance (adaptability) of a seed source is conceptually integrated with where it is used. To facilitate the practical applications of the model, it is necessary to evaluate a seed source over an interval rather than at a point as detailed and exemplified later. In practice, breeders and foresters are willing to accept some loss in order to achieve a cost-effective operation by opting for a zone of reasonable size. In this sense, the model we propose is a process of optimisation under constraints (Maynard Smith 1978). This model concept seems to fit the planning mode of common practice in operational tree improvement.

Attempting to facilitate the presentation, we chose to develop the model concept first relating to a natural seed source corresponding to provenance,

whose adaptability can be traced to its origin, which serves as a reference population for composite seed sources. The model application is extended to composite seed orchard seed and clonal material. Functional characteristics of the model are described below.

Model description

The basic functional model is to express the performance of a seed source as a function of site type value (a response curve):

$$Y(X) = \frac{A}{1 + \left[\frac{X-B}{C}\right]^2} \quad (1)$$

Graphic illustration of the model is given in Figure 1. Elements of the model are defined as follows.

X = Site type value, any quantitative variable which is used to characterise the environment of planting sites in one dimension, e.g. latitude, elevation, site severity index or heat sum, etc. Site type value does not need to be physically contiguous and it can be a derivation combining many elements (an index). But the model demands that the site type is classified by a single index (factors not covered by that index will appear as statistical noise). Site requirement value is a way to attach a value to site type. Latitude (adjusted to constant elevation) is used as a measure of site type value for Scots pine in Sweden in this study, but for other situations there are certainly more relevant site criteria (e.g. elevation).

Y = Performance of a seed source (at X). Yield is commonly used as an indicator of performance in practical application. Any performance trait can be considered as long as the trait response function over the environmental gradient fits the basic biological and mathematical features of the model.

A seed source can be characterised by three parameters, A , B , and C , as defined below. Performance of a seed source over sites can be predicted based on the estimates of these three parameters. A seed source can be e.g. a provenance, a seedlot from seed orchard or a vegetative propagule. Algebraic derivation for estimates of these parameters for a composite seed source (a seed orchard recruited over a range of provenances) will be described later.

A = Optimum performance of a particular seed source which is the height (Y) at vertex of the response curve in Figure 1. Different seed sources can have optimal performance on the same site (B) and still be different in performance, e.g. because it is improved materials.

B = The site requirement value of a particular seed source. That is the site type value at which a particular seed source attains its optimal performance (optimally adapted); the site type value at which performance of the optimal

seed source equals A . We assume an optimum seed source exists for each site type value. Note that the B -value for a seed source is where it is optimally adapted, not where it comes from. Thus “origins” are characterised by the value on the X -axis, where they are the optimally adapted.

C = Flexibility of a particular seed source can be defined as the distance between the X values measured symmetrically around B , where expected performance of the seed source is $Y = 0.8A$ (Figure 1). The performance of that seed source is more than half the maximum performance ($>0.5 A$) for sites (X -values) between $B - C$ and $B + C$. These characteristics reflect the nature of the chosen mathematical function. The flexibility is useful when extending the use of a seed source from a point to an interval. The range of sites where a seed source has an acceptable performance is proportional to C ; in other words, the C -measure provides the biological determinant scaling the width of a zone as well as a measure of adaptability of a seed source. Therefore, the width of a zone and the performance of a seed source are conceptually integrated.

Note that the parameters A , B and C describing the system does not just reflect biology, but also reflect the choice of performance criteria (it can be an economical value). A , B and C define the profile of population performance across environmental gradient, similar to the concept of norm of reaction (Gomulkiewicz and Kirkpatrick 1992).

Mathematically, this function is known as the Cauchy function. Response of seed sources is assumed to be symmetrical over the environmental gradient of planting sites, and variation among planting sites can be expressed in one dimension. Raymond and Lindgren (1986, 1990) used this model, and this study is an extension of that work.

The model can further be simplified to augment the basic characteristic of the function by scaling the Y - and X -axis in standardised units:

$$y(x) = \frac{1}{1 + x^2} \quad (2)$$

where $x = (X - B)/C$ and $y = Y/A$.

This is a standardisation of the Cauchy distribution; seed source performance y is scaled to its optimum, and x to the distance from the site where the seed source is optimal, expressed with C as the units. Therefore, y becomes a relative measure and is always ≤ 1 . Figure 1 can be viewed as an illustration of this simplification. This simplified form facilitates generalisation and comparison in applications.

To apply the model as a decision-making aid in the optimisation process, we need both point (single site) and average (across sites) estimates of seed source performance.

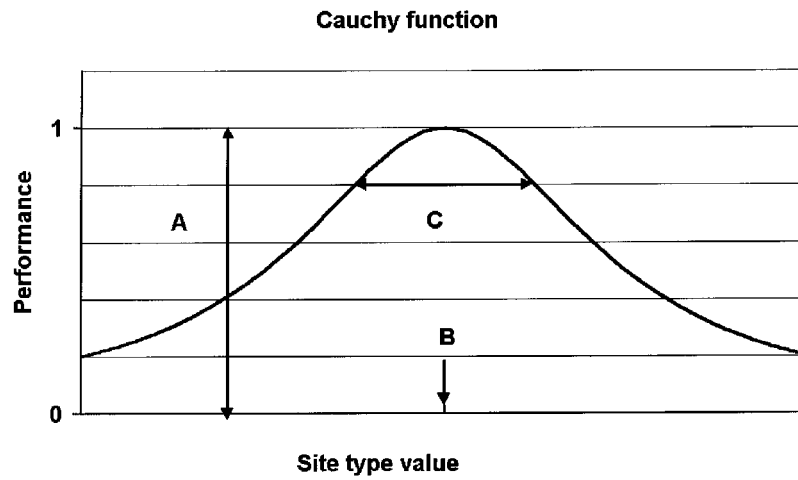


Figure 1. Graphic description of the model derived from the Cauchy function (Expression 1). The performance of a seed source across site type values is described by three parameters, which characterise the seed source: A = optimum performance of a seed source at site requirement value B ; C = flexibility of a seed source, equivalent to extent of the zone within which the seed source achieves above 80% of its optimum performance. See text for details.

Loss of performance at a single site

When a seed source is planted at marginal sites (sites distant from the optimum for the seed source), its performance will be inferior to an optimal seed source. Expression (3) (easily derived from Expression 2) can be used to calculate the loss in performance:

$$L_1(x) = 1 - y(x) = \frac{x^2}{1 + x^2} \quad (3)$$

The magnitude of loss depends on the distance from where the seed source is optimal as illustrated in Figure 1. Relative loss of using a non-optimal source in relation to distance from the optimal is presented in Figure 2, and numerically illustrated by using the Swedish Scots pine data in Table 1 (column 2). As expected, loss increases with distance from the optimum.

Average loss of performance over a seed zone

Expression (3) gives performance of a seed source at a single site type. If a seed source is used over a range of site types (within a zone encompassing a range of site types), its average performance can be approximated by the

integral of Expression (2), assuming all site type values are equally common. The general form of the integral is:

$$\int \frac{dx}{1+x^2} = \arctan x \quad (4)$$

Considering a zone with boundaries defined by z in units of C from the zone centre, B , average performance of a seed source can be approximated by integrating Expression (1) resulting in Expression (5). Expression (5) gives the average performance ($\bar{Y}$) over a seed zone extending from $B - Cz$ to $B + Cz$, where the zone is symmetric around the site type value B , where the seed source has its optimal performance (Figure 1).

$$\bar{Y}(z) = \frac{A}{2Cz} \int_{B-Cz}^{B+Cz} \frac{dX}{1 + \left(\frac{X-B}{C}\right)^2} = \frac{A \arctan z}{z} \quad (5)$$

From Expression (5), the average loss (L_2) by planting the same seed source over a range of site types instead of at a single site type where it is optimally adapted:

$$L_2(z) = 1 - \frac{\arctan z}{z} \quad (6)$$

Conceptually, it is the loss in relation to zone size – increasing loss with increasing zone size. Zone size is measured by z , the distance from where the seed source has its optimum to the fringe of the zone. This loss is expressed as a fraction of the average if an optimal seed source is used at individual site types, as graphically illustrated in Figure 2 and numerically illustrated in Table 1 (column 3) by the Swedish Scots pine example described below. The reasoning above is easily extended to asymmetric zones by regarding such a zone as two separate zones, one above and one below B .

Comparison with other functions

Other mathematical functions with similar function shape to the Cauchy can be used in describing performance of a seed source across sites. Figure 3 presents such a comparison of four different mathematical distributions: Cauchy, Normal, Beta and Parabola. The fittings near the optimum are indistinguishably similar among the four functions (provided the parameters controlling them are properly chosen), but their differences become increasingly evident where performance is low (Figure 3). In terms of practical applications, all four functions can work equally well in the central region where the optimal seed source is most commonly used, whereas performance estimates of using a seed source beyond the optimal region vary among

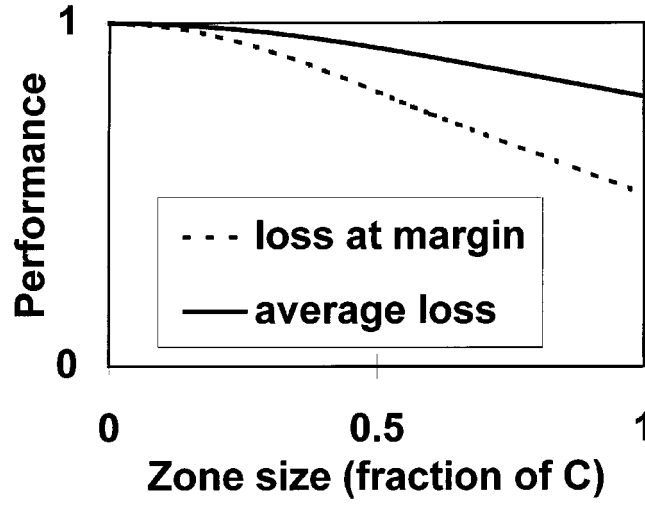


Figure 2. Loss prediction in relation to zone size (measured as distance to centre of zone in units of the flexibility parameter C). The loss of performance at a single site type in relation to increasing distance from the optimum (zone centre) is shown by a dashed line; and the average loss in relation to increasing seed zone size is shown by a solid line.

functions. We argue that the Cauchy is preferable because its parameters are easy to interpret biologically and is more reasonable at some distance from the optimum; the normal has no integral; the beta is more complex with more degrees of freedom; and the parabola is biologically unreasonable (performance can be negative).

At the optimum, the Cauchy becomes identical to a suitably scaled parabola, and in an interval close to the optimum, the Cauchy can be well approximated by a parabola. This can be realised by considering

$$\frac{1}{1+x^2} \rightarrow 1-x^2 \text{ when } x \rightarrow 0$$

The parabola is easy to handle mathematically. Parabola approximation can be used in estimating the average loss over the interval close to the optimum ($z < 0.2$) (Table 1), as shown in Expression (7), a simplified form of Expression (6):

$$L_2(x) = \frac{z^2}{3} \quad (7)$$

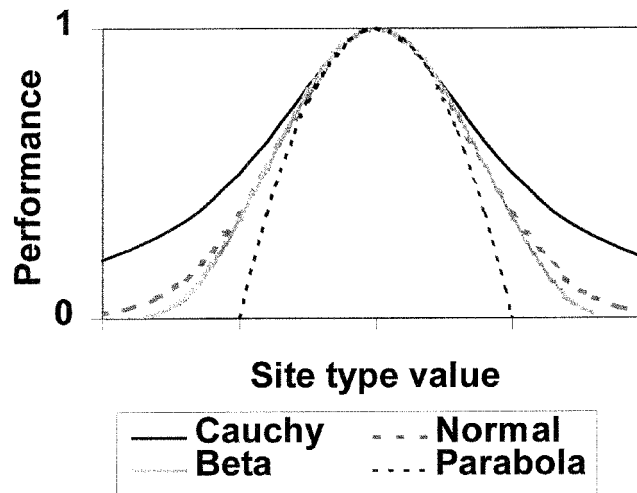


Figure 3. Comparison among four mathematical functions; the difference is negligible if only the range close to the optimal site requirement value is considered, but becomes important if the comparison is extended over a wide range. The parabola shown is identical to the Cauchy at optimum.

Model application to a composite seed orchard

If all plus trees were from the same provenance, we could regard a seed orchard crop as corresponding to a provenance with the same B and C , but a higher A . But seed orchards are often composed of selections extending across a large area rather than a single origin. We cannot evaluate that mathematically for the Cauchy, but we have been able to evaluate for the parabola, thus the formula obtained is reliable only rather close to the optimum and when plus tree origins have a limited range. The expected performance of the cross between plus trees from two provenances optimally adapted at B_1 and B_2 (site requirement values) can be calculated by the parabola approximation as reasoned above, and expressed as

$$Y(X)/A = 1 - (0.5(B_1 + B_2) - X)^2/C^2 \quad (8)$$

Extending the concept, we can estimate the average performance over all combinations of crosses in a seed orchard by integration using Expression 8. The B -value of a seed orchard is the pooled average of B -values representing the possible provenance hybrids in the seed orchard. Assume that provenances with optimal adaptation to site types between $B - Cv$ and $B + Cv$ are equally represented; that the seed orchard is random mating, and that the progeny of a provenance cross behave as a seed source with optimal adaptability (B -value, site requirement value) intermediary to the parents. The

sum over all possible crosses is formed as a double integral, one for the summation of the males and one for that over the females. The average is $\bar{Y}$ and is derived from integration of the following equation:

$$\bar{Y}(X) = \frac{A}{[2Cv]^2} \int_{B_2=B-Cv}^{B+Cv} \int_{B_1=B-Cv}^{B+Cv} 1 - \left(\frac{0.5(B_1 + B_2) - X}{C} \right)^2 dB_1 dB_2$$

Evaluation of this integral and algebraic simplifications lead to Expression 9,

$$\bar{Y}(X) = A \left[1 - \frac{v^2}{6} - \frac{(X - B)^2}{C^2} \right] \quad (9)$$

Note that this expression is similar to (8), but a term for the variation of origins in the seed orchard is added.

The equation derived above gives the performance on individual site types, but we are interested in averages over a seed source zone. Assume the seed zone has centre in B and extends between $B - Cz$ and $B + Cz$ with all site requirement values equally common. The average over the zone of size $2Cz$ is $\bar{\bar{Y}}$.

$$\bar{\bar{Y}} = \frac{A}{2Cz} \int_{B-Cz}^{B+Cz} 1 - \frac{v^2}{6} - \frac{(X - B)^2}{C^2} dX = A \left(1 - \frac{z^2}{3} - \frac{v^2}{6} \right) \quad (10)$$

A loss function can be formulated (in a similar manner as for seed source from a single provenance) as follows:

$$L_3(v, z) = \frac{z^2}{3} + \frac{v^2}{6} \quad (11)$$

This function is illustrated in Figure 4 with Swedish Scots pine data as described below.

3. Possible applications illustrated by Scots pine in Sweden

What is needed to apply the model are measures of performance across sites for seed sources. Flexibility (C) can be estimated based on these measures. The same Scots pine data evaluation as that presented by Raymond and Lindgren (1990) from a large provenance testing in Sweden (over a period of 25 years) are used here to demonstrate the application of our model. Performance was estimated as the product of height*survival instead of height itself, which works better as predictor of mature production (Marklund 1981). Raymond and Lindgren (1990) used “equivalent latitude” (denoted as latitude*) as site type value. Latitude* re-scales the combination of latitude

and altitude of planting site into a one-dimensional scale as: $\text{Latitude}^* = \text{Latitude} + (\text{Elevation} - 300 \text{ m})/300 \text{ m}$. This re-scale takes into consideration the fact that latitude is the most important factor for site classification in Sweden, and that 300 m is the typical elevation of forest land in northern Sweden (and so was chosen as the benchmark elevation). C -values of Scots pine in Sweden based on provenance testing results ranged between 4 and 6 latitude* for different provenances; we used 5 in our numerical examples (Table 1). This means that if a provenance is used on a site five latitudes* from its optimum (from the site requirement value of the provenance) its production is expected to be half that of a provenance optimally adapted to that site. If a symmetric zone five latitudes* wide is applied, the performance will be at least 80% (Table 1, column 1) and on an average 92.7% (Table 1, column 3) of that if fully adapted provenances were matched with each site type (see definition of C parameter).

Needless to say, the above posit (assumption) is somewhat simplified and generalised when applied to the following examples, even for Scots pine in Sweden where there are other relevant factors to consider. This is necessary in order to highlight the model's broad applications.

The flexibility (C) cannot be determined for the harshest provenances because there are none or not many sites where they are "overhardy", and it is likely the function is not symmetric around the optimum latitude* for these provenances. Too far to the north, a provenance may not survive at all while too far to the south it will just grow slow. As long as the considered ranges around optimum are relatively small, this lack of symmetry will not be quantitatively important. In Sweden practical considerations are often done based on an EXCEL spreadsheet (Andersson 1996). The spreadsheet returns the "performance" at a site (characterised by altitude and latitude) as a function of the latitudinal transfer (the altitudinal transfer is considered of low importance). It seems to be a reasonable symmetric response within a latitude from the optimum where the optimum provenance is south of latitude 67 or within 2 latitudes when it is south of latitude 65. As far as the suggested ranges are not larger than that, a symmetric model is likely to give useful results.

Adequacy of a seed transfer guideline

The model provides quantitative evaluation of the effectiveness of a seed transfer guideline in terms of loss of productivity. Using $C = 5$ latitude* to guide seed transfer of Scots pine is within the limit of the current seed transfer guideline in Sweden (Skogstyrelsen 1995). The model estimated the loss of productivity at a maximum of 20% and average 7% (Table 1), although it is certainly much less as the rules are applied in practice. Will it be worthwhile

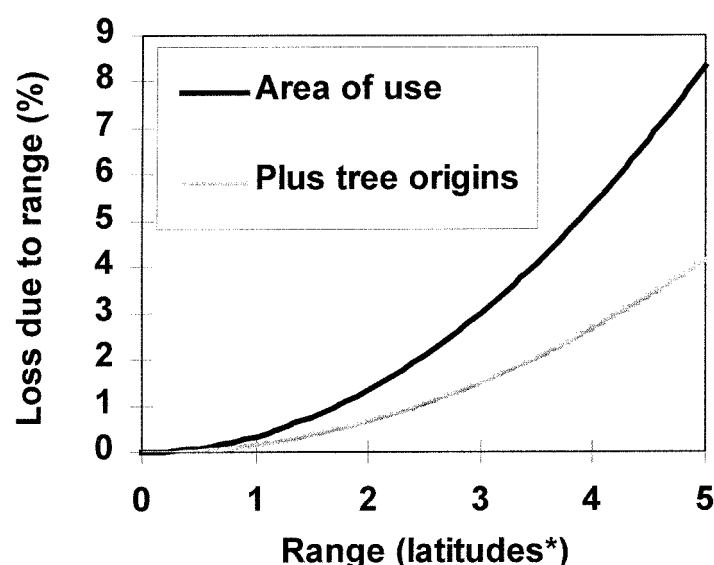


Figure 4. Predicted relative volume production loss for seed orchard seeds of Scots pine in Sweden as a function of the range over which plus trees are recruited from for the orchard (lower gray line) and the range of the area where the seeds are used (upper black line), derived from equation 11. The flexibility has been set to $C = 5$ latitudes*. Note that the z or v units are a factor of 10 smaller than the latitudes*. The ranges used may be in the magnitude 2 latitudes*, which does not give reason for alarm.

to attempt to further curtail the loss by imposing a more stringent guideline? Further improvement can probably be achieved more efficiently through local considerations rather than stringent regulations.

The intention of seed transfer rules, like most forest practice laws, is for its broad applicability, not to prescribe specifics for local operations. A local forest manager knows better about the planting site, the management goal, and other factors specific for a decision than could be codified in any binding law. For the case of Scots pine in northern Sweden, Rosvall et al. (1998) listed and quantified these factors which should be considered locally in decisions on seed transfer. From this perspective, a modelling approach, as described here, seems to be particularly proper in quantifying seed transfer (mathematical abstraction highlights the norm of a natural phenomenon). An illustration of the likely losses as a function of the range from which plus trees are recruited to a seed orchard and the range over which the seed orchard material is used for Scots pine in Sweden is given in Figure 4.

Table 1. Predicted loss in relation to increasing zone width (due to decreasing optimal match of site types with seed sources) using the same Swedish Scots pine data as Raymond and Lindgren (1990).

Area the same material is used over (latitudes*)	Loss at fringe of area of use (L_1 , Eq. 3), %	Loss over the whole area (L_2 , Eq. 6), %	Zone size expressed as a fraction of C from centre to fringe (= lat*/10)
0	0	0	0
1	1.0	0.3	0.1
2	3.8	1.3	0.2
3	8.3	2.8	0.3
4	13.8	4.9	0.4
5	20.0	7.3	0.5

Balance between number and size of seed zones

From a biological standpoint, increasing the number (or reducing the size) of zones would be expected to improve the performance (productivity) in reforestation resulting from improved match of seed sources with planting sites as explained before. But it is not free of cost. Obviously, cost increases with increasing number of zones in terms of seed and nursery stock production, storage and delivery, and administration of regulations and record keeping, etc. It is important in a seed transfer guideline to consider the trade-off of both biological and operational, and administrative efficiencies. The model developed here offers a useful aid in decisions on optimising this trade-off.

Considering Table 1, breeders may have no difficulty with zone width not extended over two latitudes*, but feel uncomfortable with using the same Scots pine material over more than three latitudes* with potential loss at fringe of over 8% and on average nearly 3%. Other considerations related to optional cost and efficiency can then be factored in for a final decision.

This process offers a quantified way to aid decision-making balancing the increasing operational cost (efficiency) with potential loss of productivity by weighing their relative significance. We believe a modelling approach like this offers a dynamic optimisation process in decision making in deployment of genetic materials.

Range of the use of seed orchard seeds

Assuming genetic worth of seed orchard seeds 10 percent better (have ten percent higher A) than a natural seed source (provenance), and adaptability due to the wide range of parental origin of the former is not a concern, Table 1 (column 2) suggests the seed orchard seeds would outperform the natural seedlots over three latitudes* (10%–8.3%). Thus it can be argued in favour of planting seed orchard seeds over a greater range, since possibility of better local adaptation of local seeds is unlikely to compensate for the higher gain of seed orchard seeds.

Number of seed sources needed for Sweden

Roberds and Namkoong (1989) suggested that four provenances (thus four non-overlapping zones) are adequate for Scots pine reforestation in Sweden; their model (based on similar data as used in this study) estimated a loss of about 5.7% compared with using a large number of zones. If Sweden was divided into four zones, as Roberds and Namkoong's model suggests, each zone width would extend over four latitudes*. According to Table 1 (column 3), the loss would be 4.9%, so the two models agree. But the loss at the fringe of the zones would be 13.8% (Table 1, column 2) and that may be found unacceptable. If the number of zones were doubled to eight (zone width reduced to two latitudes*), loss would be reduced from 4.9% to 1.3% and the fringe loss would be reduced to 3.8%. This is enough justification to have more than four zones.

Long term breeding and range of origins to be included in future seed orchards

A main purpose of long-term breeding is to sustain future seed orchards (Rosvall 1999). The model can be used to assist the evaluation of structure and organisation of breeding populations in terms of long-term adaptability and flexibility. For example, the Swedish breeding material of Scots pine is planned to be structured in 24 subpopulations with 50 selections each (Wilhelmsson and Andersson 1993). The division in subpopulations is not final yet. Each subpopulation would be propagated from a founder population of 50 tested plus trees. Figure 4 suggests there is little risk of impairing adaptability if the initial origins composing a subpopulation covered two latitudes*. Swedish forestland covers around 16 latitudes*. Therefore, future seed orchards can draw materials from several subpopulations without risking serious maladaptation, but with the advantages of high selection intensity (resulting in higher gain), low inbreeding and large diversity in seed orchard

crops. According to Figure 4, adaptability value of the seed orchard decays only about two percent when the origins of the plus trees cover a range of 4 latitudes*. Scots pine seed orchards in Sweden seldom cover such a wide range of origins, thus it is not likely better adaptation can be obtained by narrowing the range of origins included compared to that in current orchards. At the establishment of a future seed orchard, it can however be worthwhile to consider more than 20% of the subpopulations as potential recruitment population. It may be argued that local adaptations could then be lost, but local adaptations are preserved in the breeding populations, and anyway it is likely that gene migration by pollen over latitudes is common, smoothing out local adaptations.

As the number of subpopulations is large enough to maintain sufficient local adaptation and as future seed orchards can be drawn from many subpopulations, it increases the flexibility to cope with future uncertainties through variable genetic management of the multiple populations. Such traits may be different wood products to meet future markets or tolerance of hostile environment in case of climate change.

4. Discussion

By integrating zone size with seed source adaptability and performance, the model offers the conceptual framework of an optimisation process in dynamic rather than static manner – zone size varies according to the particular characteristics of a seed source. Zonation is viewed as a process (dynamic) rather than the delineation of boundaries (static). Zonation and seed transfer in forest tree improvement will likely be a dynamic process in the future and modified continuously. Rather simple quantitative assessment based on theoretical models like this one, as illustrated in Figure 4 and Table 1, seems to offer a viable alternative for the needed future dynamics.

Predictability of model fitting depends on a realistic estimate of the parameters. Practical applicability of the model hinges on a reasonable estimate of the C parameter. It is possible to speculate if C is different for different materials or how C will change during breeding, but we feel there is insufficient results presented to justify that. We believe it can just be seen as a constant for provenances over an area. For example, $C = 5$ latitudes* represents the best estimate of Scots pine provenances in Sweden (Raymond and Lindgren 1990), and a C -value of 6 or 7 latitudes* the most proper estimate for lodgepole pine provenances in northern Sweden (Lindgren et al. 1993). Practical seed supply for those species will mostly come from seed orchards, and we have shown how C of these crops can be derived. It would probably not be very difficult to get C estimates (considering relevant factors for site classifi-

cation and adaptation criteria) for other species and cases where international provenance trials cover wide areas. Probably a number of such “case studies” would give a sufficient ground for C estimates of many cases, which are not directly covered by the studied cases. Substantial provenance and progeny testing results of commercial species are available in all major forest regions in the world. Estimates of the parameters required by the model is often possible, even if experimental limitations cause considerable uncertainty in the estimates. Estimating these parameters for synthetic seed sources can be done as illustrated for composite seed orchard seeds (Expressions 8 to 11 supply the theoretical framework). Despite the approximate nature of these parameters, the results come out reasonably realistic, as exemplified by the application to the Scots pine case in Sweden. Observed variation between provenances were between $C = 4$ and $C = 6$ (Raymond and Lindgren 1990) and this observed variation may not be real but just statistical noise. Thus, it may be a basis to believe that C is a characteristic for a species and region rather than a characteristic of the provenance. The parameter A is often seen as a constant in our reasoning about provenances, that tends to make the results related to some average of materials. If experimental data identifies some provenances as better than others from equivalent sites, the model can be used to analyse over what site range such superior provenances can be used. A better fit could probably be obtained using a more complex model that likely would require much sophisticated data, which are seldom available. There are probably many situations in practical forestry where the use of more complex models cannot be profitably implemented. In facing considerable future uncertainty, further fine-tuning of the modelling process probably does not serve a practical purpose.

The model may work best for species with a wide continuous distribution like Scots pine and in regions that are not close to the border of the species' natural distribution. The model may work less satisfactorily in periphery regions where environment tends to be extreme and there the concept of an optimal adaptation may be less relevant (as no materials can be regarded as “well” adapted). Application of the model in periphery regions ought to be practised with caution.

Models fitting mathematical functions have been suggested as tools of optimisation to maximise efficiency in deploying seed sources in tree improvement and reforestation (Roberds and Namkoong 1989; Raymond and Lindgren 1990). Raymond and Namkoong (1990) and Westfall (1992) discussed the merits of this approach compared with alternatives as the classical regression method (Campbell 1991; Rehfeldt 1990). A disadvantage with response functions is that they require rather large and specific data sets. The difference between a “free” regression and the fit to a mathema-

tical function is that in the later case, a hypothesis (or knowledge) about the general shape of the response function is used, making a better use of the available degrees of freedom for the fit if the hypothesis is reasonable. Each mathematical function has its pros and cons. The current approach (Cauchy-function) can be criticised for considering site classification in a single parameter; it gives no other option to simultaneous consideration of different trait than forming an index of them; and it constrains the possible type of genotype by site interaction (Westfall 1992). Site environment can be of infinite dimensions, component traits of adaptability are numerous and complex biologically, and it is a daunting task to decompose their interactions. For simple operational application, it is very desirable to have a single dimension. For practical applicability, large efforts must be made to reduce problems to one dimension, and the problem is rather to identify the most important dimension (in terms of composite indices describing a site and a genetic material as powerful as possible with a single variable). Experimental materials may seldom support that added principal components contribute much added explanation of variance. We believe (as we have demonstrated for the example with Scots pine in Sweden) that it often is possible to reduce the problem to a single most important dimension.

Mathematical diagnosis of all one variable functions is not the intention of this paper. It appears that all four models are similar if only the central region is considered, but may be very different at the outer ends (Figure 3). In a practical sense, fitting different functions would have produced similar conclusions if applied to a narrow range of provenance samples or site environments and choice of function may be a matter of preference rather than substance. Model fitting seems to be sensitive to site environment at the periphery (Figure 3); sites at the periphery anchor the response functions and tend to govern the parameters of the curves. In other words, model predictability in central regions is not independent of other regions. The Cauchy has the advantage that it will be rather robust to variations in the performance of badly adapted provenances. More empirical verification with data from different species in different regions may be of value to test the model's broad applicability.

A high proportion of resources in tree improvement is usually directed towards selection and breeding. Efficient deployment of improved materials receives much less attention. As breeding cycles advance, realisation of genetic gain will become increasingly dependent on precise genotype-site match. Considering seed source and zone as one rather than separate entities as expounded in the modelling approach in this paper offers one valuable process, at least in concept.

In our view, the method for optimising future zone size (deployment strategy) will likely be a trade-off process between maximising biological potential (e.g. genotypes with broad adaptability vs. site specific) and constraints imposed by cost/benefit considerations. The modelling approach, as presented in this and other papers, provides one-dimensional quantification of optimisation considering only the biological and production aspect. Broadening the application, cost-benefit constraints have to be incorporated into the modelling process.

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