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Forest Ecology and Management 136 (2000) 107–119

Forest Ecology
and
Management

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Genotype \times environment interactions in *Alnus rubra*: developing seed zones and seed-transfer guidelines with spatial statistics and GIS

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Received 20 May 1999; accepted 17 September 1999

Abstract

Multiple provenance trials of red alder (*Alnus rubra* Bong.) were used to demonstrate how geostatistical methods can be applied to develop better seed-transfer guidelines and seed-procurement zones for forestry. Height and survival of 65 provenances from British Columbia were measured at four test sites. Significant genotype \times environment interactions were found at the population and family level. Provenances close to each planting site showed superior performance in growth and survival, suggesting adaptation of red alder to local environments. The environmental basis of local adaptations was evaluated using redundancy analysis. Geographic and climatic variates accounted for approximately equal amounts of the variation in height growth (21 and 23%, respectively), while geographic variates accounted for 60% of the variation in climatic variables. Loadings of the redundancy variates suggested that both, gene flow and selection by environmental factors shaped geographic patterns of genetic differentiation in red alder. Performance of seed sources at unknown locations was predicted with ordinary kriging throughout the natural range of red alder in British Columbia. General seed-transfer guidelines were then generated with principal component analysis of predicted reaction norms. We found clinal differentiation of reaction norms along the coast from northwest to southeast. Further, the Georgia depression was identified as an area of genetic differentiation. Based on predicted height and survival at two trials that most realistically represented operational planting sites, we derived simple rules for seed transfer. A transfer of 100 km in either direction along the coast was associated with a decline of 2.5% in survival, and \approx 5 cm in 2-year height. Finally, we showed how maps of predicted performance and associated variance surfaces can be used to develop seed zones for specific objectives, where seed zones are given as maps of probabilities of a seed source performing above or below a given threshold for any combination of traits. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Red alder; Genecology; Seed zones; Seed transfer guidelines; Kriging; British Columbia

1. Introduction

A critical decision in forest resources management is the choice of seed sources for reforestation to ensure

a successful crop. Seed zones and seed-transfer guidelines are essential tools in assisting this decision. There are two common approaches to quantify the distance of seed transfer and to determine the size of seed zones. One strategy attempts to minimize the risk of planting poorly adapted trees, using regression models of provenance (seed source) performance over geographic coordinates to scale seed transfer (e.g.

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Campbell, 1983, 1986, 1991; Rehfeldt, 1985, 1991, 1995; Thomas et al., 1990; Russell, 1998). This approach implicitly assumes that local sources are optimal and often imposes a linear relationship between provenance performance and geographic variables. Local optimality is a subject of considerable debate (Namkoong, 1969; Mangold and Libby, 1978; Matyas, 1990), and a linear mode of geographic variation may not be appropriate, particularly in regions with highly heterogeneous environment like British Columbia. The advantage of this approach is that information about genetic differentiation in growth and adaptive traits can quickly be obtained from single provenance tests, greenhouse trials with seedlings, or laboratory experiments. A more advanced strategy aims at maximizing productivity by selecting the best provenances for a defined planting environment. This approach relies on mathematical functions to model response of genotypes to environmental gradients (Raymond and Namkoong, 1990; Raymond and Lindgren, 1990; Roberds et al., 1990). For practical application, however, this methodology requires extensive data from multiple provenance tests close to rotation age for each potential planting environment, which is rarely available (Ying, 1997).

In this report, we apply geographical information systems (GIS) and advanced statistical methodology to seed transfer concepts developed by (Campbell, 1983, 1991) and (Rehfeldt, 1985, 1991, 1995). The use of GIS has been previously explored for the development of seed zones (Parker, 1991; Parker and Nienhuis, 1996), and recently geostatistical software has become available that is compatible with most commercial GIS (Pebesma and Wesseling, 1998). We replace regression methods with ordinary kriging, where variation in provenance performance is modeled by a stochastic surface of best linear unbiased predictions. The crucial advantages of this methodology are the ability to model heterogeneous surfaces and that the prediction surface is accompanied by a surface of variance estimates which depend on the density of samples and the residual sampling error (Burrough and McDonnell, 1998). We utilize this estimation variance surface to map probabilities of a seed source performing above or below a given threshold and in this way develop seed zones. This method reflects the uncertainty due to sampling as

well as random genetic variation, and allows for flexible zoning according to the forester's objectives and willingness to take risks. Finally, we discuss how advanced forms of kriging in combination with GIS can be used to effectively detect and manage small-scale genetic variation, and how to identify sampling locations of seed sources that have high probabilities of superior performance.

Red alder (*Alnus rubra* Bong.) possesses substantial genetic variation in several growth and adaptive traits and the use of selected genotypes can enhance site productivity and reduce the risk of maladaptation (Stettler, 1978; DeBell and Wilson, 1978; Ager, 1987; Hook et al., 1990; Agar and Stettler, 1994; Dang et al., 1994; Xie and Ying, 1994; Hamann et al., 1998). Maximizing site productivity requires results from long-term provenance tests on multiple sites in order to accurately identify seed procurement zones where productive seed sources exist for a particular planting environment. Since red alder provenance trials in this report are only a few years old and the four test sites available do not sample all the species' potential planting sites, it is prudent to model geographic patterns of genetic variation aiming primarily at reducing the risk of planting maladapted seed sources. Since data from four sites are available, we can, however, test the assumption of local optima to some degree and investigate family stability over these planting environments. We further show how information from several traits or planting sites can be combined with GIS to derive general transfer guidelines. For demonstration of the methodology, we also derive maps aiming at maximum site productivity in multiple traits based on preliminary seedling data from one red alder provenance trial.

2. Material and methods

2.1. Study area and data

The British Columbia Ministry of Forests established three long-term provenance tests in the spring of 1994, two on the southern Vancouver Island at Bowser and Saanich, and one on the north coast at Terrace. One short-term test was planted in 1992 at Surrey (Fig. 1). The plantations were evaluated for height and survival after two growing seasons. Details

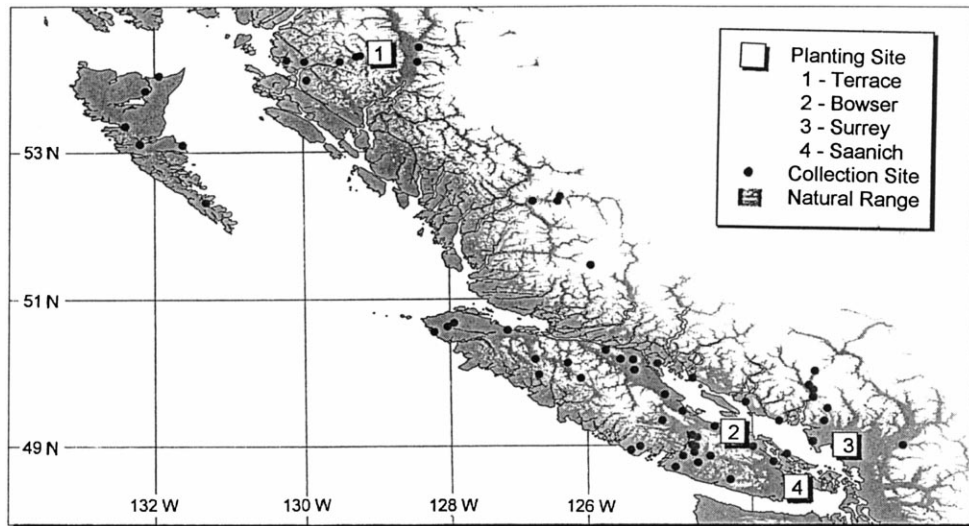


Fig. 1. Natural range of red alder in British Columbia, locations where seeds have been collected, and sites where test plantations with these provenances have been established.

about the experimental design, testing stock, and silvicultural treatments were described in Xie and Ying (1994) and Hamann et al. (1998). The major contrast between the southern planting sites was associated with moisture availability. The Surrey planting site was irrigated, prime agricultural land, while Bowser had medium and Saanich low precipitation. The Terrace planting site had a shorter growing season and a lower annual temperature than the southern planting sites. The number of provenances in each test varied between 50 and 70 with the numbers of families per provenance ranging from two to five. The Surrey trial also contained some bulk seed lots from Oregon and Alaska. Only 113 families that were common to all test plantations were included in the analysis of genotype \times environment interactions.

Climatic data of planting sites and collection sites was obtained from 55 weather stations not further away than 30 km, and not >100 m different in elevation from the collection site (Environment Canada, 1982). Climate variables were constructed using mean values for the period from 1951 to 1980. The climate variables considered were mean annual temperature, mean annual precipitation, July temperature, July precipitation, and days of the year (1–365), when the mean daily temperature first rises above and then falls below 5°C indicating the beginning and the end

of the growing season. Geographic variables used were latitude, distance to the coast, and altitude. Distance to the coast was chosen instead of longitude, since longitude is confounded with latitude due to the southeast to northwest oriented coastline of British Columbia. The distance to the coast for mainland provenances between 49 and 51°N latitude was measured from the west coast of Vancouver Island.

2.2. Statistical analysis

The experimental design at all sites was a split plot design with provenances in main plots, and families in five-tree row subplots. The Surrey trial had four blocks, while the other trials had blocks. Variance components were estimated using the restricted maximum likelihood method (SAS Institute, 1997) according to the following model:

$$Y_{ijkl} = \mu + S_i + B(S)_{j(i)} + P_k + P \times S_{ik} + \varepsilon 1_{jk(i)} \\ + F(P)_{l(k)} + F(P) \times S_{il(k)} + \varepsilon 2_{jl(ik)} + s_{m(ijkl)}$$

where Y is the measurement of seedling mat site i in block j from provenance k and family l ; μ the overall mean; S , $B(S)$, P , and $F(P)$ the effects of site, block within site, provenance, and family within provenance, respectively; $P \times S$ and $F(P) \times S$ the

interaction effects of site with provenance and site with family within provenance; and ε_1 , ε_2 , and s the main plot error, subplot error and sampling error, respectively. We assume that provenances are a random sample from a larger population about which inferences are to be made and, therefore, are random effects. Planting sites are considered random since they were not selected for particular environmental conditions.

Genotype \times environment interactions, as well as the main effects, were illustrated by plotting provenance means summarized by geographical regions. Genotype \times environment interactions at the family level were investigated with multivariate analysis of reaction norms. Reaction norms are usually referred to as response functions of a genotype to different environments. Because only four planting sites were evaluated in this study, fitting response functions is not feasible. Instead, we use the term reaction norm to describe the phenotypic response of genotypes to four environments, using a multi-dimensional coordinate system, where the axes represent performance at different environments. We then used principal component analysis to visualize this coordinate system in two dimensions. Families with similar norms of reaction, regardless of absolute performance, will be located close to each other in a plot of principal component scores and may be comprised of seed zones or breeding zones, if they are geographically clustered.

In order to guide the decision whether seed-transfer rules should be based on climatic or geographic variables, we investigated the environmental basis of genetic differentiation with redundancy analysis. This procedure determines how much of the variation in provenance performance could be explained by geographic variables or, alternatively, by climatic variables. Further, the variance that could be accounted for by geographic variables in climatic data was identified. Calculations were performed with the interactive matrix language (IML) of the SAS statistical software package according to algorithms developed by van den Wollenberg (1977).

2.3. Geostatistical analysis

To predict performance of a seed source at an unsampled location, we used ordinary kriging based on provenance means separately for each trial. The

kriging method yields smoothed, but varying surfaces and provides the best linear unbiased prediction of data values at unsampled points by dividing spatial variation into spatially autocorrelated variation, and spatially uncorrelated error variation. Predictions are calculated based on a variogram, where squared differences among all pairs of sample points are fitted as a function of their Euclidean distances.¹ We used a spherical function that starts at a minimal value at zero distance (indicating the highest spatial dependence), increases linearly at first and then gradually approaches a maximum value (indicating no spatial dependence beyond a certain distance among sample points). This function was then used to calculate the value and the associated variance of an unknown point. The program GSTAT by Pebesma and Wesseling (1998) was used to fit variogram models and to generate maps of predicted values and variances.²

The raw maps of predictions and associated variances were then transformed with the GIS software IDRISI. Seed-procurement zones are given as maps of probabilities that a seed source exceeds a threshold performance. These probabilities were calculated with the IDRISI module PCLASS, which integrates areas under the normal curve based on the map of predictions and the corresponding estimation variance surface. Seed-transfer guidelines can be read directly from maps of predicted values. Alternatively, the four prediction maps corresponding to the test sites were summarized by using differences in reaction norms as a measure of genetic differentiation. The predicted norm of reaction at a map location consists of the four values at corresponding locations of the individual prediction maps. To visualize geographic differences in reaction norms, we reduced the number of dimensions with principal component analysis using the IDRISI module PCA. This module returns a set of orthogonal maps and their component loadings with the original maps. Since every planting site should be considered with equal weight, we extracted orthogonal variates from correlation matrices. The resulting principal component score represents the predicted norm of reaction at a geographic location, so that the maximum variance in the original maps is accounted for. Conceptually,

¹ Refer to Chapter 6 of Burrough and McDonnell (1998) for a thorough introduction to geostatistical methodology.

² Software available at <http://www.geog.uu.nl/gstat/>

Table 1
Analysis of variance and estimated variance components for height

Source of variation	df	MS	$p > F$	Variance component	(%)
S	3	6195833	>0.0001	4159.598	(0.733)
B(S)	9	28958	>0.0001	53.186	(0.009)
P	40	12525	>0.0001	31.573	(0.006)
P × S	120	6065	>0.0001	40.942	(0.007)
Error 1	360	3742		218.092	(0.038)
F(P)	68	3719	>0.0001	28.638	(0.005)
F(P) × S	203	2086	>0.0001	59.170	(0.010)
Error 2	598	1290		64.559	(0.011)
Sampling error	4620	1019		1019.926	(0.180)
Corrected total	6021				

this cartographic analysis corresponds directly to the sample based evaluation of family reaction norms in the previous section.

3. Results and discussion

3.1. Genotype × environment interactions

The analysis of variance shows significant genotype × environment interactions at all levels of the sampling design (Table 1). Since site × provenance and site × family interactions are significant, main effects cannot be interpreted easily. However, the large variance component attributable to planting site indicates a major main effect which is illustrated in Fig. 2, where performance of provenances at the four planting sites is summarized according to their regional origin. Fig. 2 also illustrates that performance of seed sources is generally best at the planting site located in the same region. It is particularly apparent for survival that seed sources from the northern mainland perform best at Terrace, and seed sources from east Vancouver Island perform best at Saanich. At Surrey, where growing conditions were kept optimal with artificial fertilization and irrigation, differences among seed sources from BC were minimal in both, height and survival and only provenances sampled from far south in Oregon and far north in Alaska revealed a substantial decline in height and survival. This seems to suggest that 'ideal' site conditions do not provide an effective screening of provenance adaptability.

Principal component analysis of family means for height at four planting sites yielded two components

with eigenvalues >1, which account for 44 and 24% of the total variance. Component loadings in Table 2 reveal similar contrasts for both these components among Terrace and the southern planting sites, being orthogonal in a slightly different weighting of the southern sites. In Fig. 3, the top 10 families at each site are identified with letters in a plot of the first two components. If we define stable families as those that rank consistently high or low at both, the Terrace and the southern sites they would be found near the center of Fig. 3, delimited approximately by a circle, whereas families that perform well either at just Terrace or at the southern sites would be scattered in the periphery. Fig. 3 shows that the 10 best performing families are mostly unstable following the above definition, with the exception of some of the best performing families at Surrey which are located closer to the center. Also, the geographic origin of the top performing families was almost exclusively the same region where the planting site was located (data not shown).

The presence of significant genotype × site interactions at both the provenance and family levels implies changes in the relative performance of genotypes from one environment to the next, or changes in absolute differences between genotypes that leave the

Table 2
Eigenvectors of the first two principal components for height measurements from four planting sites

	PC-1	PC-2
Surrey	0.599	0.182
Saanich	0.547	-0.047
Terrace	-0.271	0.927
Bowser	0.517	0.325

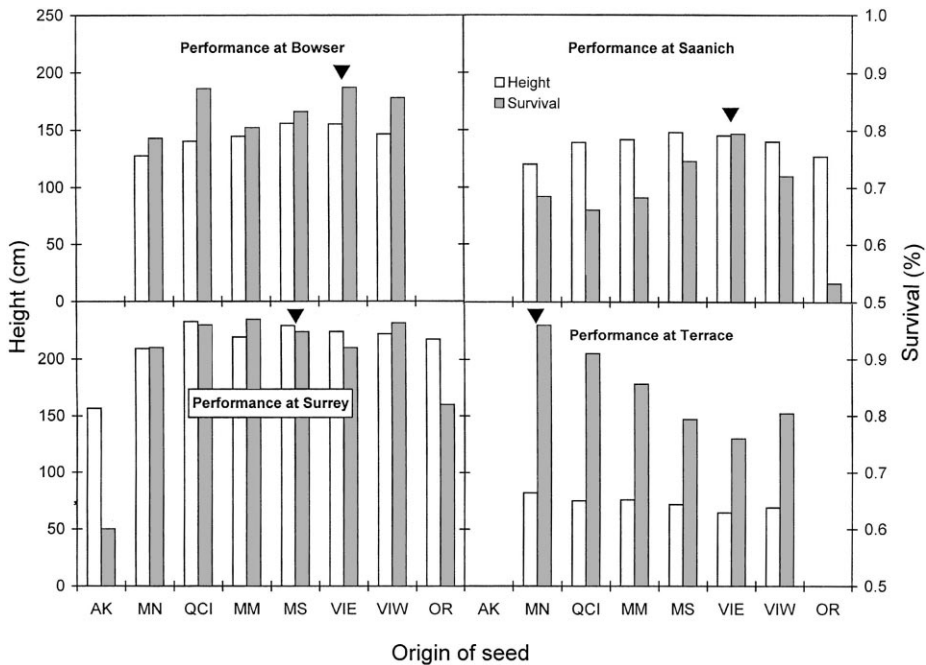


Fig. 2. Performance of provenances summarized by regions at the four planting sites. Regions of origin are Alaska (AK), British Columbia mainland north 53° to 55°N (MN), mainland middle 51° to 53°N (MM), mainland south 49° to 51°N (MS), Queen Charlotte Islands (QCI), Vancouver Island west coast (VIW), Vancouver Island east coast (VIE), and Oregon (OR). Arrows (▼) indicate in which region the planting site is located.

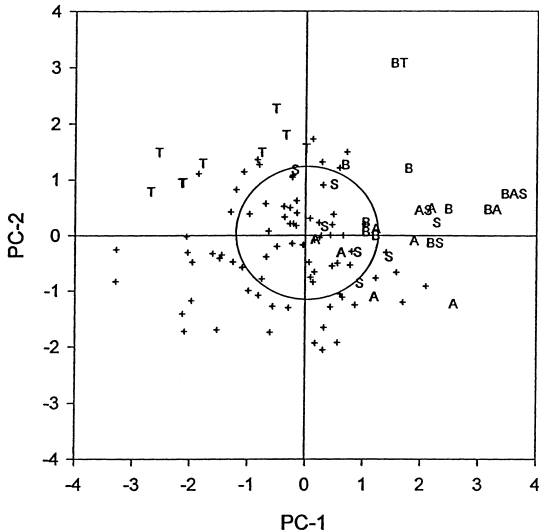


Fig. 3. Plot of the first two principal components extracted from height data for four planting sites. Letters refer to the 10 best performing families at Bowser (B), Saanich (A), Surrey (S), and Terrace (T).

rank order unchanged. Fig. 2 confirms that provenance rank changes occur between sites, both for height and survival. Principal component analysis of family means showed that this also holds true at the family level, at least for the top performing families between Terrace and the southern sites (Table 2, Fig. 3). These results suggest that breeding for stable genotypes, or using a single breeding or seed zone for red alder in British Columbia is not biologically reasonable. Further, the results validate the assumption that genotypes are adapted to a limited range of environments. Local adaptedness (or optimality) is often assumed without further testing. However, if environmental conditions have changed faster in the recent history of a species than the process of adaptation, populations may not be optimally adapted to current environments (Matyas, 1990). Moreover, optimal adaptation may not be necessary, depending on the objectives of the forester. If the planted stand need only to produce a marketable product, local populations (optimally adapted to long-term environments) may be less desirable than imported sources (Namkoong, 1969).

Further, growth rate may not generally be identical with adaptation to a certain site. Local populations could be slow growing but well adapted to long-term environmental conditions; while introduced populations may be fast growing but less adapted to extreme environmental conditions at the site. In the case of red alder, however, growth rates as well as survival are maximal at the site of seed origin and there is no indication that growth rates do not reflect adaptation to local environments. The reason may be that initial growth rates are an important fitness trait in a pioneer species. Further, the limited life span of red alder and its early age of reproduction, make it less necessary for this species to be conservative with respect to long-term survival.

3.2. Environmental basis for genetic differentiation

Redundancy analysis shows that geographic and climatic variables explain approximately equal amounts of variance in height measurements at the four planting sites (Tables 3 and 4). In both cases, the first pair of three orthogonal linear combinations accounts for almost all the variance explained (23% for climatic variables and 21% for geographic variables). Loadings of redundancy variates reveal that a long growing season with less extreme temperatures,

low precipitation and high average temperatures at the seed source are associated with contrasting performances at the southern sites (above average) and Terrace (below average). The same contrast can be found mainly as a function of latitude (Table 4), and, in fact, geographic variables account for a large proportion of variance in the climatic data set (Table 5). It should also be noted that elevation is an important predictor for climatic variables but not for provenance performance (Variate 1 in Tables 3 and 5).

If climatic conditions are sufficiently dissimilar for differential selective forces to act, the populations are expected to be differentiated in patterns associated with environmental variables. On the other hand, effectiveness of selection can be neutralized if gene flow across environments is substantial. The resulting cline might then be more accurately predicted by geographic variables. The fact that much of the variation in red alder can be explained by the variable latitude, while the other geographic variables that represent less geographic distance are of minor importance (Table 4, Variate 1), indicates that gene flow may be an important factor in shaping the adaptive landscape of red alder in British Columbia. This is supported by the observation that elevation is an important factor in explaining variation in climatic

Table 3
Loadings of redundancy variates and variance explained in height by climatic variates

Variable	HEIGHT1	HEIGHT2	HEIGHT3
Height at Surrey	0.446	0.471	-0.292
Height at Saanich	0.431	-0.416	-0.120
Height at Bowser	0.872	0.211	0.403
Height at Terrace	-0.657	0.243	0.644
	CLIMATE1	CLIMATE2	CLIMATE3
Season beginning	-0.702	0.172	0.029
Season end	0.500	0.157	-0.354
Temperature maximum	-0.461	-0.181	0.360
Temperature minimum	0.364	0.485	0.371
Temperature, July	0.424	0.274	0.547
Temperature, Year	0.812	0.411	-0.075
Precipitation, July	-0.465	-0.043	-0.225
Precipitation, Year	-0.033	-0.325	-0.533
	Variance explained in HEIGHT by CLIMATE		
Proportion	0.228	0.025	0.020
Cumulative	0.228	0.253	0.273

Table 4
Loadings of redundancy variates and variance explained in climatic variables by geographic variates

Variable	HEIGHT1	HEIGHT2	HEIGHT3
Height at Surrey	−0.385	0.582	−0.353
Height at Saanich	−0.511	0.134	0.418
Height at Bowser	−0.852	0.495	0.011
Height at Terrace	0.625	0.627	0.417
	GEO1	GEO2	GEO3
Latitude	0.894	0.445	−0.058
Distance	−0.340	0.161	0.927
Elevation	0.116	−0.868	0.483
Variance explained in HEIGHT by GEO			
Proportion	0.206	0.008	0.002
Cumulative	0.206	0.214	0.216

variables at the provenance locations (Table 5, Variate 1), but accounts for very little variation in provenance performance (Table 4, Variate 2). Genetic differentiation of provenances over elevational gradients may have effectively been prevented by gene flow over relatively short distances. Loadings of the first climatic variate explaining provenance performance shows trends associated also with latitude, i.e. longer growing season, smaller temperature extremes that are also associated with latitude. This indicates that patterns of genetic variation described by geographic variables

relate directly to environmental variables that plausibly reflect the effects of natural selection. In summary, it can be said that gene flow among populations may prevent local adaptations on a fine scale and geographic variables can be used to predict the adaptive landscape of red alder with reasonable accuracy.

Results of the redundancy analysis suggest that we can model provenance performance with ordinary kriging, because elevation and climatic variables do not account for much additional variation in provenance performance. There are also practical advan-

Table 5
Loadings of redundancy variates and variance explained in climatic variables by geographic variates

Variable	CLIMATE1	CLIMATE2	CLIMATE3
Season beginning	−0.317	0.784	0.158
Season end	0.405	−0.726	−0.378
Temperature maximum	−0.193	0.606	0.276
Temperature minimum	0.411	−0.523	−0.411
Temperature, July	0.522	−0.294	0.671
Temperature, Year	0.194	−0.948	0.068
Precipitation, July	0.145	0.055	−0.918
Precipitation, Year	−0.331	−0.221	−0.809
	GEO1	GEO2	GEO3
Latitude	0.642	0.666	−0.380
Distance	0.021	0.175	0.984
Elevation	−0.867	0.455	0.204
Variance explained in CLIMATE by GEO			
Proportion	0.418	0.176	0.015
Cumulative	0.418	0.593	0.609

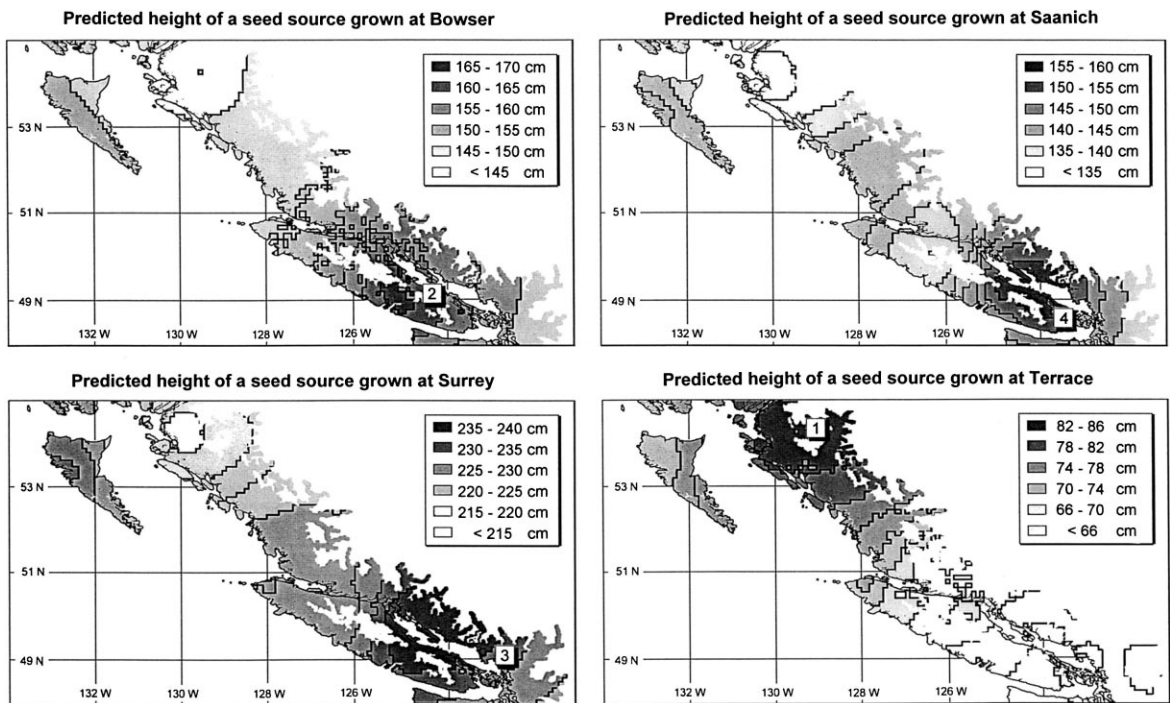


Fig. 4. Best linear, unbiased predictions of seed source performance obtained with the kriging method. The different shades represent expectations of height growth when seeds are collected at a geographic location and grown at one of the four planting sites. One contour interval is equivalent to 0.25 standard deviation in height growth at a planting site.

tages in restricting the model to spatial variables. Seed-transfer rules derived with advanced kriging methodology that includes additional information, such as climatic variables, are not as simple to use and require subsequent management of a species with GIS, which will be discussed later.

3.3. Seed-transfer guidelines

Predicted values of seed sources for height at each individual planting site are shown in Fig. 4. Height growth of provenances originating near planting sites are apparently higher than provenances from elsewhere, and the line where relative performance of provenances at the southern planting sites (Bowser, Saanich, and Surrey) exceeds those at northern planting site (Terrace), and vice versa, lies approximately half way between the planting sites. Hence, there are opposite trends in provenance performance along the mainland from southeast to northwest of approximately the same magnitude. Moreover, there appears

to be a local differentiation in the region of the Georgia depression (the southeast region of Vancouver Island, Gulf Islands, and the mainland across the Strait of Georgia). Provenances from this area have above average height at the southern plantations, and grow especially well at Saanich, the driest planting site. Similar maps are obtained for survival (data not shown).

Under the assumption that local populations are optimal and that the deviation of a provenance mean from a local source in either direction represents the same magnitude of suboptimality, we can develop general seed-transfer guidelines. This allows the generalization that moving a provenance from a location at, say, Terrace to a location midway between Terrace and Surrey has the same effect as moving a provenance from this midway position to Surrey, although the former transfer has not been tested. The principal component analysis identifies one variate with an eigenvalue >1 , which accounted for 79% of the variation in height growth. The resulting maps of scores for

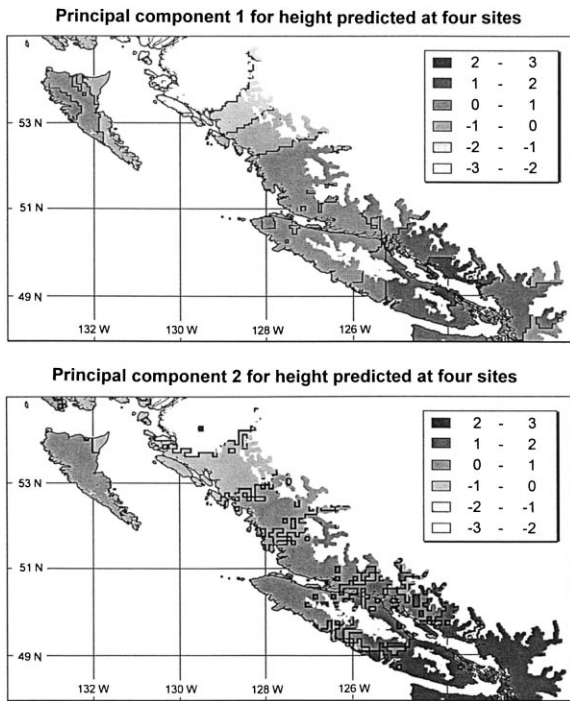


Fig. 5. Cartographic principal component analysis for predicted height growth at four planting sites (Fig. 4). The first principal component (upper map) that explains most of the variance in performance at the individual sites can be used to guide seed transfer.

the first two principal component are shown in Fig. 5. Trends for height at each of the four planting sites can effectively be reduced with principal component analysis to one dimension. The prevalent differentiation of reaction norms occurs along the coast from northwest to southeast. The component loadings in Table 6, or directly the predicted values in Fig. 4 provide insight into the direction and magnitude of changes in growth and survival if provenances are moved

Table 6

Eigenvectors of the first two principal components for predicted height at four planting sites

	PC-1	PC-2
Surrey	0.751	0.522
Saanich	0.675	0.661
Terrace	-0.644	-0.796
Bowser	0.863	0.448

perpendicular to the contours in Fig. 5. A transfer of a seed source by a distance of 100 km (scale varying due to map projection) in northeast–southwest direction roughly corresponds to one contour interval or 0.25 standard deviations in height growth at each planting site. The forester must then decide how much decline in height is acceptable. If a decrease of one standard deviation below the best performing provenances is acceptable, then a 400-km transfer in either direction along the coast may be allowed. Convenient rules to limiting seed transfer can also be derived for survival at mainland provenances. A transfer of a seed source by 100 km in the southeast–northwest direction is associated with a decline in survival by around 2.5 percentage points (data not shown).

Interpreting principal component scores as differences in reaction norms is potentially problematic. Although different scores indicate different reaction norms, the same score does not necessarily imply that the reaction norms are the same, and that seeds can be transferred among these regions without danger of poor adaptation. This problem should be kept in mind, especially when areas with the same score are not physically connected on the map. If such areas are in fact different, it should not be possible to reduce the dimensions to one with principal component analysis, and the second orthogonal map of component scores will reveal which areas with the same score in the first component map have different reaction norms. Areas north and south of the Georgia depression have a different score in the second principal component (Fig. 5, lower map). However, the second variate accounts for little variation and may be neglected. Parker (1991) in a similar situation overlays several maps of component scores with GIS, but the components are not weighted according to the variance they explain. An objective solution would be the calculation of Mahalanobis distance among reaction norms at two locations of interest and then to set a maximum threshold for a distance where seed transfer is allowed. This matrix of distances, however, cannot be visualized as a map, but must be queried for each case of interest.

3.4. Seed procurement zones

Seed zones based on a single trait may be read directly from the prediction maps. Having an estima-

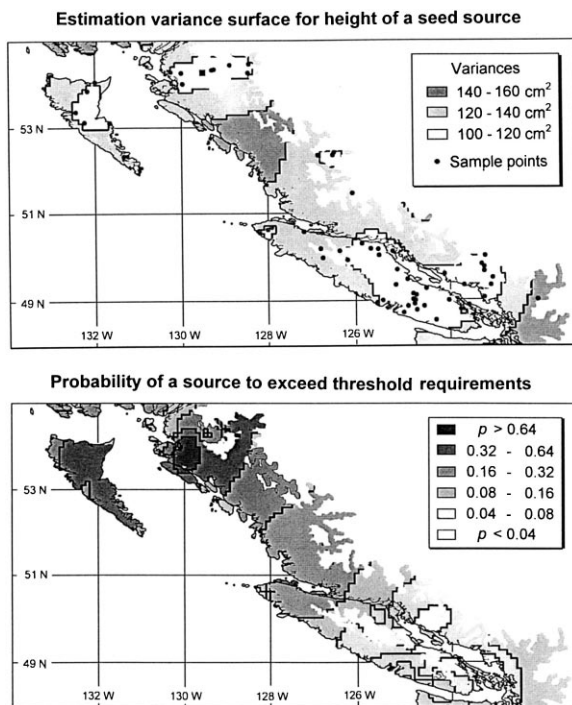


Fig. 6. Estimation variance surface for height of a seed source grown at Terrace (upper map) and derived probabilities of a seed source exceeding a threshold of 80% survival and a threshold for height of one-half standard deviation above the Terrace site mean (lower map).

tion variance surface available, it seems much more sensible to express a seed zone in terms of probabilities of superior performance. Probabilities for specific objectives may be calculated according to the following example for the Terrace planting site (Fig. 6). The variances of the predictions are largest in regions where few sample points are available, and smallest in areas covered with many samples (upper map in Fig. 6). Given the threshold of height growth being larger than one-half standard deviation above the Terrace site mean and at least 80% survival, probabilities of a provenance performing to these expectations are shown in the lower part of Fig. 6. Again, the highest probabilities of a provenance meeting the requirements can be expected, if the seed source close to this planting site is chosen.

An alternative and perhaps more flexible way to combine information about several traits is the use of GIS based decision support systems, particularly if the

number of traits under consideration is large and of different importance to the forester. IDRISI modules, such as WEIGHT, FUZZY or MCE cope with threshold requirements (e.g. provenance must be frost hardy to -10°C , with 90% probability), non-linear weighting of traits (e.g. a sigmoidal value function for survival), and relative importance of different traits. Maps of predictions or maps of probabilities of single traits performing to expectations are suitable input data for these modules to generate seed zones based on multiple criteria.

3.5. Potential applications

In this report, we presented the simplest case of how kriging could be used to derive better guidelines for forestry purposes. Ordinary kriging is sufficient for red alder or other species with little genetic differentiation on a small geographic scale. The greatest potential for the application of kriging methodology and GIS-based management of a genetic resource, however, lies in species which are highly differentiated over a complex environment, such as ponderosa pine (Rehfeldt, 1991) or interior Douglas-fir (Campbell, 1979; Rehfeldt, 1983). Co-kriging has been developed for the mining industry to predict the location of mineral deposits based on sample cores and additional (easy to obtain) geological information. The method could similarly be used in forestry to predict the location of top performing seed sources based on a sample provenances and additional climatic information. Covariates must be sampled or modeled at both, the source and prediction locations and may include nominal data such as biogeoclimatic zone, soil type, or aspect, as well as continuous variables such as elevation, precipitation or other climatic variables. With co-kriging, it is possible to optimally exploit a genetic resource by identifying sampling locations with the highest likelihood of productive seed sources. In addition to enhanced accuracy of the predicted performance, co-kriging may also be used to test current zoning (by using existing seed zones as covariates), or to provide insight into the genecology of species (by partitioning of variance components due to covariates). If several environmental factors rather than geographic variables prove to be important for the species genetic differentiation, seed-transfer rules will be more com-

plex and GIS based management of a species will likely be necessary to match source and planting environments.

Acknowledgements

This study was supported by a research grant of Forest Renewal British Columbia. We thank Dr. Brian Klinkenberg of the Department of Geography, University of British Columbia, for his assistance with the geostatistical analysis. Arrangement of a planting site and plantation maintenance by the Ministry of Forests Nursery at Surrey is gratefully acknowledged.

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