

Utilization and management of red alder genetic resources in British Columbia

by

Andreas Hamann

B.Sc., University of Hamburg, Germany 1991

M.Sc., New York State University, Syracuse 1995

A thesis submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

in

The Faculty of Graduate Studies
(Department of Forest Science; Faculty of Forestry)

We accept this thesis as conforming to the required standard

The University of British Columbia

July 1999

© Andreas Hamann, 1999

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Forest Science

The University of British Columbia
Vancouver, Canada

Date Sep. 9, 1999

Abstract

In this thesis genecology, phylogeography, and quantitative genetics of red alder were investigated. Further, literature with respect to red alder product values, market demand, forest resources, and red alder biology were reviewed. Implications of these aspects for genetic resources management were evaluated and a breeding strategy for red alder in British Columbia was developed.

Genetic differentiation among provenances in British Columbia was investigated based on six polymorphic allozyme loci and measurements of six quantitative traits. Multivariate analysis revealed complex associations of quantitative traits with the latitude, distance to the coast, and elevation of the seed source. Nei's genetic distance revealed a strong differentiation among island and mainland provenances at one allozyme locus. This differentiation can be interpreted as a result of migration from two different refugia since the last glaciation.

Adaptation of red alder provenances was investigated based on trials in multiple planting environments. 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. Seed transfer guidelines and seed procurement zones were developed under the assumption of local optimality using improved methodology based on risk associated with seed transfer.

In order to assess the potential benefits from selection and evaluate different options for tree improvement, genetic parameters for growth and adaptive traits were estimated from progeny tests. Estimated heritabilities for growth and adaptive traits were moderate with values between 0.30 and 0.50. Genetic gain in growth traits from individual selection would range from 25 to 35%. Small improvements (approximately 5%) would indirectly be achieved in the form score due to positive genetic correlations. Removal of spatially autocorrelated error variation in field experiments increased heritabilities and gains from selection.

A multiple population breeding strategy for uncertain climatic conditions in British Columbia was derived as a synthesis, using information on geneecology, risk associated with seed transfer, and genetic parameters. Six breeding populations of red alder, some with novel trait combinations, were found to be necessary to cope with possible effects of climatic warming in British Columbia.

Table of contents

Section	Page
Abstract	ii
Table of contents	iv
List of tables	viii
List of figures	x
Acknowledgements	xiv
 Chapter 1. Introduction	 1
 Chapter 2. Literature Review	 4
2. 1. Red alder biology and silviculture	5
2. 1. 1. Botany, taxonomy, and distribution	6
2. 1. 2. Ecology and life history	8
2. 1. 3. Special properties	10
2. 1. 4. Reproduction and propagation	13
2. 1. 4. Plantation establishment and tending	15
2. 1. 6. Implications for tree improvement	16
2. 2. Economic aspects	17
2. 2. 1. Value of red alder products	18
2. 2. 2. Growth and yield	20
2. 2. 3. Resource utilization in B. C.	24
2. 2. 4. Implications for tree improvement	26
2. 3. Genetic resource management	27
2. 3. 1. Genetic variability in red alder	28
2. 3. 2. Seed procurement	32
2. 3. 3. Tree improvement	35
2. 3. 4. Options for red alder	37
2. 4. References	40

Chapter 3.	Allozymic and quantitative trait variation in <i>Alnus rubra</i>: geographic patterns and evolutionary implications	55
3. 1.	Abstract	55
3. 2.	Introduction	56
3. 3.	Material and Methods	57
3. 3. 1.	Study area and plant material	57
3. 3. 2.	Data collection	59
3. 3. 3.	Statistical analysis	60
3. 4.	Results	61
3. 4. 1.	Population differentiation	61
3. 4. 2.	Simple correlation among variables	65
3. 4. 3.	Canonical correlation and redundancy analysis	67
3. 5.	Discussion	71
3. 5. 1.	Differentiation in quantitative traits	71
3. 5. 2.	Allozymic differentiation and evolutionary history	73
3. 6.	References	76
 Chapter 4.	 Genotype \times environment interactions in <i>Alnus rubra</i>: developing seed zones and seed transfer guidelines with spatial statistics and GIS	 79
4. 1.	Abstract	79
4. 2.	Introduction	80
4. 3.	Material and Methods	82
4. 3. 1.	Study area and data	82
4. 3. 2.	Statistical analysis	84
4. 3. 3.	Geostatistical analysis	86
4. 4.	Results and Discussion	88
4. 4. 1.	Genotype \times environment interactions	88
4. 4. 2.	Environmental basis for genetic differentiation	93
4. 4. 3.	Seed transfer guidelines	97
4. 5. 1.	Seed procurement zones	101
4. 5.	Recommendations	102
4. 6.	References	103

Chapter 5.	Estimation of genetic parameters in <i>Alnus rubra</i>: improving breeding values with kriging	107
5. 1.	Abstract	107
5. 2.	Introduction	108
5. 3.	Material and Methods	110
	5. 3. 1. Field experiments	110
	5. 3. 2. Parameter estimates	111
	5. 3. 3. Spatial analysis	113
5. 4.	Results and Discussion	114
	5. 5. 1. Genetic parameters in red alder	114
	5. 5. 2. Improved estimates for selected traits	118
5. 5.	Conclusions	125
5. 6.	References	126
Chapter 6.	A multiple population breeding strategy for uncertain climatic futures: genecological studies and selection experiments with <i>Alnus rubra</i>	129
6. 1.	Abstract	129
6. 2.	Introduction	129
6. 3.	Material and Methods	132
	6. 3. 1. Selection experiments	132
	6. 3. 2. Breeding techniques	135
	6. 3. 3. Genecological aspects	137
6. 4.	Results and discussion	137
	6. 4. 1. Genetic parameters and response to selection	137
	6. 4. 2. Possible response to climatic warming	140
	6. 4. 2. Required breeding populations	147
6. 6.	Recommendations	150
6. 6.	References	151

Chapter 7. Summary and recommendations 155

Appendices 159

A. 1. Layout of B. C. provenance trials at Surrey	159
A. 2. Layout of B. C. provenance trials at Saanich	166
A. 3. Layout of B. C. provenance trials at Bowser	169
A. 4. Layout of B. C. provenance trials at Terrace	172
A. 5. B. C. provenance information	175
A. 6. Layout of Alaska provenance trial	177
A. 7. Alaska provenance information	182
A. 8. Layout of selection experiment	183
A. 9. Information on selected parents	185
A. 10. Layout of Idaho/B. C. provenance trial	188
A. 11. Idaho/B. C. provenance information	189

List of tables

Chapter 2.

- | | |
|---|----|
| 2. 1. Yield at peak mean annual increment (MAI) for median site indices for species in the Vancouver forest region (Peterson 1996). | 21 |
| 2. 2. Yield of red alder at rotation age for different site qualities in the Vancouver forest region (Peterson 1996). | 21 |

Chapter 3.

- | | |
|--|----|
| 3. 1. Allele frequencies for 19 red alder populations from British Columbia. Monomorphic loci and the least frequent allele of each polymorphic locus are omitted. | 63 |
| 3. 2. Component loadings of the first two principal components for six quantitative traits. | 64 |
| 3. 3. Simple correlations among quantitative traits and geographic variables based on population means. | 66 |
| 3. 4. Summary statistics and regression coefficients for quantitative traits based on population means. | 66 |
| 3. 5. Correlations between original variables and their canonical variates. | 68 |
| 3. 6. Correlation analysis of the relationship between pairs of canonical variates. | 68 |

Chapter 4

- | | |
|---|----|
| 4. 1. Analysis of variance and estimated variance components for height. | 89 |
| 4. 2. Eigenvectors for the first two principal components for height measurements from four planting sites. | 92 |
| 4. 3. Loadings of redundancy variates and variance explained in height by climatic variables. | 95 |
| 4. 4. Loadings of redundancy variates and variance explained in height by geographic variables. | 96 |

4. 5.	Loadings of redundancy variates and variance explained in climatic variables by geographic variables.	96
4. 6.	Correlations between climatic variables and geographic variables	96
4. 7.	Eigenvectors for the first two principal components for predicted height at four planting sites.	100

Chapter 5

5. 1.	Variance components and individual heritabilities for B. C. provenances evaluated at Surrey (unless planting location specified otherwise).	115
5. 2.	Genetic correlations (upper right) and phenotypic correlations (lower left) for traits evaluated at age four.	115
5. 3.	Variance components and individual heritabilities using the normal model (N), and after adjustment for spatially autocorrelated variation (A).	124
5. 4.	Genetic correlations before (upper right) and after (lower left) adjustment for spatially autocorrelated error variation. Standard errors are given in parentheses.	124

Chapter 6

6. 1.	Weights for restricted selection indices.	138
6. 2.	Estimated variance components and heritabilities for traits based on full-sib offspring of controlled crosses.	138

List of Figures

Chapter 2

- | | |
|--|----|
| 2. 1. Natural range of red alder in the Pacific Northwest (adapted from Harrington (1990)) and a more detailed map showing outlying populations in Idaho (adapted from Johnson (1968a)). | 7 |
| 2. 2. Price development of red alder saw timber quality logs over the past two decades compared to softwood species (data from Oregon Ministry of Forests (1999)) | 19 |
| 2. 3. Change of red alder log prices over the past two decades compared to changes in log prices of softwood species (data from Oregon Ministry of Forests (1999)). | 19 |
| 2. 4. Site index curves for red alder and Douglas-fir, the latter representative of most other conifers in coastal British Columbia (From: Thrower and Nussbaum 1991). | 23 |
| 2. 5. Quality of stands in British Columbia by regions (data from Massie (1996) summarized by the following regions: NC, North Coast; MC, Mid Coast; GD, Georgia Depression; QCI, Queen Charlotte Islands; VIW, Vancouver Island Westcoast). | 25 |
| 2. 6. Ownership of stands in British Columbia (data from Massie (1996) summarized by the following regions: NC, North Coast; MC, Mid Coast; GD, Georgia Depression; QCI, Queen Charlotte Islands; VIW, Vancouver Island Westcoast). | 25 |

Chapter 3

- | | |
|---|----|
| 3. 1. Location of provenances and planting site for B. C. red alder provenance trial. Symbols represent regions, and numbers refer to provenances essayed for allozyme frequencies. | 58 |
| 3. 2. Dendrogram of 19 B. C. red alder provenances using UPGMA clustering technique for Nei's unbiased genetic distance. Symbols refer to regions specified in Figure 1. | 62 |
| 3. 3. Dendrogram of 19 B. C. red alder provenances using UPGMA clustering technique for Mahalanobis distances derived from quantitative traits. Symbols refer to regions specified in Figure 1. | 62 |

3. 4.	Plot of the first two principal components for 65 B. C. red alder provenances based on 6 quantitative traits. Symbols refer to regions specified in Figure 1.	64
3. 5.	Expected heterozygosities for 19 B. C. red alder provenances plotted as a function of latitude. Symbols refer to regions specified in Figure 1.	70
3. 6.	Hypothetical refugia and migration of red alder since the height of the last glaciation adapted from Pilou (1991).	70

Chapter 4

4. 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.	83
4. 2.	Flowchart of GIS operations for the development of seed transfer guidelines and seed procurement zones from general maps and from data of common garden experiments (shaded boxes are IDRISI-images, capitals denote IDRISI-modules used, and circles represent auxiliary programs used).	87
4. 3.	Performance of provenances summarized by regions at the four planting sites. Region of origins 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).	90
4. 4.	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).	92
4. 5.	Predicted height of seed sources at four planting sites. One contour interval is equivalent to 0.25 standard deviations at each site.	98
4. 6.	Scores of the first (upper map) and second (lower map) principal component of predicted height at four planting sites.	99
4. 7.	Variance of predicted height growth (upper map) and probabilities of a seed source having superior performance in two traits at Terrace (lower map).	99

Chapter 5

5. 1. Genetic intraclass correlations for traits in B. C. provenances evaluated at the Surrey-I plantation. Effects due to regions are based on groups of provenances defined in Figure 3. 1. 116
5. 2. Residual error variation after analysis of variance at the Saanich field trial. Light shades indicate negative residuals, dark shades represent positive values. 120
5. 3. Semivariograms for height at the Saanich trial (above), and bud break at the Surrey-II trial (below). 121
5. 4. Variation due to autocorrelation in residuals values for height, predicted by the kriging method, at the Saanich field trial. Light shades indicate negative residuals, dark shades represent positive values. 122
5. 5. Variation due to autocorrelation in residuals values for height, predicted by the kriging method, at the Surrey-I (left) and Surrey-I (right) field trials. Light shades indicate positive residuals, dark shades represent negative values. 123

Chapter 6

6. 1. Selection scheme for breeding experiment (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, population based on parents selected for the same trait or trait combination; y, population based on parents selected for different traits). 133
6. 2. Mating design for breeding experiment (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, cross among parents selected for the same trait or trait combination; y, cross among parents selected for different traits). 134
6. 3. Population means for parents and offspring (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, population based on parents selected for the same trait or trait combination; y, population based on parents selected for different traits). 139

6. 4.	Growth rates during the second growing season for provenances summarized by regions of origin	141
6. 5.	Date of budbreak predicted for provenances when grown at the Surrey planting site. Contours are drawn at intervals of approximately 0.25 standard deviations.	141
6. 6.	Proposed multiple breeding populations for current (dark circles) and possible future (light circles) climatic conditions (NC, British Columbia north of 51°N latitude; GD, Georgia Depression; VIW, Vancouver Island Westcoast).	149

Acknowledgments

My work builds on a project initiated by the Ministry of Forestry in 1992 with a provenance trial including 65 B. C. seed sources of red alder. In 1994 three other genetic trials with the same seed sources were established. I utilize data from two year evaluations for quantitative traits, conducted by the Ministry and allozyme data generated by Yousry El-Kassaby (4-year evaluations and trial establishments from 1996 on were carried out by myself).

This research was supported by a research grant of Forest Renewal British Columbia. I thank my supervisor Gene Namkoong, and my committee members Sally Aitken, Cheng Ying, and Kermit Ritland for help and advice throughout the study. Field and laboratory work by Jodie Krakowski is gratefully acknowledged, and I would like to thank Tony Willington of the Ministry of Forests Nursery at Surrey for providing planting sites and plantation maintenance.

Chapter 1. Introduction

Red alder (*Alnus rubra* Bong.) is the most common and wide ranging hardwood in the Pacific Northwest. The species has attracted considerable attention as a potential reforestation species because of its fast growth and its ability to symbiotically fix nitrogen. While many aspects of the species ecology and management are well researched, there is little information on genecology, population genetics and quantitative genetics of red alder. Consequently, no tree improvement or genetic resources management has been attempted until now. In fact, management of the species in the Pacific Northwest has only recently been initiated, although the value of its wood products and its ecological benefits have been recognized widely for decades.

During the last two decades, incentives have increased to develop an intensive forestry management system for red alder. Its abundance and low cost on markets in Washington and Oregon has made it one of the few hardwoods in the Pacific Northwest with major economic importance. Strong and consistent markets have developed particularly for high quality red alder lumber in North America and overseas, and harvest of most good quality stands in the United States has already lead to shortages and projected declines in the supply of red alder. In the same period, changes in forest management practices have taken place with emphasis on ecologically sound and sustainable use of forest ecosystems. An intensive management program for red alder would diversify softwood-oriented plantation forestry, and add an ecologically important component of coastal ecosystems to forestry in British Columbia.

Despite its reputation of growing everywhere where it is not wanted, natural regeneration of red alder is inadequate in many cases. If the establishment of high quality red alder stands is a primary objective, adequate regeneration can only be achieved by planting. The decision to

regenerate a species by planting, however, entails the need to manage the genetic resource at some level to avoid planting maladapted trees. It also opens up the opportunity to improve a forestry program by planting selected genotypes. In this thesis I investigate genecology, phylogeography, and quantitative genetics of red alder. Implications of these aspects for genetic resources management will be discussed in depth, and this thesis is intended to provide a framework for genetic tree improvement of red alder in British Columbia.

Overview of chapters

In the literature review (Chapter 2) I briefly introduce the species and summarize knowledge of red alder genetics as well as aspects of red alder biology, silviculture, and economics that are relevant background for genetic resources management. Based on a review of red alder product values, a market analysis, and a red alder resource inventory for British Columbia, I will evaluate possible breeding objectives for red alder, and discuss them in the context of approaches for applied genetics programs taken for sympatric conifer species in the Pacific Northwest and hardwoods elsewhere.

An assessment of geographic variation in a forestry species (Chapter 3) is a necessary first step towards intensive genetic management. Amount and patterns of genetic diversity in a species must be understood in order to manage a forestry species responsibly and effectively. In this section I describe genetic variation in both quantitative traits and allozymes, and investigate how closely attuned this variation is to geographic variables. Adaptation of red alder provenances along environmental gradients is investigated with regression- and multivariate analysis of growth and adaptive traits. Geographic patterns in allozyme frequencies are interpreted with respect to evolutionary history since the last glaciation.

A second step toward genetic resource management is the development of seed transfer guidelines (Chapter 4). Based on provenance performance at four planting environments and climatic data for each provenance source environment, I investigate the degree of adaptation of the species to local environments, and use redundancy analysis to investigate the importance of different environmental clines. I further present improved methodology for the development of seed transfer guidelines and seed procurement zones, and illustrate its use with preliminary data from four red alder provenance trials.

The translation of breeding objectives into selection criteria depends largely on the genetic control of the traits of interest. In order to assess the potential benefits from selection and evaluate different options for tree improvement, estimates of genetic parameters are needed for traits of importance (Chapter 5). In this section I estimate heritabilities and genetic correlations for growth and adaptive traits in four progeny trials of red alder, and discuss implications for a tree improvement strategy. Further, I remove spatially autocorrelated error variation in field experiments in order to increase heritabilities, gains from selection, and precision of parameter estimates.

In Chapter 6 I develop a multiple population breeding strategy for uncertain climatic futures. Multiple populations for different climatic scenarios and different regions of British Columbia are derived as a synthesis of the three preceding chapters: I utilize information on genecology (Chapter 3), risk associated with seed transfer (Chapter 4), and genetic parameters (Chapter 5). The feasibility of the strategy is tested with a breeding experiment involving 12 populations selected for growth, bud break, and leaf abscission using different selection intensities and directions.

Aspects of a commercial breeding strategy for red alder in British Columbia are discussed in Chapter 7. While the previous section is mainly concerned with experimental breeding based on seedling evaluation, this chapter draws conclusions regarding commercial tree improvement of red alder. Important findings from all previous sections including the literature review are summarized, and recommendations for red alder management in British Columbia are made.

Chapter 2. Literature review

Red alder's potential for soil amelioration, nurse tree, fire protection and wood production have been described as early as the beginning of the century (Johnson 1917; Johnson et al. 1926) and its value as a forest tree has been emphasized ever since. Ecological and silvicultural research on red alder in the Pacific Northwest has been extensive (Trappe et al. 1968; Briggs et al. 1978; Hibbs et al. 1994), and the species has also been the object of research efforts overseas. Studies were conducted in France (du Cros et al. 1989; Hibbs et al. 1994), Scotland (Wheeler et al. 1986; McIver 1990), England (Moffat et al. 1989), and Norway (Erstad 1989). Trials have even been established in South Africa (Zwolinski 1988) and experimental mixed plantations with *Eucalyptus* and *Albizia* species were studied in Hawaii (Zou et al. 1995).

Undoubtedly, red alder owes much of its popularity as a research object to the fact that it is among the few forest trees in temperate climates that are able to symbiotically fix nitrogen. Red alder is in fact the model species for research on symbiotic relationships of plants with *Frankia* nitrogen fixing bacteria (Werner 1992). From there it has become a popular research object in forest ecology to study soil-nutrient relations and soil building processes in general. Silvicultural

implications, such as site amelioration and the use of fixed nitrogen by other plants have subsequently been studied by foresters. Many hundreds of papers on these topics are summarized in three major conference proceedings (Trappe et al. 1968; Briggs et al. 1979; Hibbs et al. 1994). Despite extensive knowledge about the species and its ecological and economic benefits, actual management for red alder has only started on a small scale in the mid 1990s, which led to the notion that red alder is a unique example in the history of forestry, where a wealth of biological and silvicultural information is available in advance of management (Tarrant et al. 1994).

The three compilations of knowledge about red alder ecology and management (Trappe et al. 1968, Briggs et al. 1979; Hibbs et al. 1994) focus on the region of the United States. This literature review has a focal relevance to red alder genetic resources management in British Columbia. The review is expanded to include recent research on biology and general aspects of red alder management since 1992, when the Hibbs et al. (1994) review was compiled. I will also allow a more detailed description than previous reviews on what is known with respect to red alder genetics and genetics of sympatric species.

2. 1. Red alder biology and silviculture

Effective genetic resource management depends to a large extent on the understanding of the species' biology. Reproductive biology of a forestry species determines the management and size of seed orchards, the viability of seed storage, the length of breeding cycles, the use of hybrids and clonal deployment. Ecological properties of a forestry species determine its suitability to be planted in open fields, to withstand pests and diseases, and cope with other stress factors. In the case of red alder, improved nitrogen fixation rates and an enhanced ability to ameliorate soils

could potentially be breeding objectives in a tree improvement program. After a short introduction of the species, I review biological and ecological properties of red alder relevant for genetic resources management.

2. 1. 1. Botany, taxonomy, and distribution

The genus *Alnus* belongs to the family Betulaceae which also contains birches (*Betula*). North American alders are divided into two subgenera which are morphologically distinct (Furrow 1979), and reproductively isolated (Bousquet et al. 1988; Bousquet and Lalonde 1991). The first subgenus (*Alnobetula*) is represented in North America by green alders. This complex (described as *Alnus viridis* (Vill.) Lam. & DC., *A. sinuata* (Regel) Rydb., *A. crispa* (Ait.) Turrit) covers the American continent north of 45° latitude from coast to coast with at least two hybridizing but genetically distinct subspecies (Bousquet et al. 1990). The other subgenus (*Glutinosae*) contains three North American species: white alder (*A. rhombifolia* Nutt.) in California, the complex of thinleaf alder (*A. tenuifolia* Nutt., *A. rugosa* (Du Roi) Spreng., *A. incana* (L.) Moench, *A. serrulata* (Ait.) Willd.) in the Rocky Mountains, and red alder on the west coast from southern California to Alaska (Figure 2.1.). Red alder overlaps in the most southern portion of its range with white alder and with its most northern populations (and outlying populations in Idaho) with thinleaf alder (Johnson 1968b). Red alder possibly hybridizes with both species to which it is closely related (Johnson 1968a; 1968b).

Red alder is the only American species of this genus that can grow into a fairly large tree. It can reach about 40 m height and 80 cm diameter and its maximum age is about 100 years. It has a smooth, thin bark, which is almost always covered with gray-whitish lichens. It has a shallow

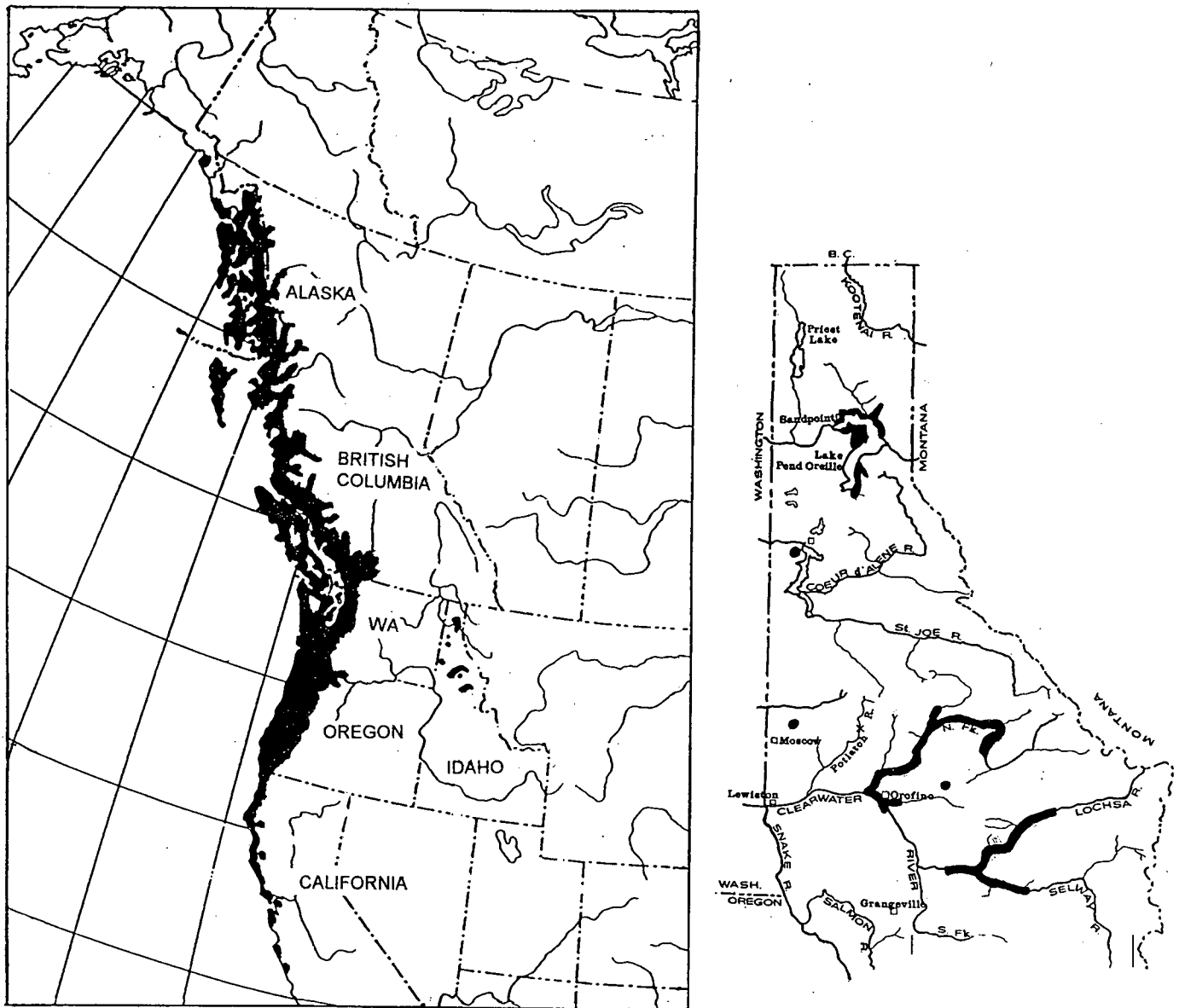


Figure 2. 1. Natural range of red alder in the Pacific Northwest (adapted from Harrington (1990)) and a more detailed map showing outlying populations in Idaho (adapted from Johnson (1968a)).

root system, but being a deciduous tree, wind throw is seldom a problem. Male and female flowers are clustered in separate catkins that are arranged in a single inflorescence with the female catkins in a distal position. What is usually referred to as “seeds” are actually winged nutlets, i.e. fruits. What is usually referred to as “cones” are the woody bracts of the female catkins (Harrington 1990). Compared to all other North American alders, red alder has relatively thick leaves, which are grayish underneath, with blunt toothed edges that tend to curl under. Red alder owes its species name to a substance in its inner bark that turns deep reddish-orange when exposed to air. Bark extracts have been used by native Americans of the Northwest to dye basket material, wood, wool, hair, and skin. Red alder bark also contains a salicylin, closely related to aspirin, and bark extractions have served as medical remedies for native Americans. Recently, several novel antibiotics with a remarkably broad spectrum against otherwise resistant pathogens, an active compound against tuberculosis, fungicides, and other pharmaceutical compounds were discovered in bark and catkins of red alder (McCutcheon et al. 1992, 1994, 1997; Saxena et al. 1995; Chen et al. 1998).

2. 1. 2. Ecology and life history

Red alder experiences a wide range of environmental conditions over its distribution from 32°N to 68°N along the Pacific coast. Its natural range is usually confined to within 200 km of the ocean and to elevations below 700 m, with a humid coastal climate characterized by cool wet winters and warm summers. Red alder occurs over a wide variety of soil types ranging from well-drained gravel and sands to poorly drained clay and organic soils. Good growth, however, is limited to a relatively narrow range of site conditions. Red alder performs poorly on older, highly weathered soils with a low pH and leached horizons. The best red alder stands occur on alluvial

soils of flood plains or upland sedimentary or volcanic soils. (Harrington 1986; Haeusler and Coates 1986). Red alder tolerates occasional flooding and restricted drainage. Its range seems to be limited by 600 mm/year of precipitation and most stands receive an excess of 1000 mm/year. In dry interior valleys, in the most southern portion of its range, and in outlying populations in Idaho, red alder is restricted to riparian forests.

Red alder occurs typically in riparian communities in pure stands or together with cottonwood (*Populus trichocarpa* Torr. & Gray), bigleaf maple (*Acer macrophyllum* Pursh), western redcedar (*Thuja plicata* Donn ex D. Don), or redwood (*Sequoia sempervirens* (D. Don) Endl.). The species, however, is not confined to waterlogged habitats, but is a natural component of upland coniferous forests dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), grand fir (*Abies grandis* (Dougl. ex D. Don) Lindl.), Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and western redcedar (Hall 1984; Holstein 1984).

Ecologically, red alder is a pioneer species with low shade tolerance, rapid juvenile growth rates, precocious and abundant reproduction, and a short life span. In conifer forests trees only become established in forest openings created from disturbance, due to the intolerance of red alder to shading. On upland sites red alder is rarely found in larger stands, but is scattered as individual trees or in small clumps (Franklin 1968, 1979; Haeusler et al. 1995). When coniferous forests are disturbed on a large scale, red alder has proven to be aggressive colonizer of upland sites. Particularly after logging it forms pure even aged stands with a dense shrub undergrowth. Widespread human disturbance in southern British Columbia, Washington and Oregon has created habitat to make red alder the most abundant hardwood in the Pacific Northwest. After oldgrowth forests were logged in the 1930's to 1950's, naturally regenerated stands of red alder make up a significant proportion of commercially available timber today. Historically population sizes were much smaller, mostly restricted to wet areas, and ephemeral in upland habitats.

2. 1. 3. Special properties

Nitrogen fixation

Alders are capable of forming an endosymbiotic relationship with nitrogen fixing bacteria of the genus *Frankia*. Although nitrogen fixing symbioses with trees are widespread in the tropics, only two genera of trees, *Alnus* and *Robinia* contribute to nitrogen fixation in temperate regions.

Frankia species are filamentous actinobacteria, which can form root nodules with trees from 24 genera and eight different families, while *Rhizobium* only infects Fabales and one genus of Ulmaceae (Brewbaker 1990; Wheeler 1991). Accumulation of soil nitrogen in pure red alder stands was found to be between 50 and 350 kg per hectare and year (Haeussler and Coates 1986), resulting in concentrations of 500 to 7500 kg per hectare in mature red alder stands (Bormann et al. 1994). Red alder is thought to be responsible for the large accumulations of nitrogen in coastal forests, and is a main source of nitrogen for other plants (Swanston and Myrold 1997). Its litter contains significant amounts of nitrogen and decomposes rapidly, forming a deep humus layer. Soil carbon in pure or mixed alder stands is largely increased compared to coniferous stands (Cole et al. 1995). For these ecological functions the species is deemed essential for the long term productivity and health of Pacific Northwest ecosystems (Bormann et al. 1994).

Because of red alder's ability to symbiotically fix nitrogen, it has been proposed that this species be grown in a mix or in alternative rotation with conifers (DeBell 1979; Miller and Murrey 1979; Comeau et al. 1995, 1996). Conifers planted after a rotation of red alder were shown to have increased growth rates compared to conifers following conifers (Atkinson and Hamilton. 1978). Mixed plantations with conifers have also been proposed, and the substantial effects of nitrogen fertilization on other plants to a distance of 15 m was demonstrated by Miller and Murray (1978) and Miller et al. (1993). However, due to its rapid initial growth red alder has a competitive edge

over conifers, and to avoid entirely suppressing conifers requires wide spacing of red alder. At low densities, however, live branches may be retained on red alder far longer than is desirable for quality saw log production (Comeau et al. 1996). Comeau and Sachs (1992) simulated various mixed plantations and suggested that the problem could be overcome by planting Douglas-fir five years before establishing red alder. Pure and mixed red alder and cottonwood biomass plantations were evaluated by Radwan and DeBell (1988). The choice between pure cottonwood and pure alder was determined by the nutritional status of the soil. Mixed plantations resulted in increased growth rates of poplars and decreased performance of red alder.

Soil building

Red alder also enhances soil properties other than nitrogen content. The general view is that nitrogen-rich litter of red alder improves turnover rates of litter from other species, particularly conifers, resulting in increased availability of most macronutrients. In contrast, Bormann et al. (1994) reported nutrient leaching under red alder stands, which was interpreted as an effect of acidification, a byproduct of the nitrogen fixation reaction. This acidification, however, also speeds mineral weathering and thus soil building. Bormann et al. (1994) concluded that deep weathered soils or nitrogen rich soils could be degraded by red alder, while young alluvial soils will be enhanced most effectively. The notion that the effectiveness of red alder for soil amelioration is context dependent was confirmed by two other studies. Giardina et al. (1995) reviewed effects of red alder on soil pH and phosphorous availability, and found that alder always has beneficial effects as a component in coniferous forests, but in pure alder stands it may degrade site quality. Compton et al. (1997) conducted a thorough study with control plots that did not contain red alder and observations over two rotations. While the first rotation of red alder had largely positive effects, a second rotation of red alder degraded the site with respect to most macro nutrients.

Other properties

Alternative rotation schemes with red alder and conifers were suggested for a second benefit in areas infected with laminated root rot fungus (*Phellinus weirii*) that affects most conifers. Red alder could be grown in pure stands to reduce the presence of the pathogen, since hardwoods are immune to this disease (Nelson et al. 1978).

Diseases that affect alder are root rot (*Armillaria* spp., *Heterobasidion* sp.), alder bark disease (*Didymosphaeria* sp.), trunk rot (*Fomes* sp., *Fomitopsis* sp., *Phellinus* spp. [not *weirii*], *Stereum* sp.) and cankers (*Nectaria* sp., *Hypoxylon* sp.), but overall decay is a minor problem. Allen (1993) showed that trees harvested at 60 to 80 years would have under 3.5% decay losses, less than most other hardwoods. Insect pests include tent caterpillars (*Malacosoma* spp.), leaf beetles (*Altica* sp., *Pyrhalta* sp.), and alder sawflies (*Eriocampa* sp, *Hemichroa* sp.). There is no pest that causes significant problems. Especially younger trees are fairly free from insect problems or recover quickly from defoliation (Harrington 1990; Markham 1996; Markham and Chanway 1998).

The deciduous canopy and the relatively low leaf area index allows high levels of understory vegetation in forests dominated by red alder (Hanley and Hoel 1996). This in turn supports a remarkably diverse wildlife community when compared to coniferous forests (McComb 1994; Wipfli 1997). In winter, red alder is an important food source for wildlife. Bark, twigs, and buds are eaten by deer, elk, and beaver, while "seeds" are consumed by small rodents and songbirds (Martin 1951; McComb 1994; Peterson 1996).

Due to fast decomposition of fallen twigs and leaves, red alder stands lack flammable understory debris, and the foliage does not carry fire well. Therefore, fire hazard is generally low and stands of red alder may be considered natural fire breaks (Worthington et al. 1962).

2. 1. 4. Reproduction and propagation

Natural regeneration

Red alder is a vigorous seed producer, and has a reputation as a forest weed. Management of red alder for most of this century was restricted to eradication of red alder in order to promote the growth of conifers. Particularly in British Columbia red alder chemical or biological eradication is the only form of management and remains an area of active research (Sieber et al. 1990; Figueroa 1991; Wall 1994; Dorworth 1995; Knowe et al. 1995; Dorworth et al. 1996). It should be noted that the development and use of biological agents for eradication of red alder could potentially be a threat to red alder plantation forestry.

Despite its reputation of growing everywhere where it is not wanted, natural regeneration is inadequate in many cases. It has been pointed out that red alder often fails to establish under the most favorable site conditions (Harrington 1990; Harrington et al. 1994; Haeussler et al. 1995). The problem is that red alder seed are very small and susceptible to desiccation and any competing vegetation. For successful development into a seedling they require optimal conditions involving many factors (Elliott and Tailor 1981a, 1981b). This results in erratic regeneration success and uneven distributions. Natural regeneration is therefore restricted to a much narrower range of conditions than for successful plantings.

Seed collection, handling, and storage

To obtain planting stock, guidelines for collection, extraction and storage of seed are available (Kenady 1978; Owens and Blake 1985; Hibbs and Ager 1989; Ager et al. 1994). Flowering generally occurs during March depending on latitude and climate. After fertilization, female catkins develop into woody catkins that contain 100 to 300 winged seeds. Catkins can be

harvested in early fall, before seeds start to shed. Seeds can be extracted by thrashing the catkins in a tumbler or by hand for small quantities after the catkins have been dried for several days at room temperature. Seeds can be stored at 2-4 °C for up to 1 year (Haeusler and Coates 1986), and at -15 °C for at least 10 years. Red alder produces peak crops about every four years with moderate to light crops in between (Kenady 1978). Given a success rate of germination and growth into a suitable seedling of 50%, 1000 catkins would be enough to plant 1 ha, which could easily be obtained from a few small branches of a mature tree.

Nursery production of planting stock

Large, high quality red alder seedlings can be produced in approximately one half growing season. Because of red alder's rapid growth, production of planting stock of the right size requires careful timing. Germination does not require any stratification but light exposure is necessary, and presoaking of seeds over night may enhance germination rates (Elliott and Taylor 1981a; Bormann 1983; Berry and Torrey 1985; Haeussler and Tappeiner 1993; Ager et al. 1994). Seeds are usually sown on the surface of a peat based potting mixture that must be kept moist at all times, preferably with a mist system (Berry and Torrey 1985). Germination rates are usually good but can be as low as 10% due to empty seed (Radwan and DeBell 1981). For this reason, seedlings are usually germinated at high densities and then shortly after germination hand-transplanted to produce containerized planting stock (Stowers and Smith 1985; Radwan et al. 1992; Ahrens 1994). For optimal health and growth of seedlings, they must be inoculated with *Frankia* from root nodules of mature trees (Sheppard et al. 1988; Wheeler et al. 1991). Inoculation methods are described by Stowers and Smith (1985) and Crannell et al. (1994).

Vegetative propagation

Plants may not be directly established by cuttings as is possible for poplars and willow. Stem sprouting after coppicing is infrequent beyond three years of age. Sprouting depends mainly on

the length of the remaining stump, age, and timing of cut (Harrington 1984; Bancroft et al. 1990). Monaco et al. (1980) found that rooting requires hormone treatment and an extended period in a warm greenhouse environment in order to achieve a reasonable rooting success. Also Radwan et al. (1989) found that rootability of red alder cuttings is largely dependent on the age of the ortet and normally requires a special rooting environment and hormone treatment. He concludes, however, that a vegetative propagation system by rooted cuttings is feasible to propagate superior genotypes for intensively managed plantation forestry. A commercial system for micropropagation was developed for red alder by Perinet and Tremblay (1987).

2. 1. 5. Plantation establishment and tending

Large, high quality red alder seedlings are not very susceptible to environmental stress, and rapid growth permits escape from competing vegetation and damage from browsing (Newton and Cole 1994). The results of Nelder plot experiments suggest that red alder should be planted at 2.5×2.5 m spacing to avoid either high early mortality or poor form. Wider spacing results in undesirable large branches (Knowe and Hibbs 1996) and reduced initial height growth, since alders are among the few species that respond with increased height growth to early competition (Hibbs et al. 1989) (more details on response to thinning in section: 2. 2. 2. Growth and yield).

Control of spacing for red alder in a sawtimber regime is also a mandatory silvicultural treatment for another reason. Mortality associated with close initial spacing results in lean and sweep of surviving trees that grow into the free crown positions. Red alder is capable of considerable deformation to seek higher light environments, and this is a major reason for reduced quality of red alder logs in natural stands (Ahrens et al. 1992). High value stands can only be achieved

through careful thinning or planting for better control over spacing and uniformity of establishment (Bormann 1985).

2. 1. 6. Implications for tree improvement

Red alder is certainly a natural candidate for intensive forestry management. Being a pioneer species that survives open field conditions and naturally occurs in pure stands, it can be expected to be a relatively unproblematic candidate for plantation forestry regarding survival, growth, and resistance to pests and diseases. Where intensive plantation forestry is warranted, genetic resource management and genetic improvement should be complementary to silvicultural prescriptions.

Large improvements in the quality of red alder stands can be expected from the use of artificial regeneration alone. Control over spacing at plantation establishment will reduce lean and sweep which are common in natural stands. The use of larger seedlings will allow stand establishment under a wide range of environmental conditions, and avoid the patchy distribution of alder regularly found in natural stands.

Breeding cycles could be as short as four years, and they are likely to be determined by the time it requires to obtain reliable progeny test results, rather than by the species reproductive biology. Production of large numbers of seeds and seedlings will require only minimal seed orchard facilities because even young trees are vigorous seed producers.

Nursery techniques for mass production of seedlings are not available and need to be developed. There are also limited opportunities for vegetative propagation, and simple coppice systems for biomass production such as those used for black cottonwood can probably not be developed for red alder. A rooted cutting propagation system for bulking up elite genotypes for deployment of clones in production plantation appears to be technically feasible.

Red alder is a very valuable species for reforestation on special sites where it outperforms any other species (Dale 1989; Erstad 1989; Moffat et al. 1989; Heilman 1990a, 1990b). A possible objective for a tree breeding program could be the improvement of traits in red alder that are responsible for site amelioration or survival on special sites. Examples are nitrogen fixation rates, nutrient content of litter, survival and growth under extreme site conditions.

2. 2. Economic aspects

Before launching a tree improvement program, the economic viability of such an effort should be examined. In this section I investigate the development of market demand and prices for red alder wood products over the last 20 years, and compare it to the major softwood species harvested in British Columbia. I also compare yield expectations for red alder wood products under different silvicultural systems with softwood species. Further, problems and potentials for red alder utilization in British Columbia are identified based on resource inventory and harvest data for red alder. Finally I discuss whether tree improvement of red alder can effectively contribute to the value of this species for forestry in British Columbia, and which breeding objectives should be pursued based on economic considerations.

2. 2. 1. Value of red alder products

Red alder wood has a fine even texture, darkens to a reddish color, and has no distinction between heart and sapwood. It has a moderate density, dries without warping and seldom splits. It is easy to work, to glue, sands and polishes easily, and stains readily (Atterbury 1978; Leney et al. 1978). These properties and particularly its uniformity have made it popular for furniture manufacturing, carving, cabinetry, paneling, and musical instruments (Resch 1988). Red alder lumber is not used for construction because it is not rot resistant. Trees less than 20 cm dbh are generally chipped for pulp or cut for fuelwood. The value of alder wood chips is less than wood chips from most other hardwoods, because a smaller volume of pulp can be obtained from the same amount of solid wood equivalent (Massie et al. 1994).

Strong and consistent markets have developed for red alder saw timber in North America and overseas. High grade logs in natural stands make up a significant proportion of harvests from natural stands in Oregon and Washington (Plank and Willits 1994), and red alder's popularity today is mainly due to its abundance and low price on commodity markets in the United States during the past 20 years (Little 1978). The most common log sizes (30 to 45 cm) had half the value of softwood logs in the 1970s. Now they are second in value only to Douglas-fir (Figure 2.2.). Since volume recovery at the sawmill is generally lower in red alder than in conifers, there is a dramatic increase in log value as the diameter increases (Plank et al. 1990). Logs of 45 cm and above of red alder are comparable in value to similar sized Douglas-fir logs (Willits et al. 1990; Plank et al. 1990). Warren (1994, cited in Daniels 1995) even reports prices of US\$ 1600 for alder compared to US\$ 1000 for Douglas-fir premium grade logs per 1000 boardfeet. These prices are partly due to over-utilization of good quality red alder stands and shortages in the supply of premium alder saw logs. In the recent past, prices of good quality red alder logs have

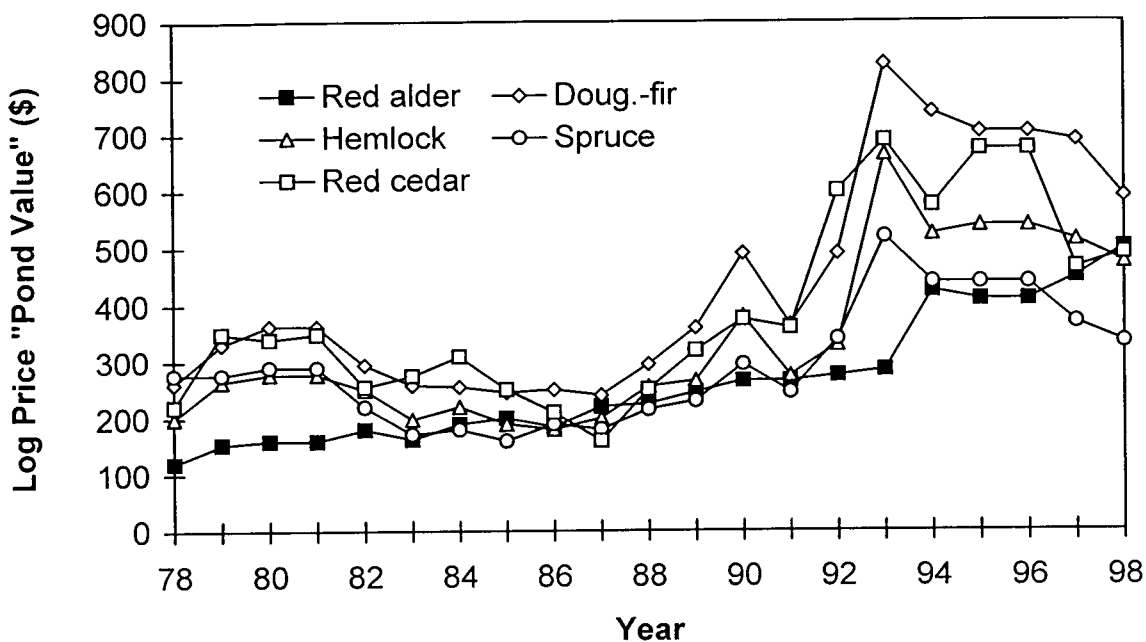


Figure 2. 2. Price development of red alder saw timber quality logs over the past two decades compared to softwood species (data from Oregon Ministry of Forests (1999))

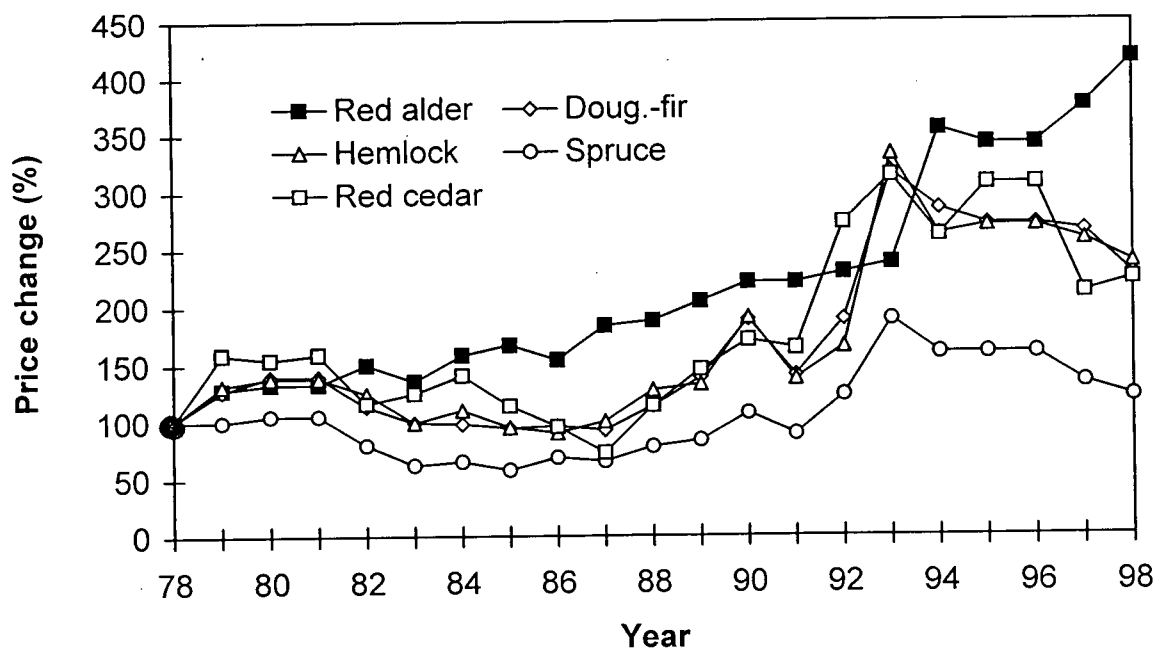


Figure 2. 3. Change of red alder log prices over the past two decades compared to changes in log prices of softwood species (data from Oregon Ministry of Forests (1999)).

increased dramatically, when compared to price development of other major saw timbers (Figure 2.3.).

In contrast, red alder chips are less valuable than chips from most other hard and softwoods. Average pulp prices for the period 1987 to 1991 were US\$ 196, 203, and 228 for 1 m³ solid wood equivalent of red alder, aspen and cottonwood chips, respectively (Massie et al. 1994). Alder wood chips and pulp are readily accepted in markets of the United States and Japan, but they have to compete with products from low cost biomass production systems on the world market. Red alder products are not used by pulpmills or papermills in British Columbia (Peterson 1996).

2. 2. 2. Growth and yield

Red alder's initial growth is rapid and height growth during the first 20 years is about 1 m per year under average site conditions in British Columbia. Thereafter it is typically 0.5 m per year until the age of 50 years (Smith 1968). Site index curves for British Columbia were developed by Mitchell (1988) and Thrower and Nussbaum (1991). Similar work for the United States was conducted by Harrington and Curtis (1986) and Harrington (1986). Compared to softwoods, rotations of alder in British Columbia will be considerably shorter. Peak mean annual increment (MAI) for volume at median site indices for the Vancouver Forest Region occurs at less than half the age for red alder than for softwoods (Table 2.1.). Rotation at maximum MAI for volume, however, is different from rotation at maximum value for sawtimber. A high log grade requires dimensions of approximately 30 cm DBH and 30 m height, which will be reached in natural stands at 40 to 60 years for median site conditions in British Columbia (Table 2.2.). This is not

Table 2. 1. Yield at peak mean annual increment (MAI) for median site indices for species in the Vancouver forest region (Peterson 1996). Median site indices are: red alder, 27; Douglas-fir, 30; western hemlock, 26; Sitka spruce, 29; western redcedar, 18 (Green and Klinka 1994).

Species	Yield [m ³ ha ⁻¹]	Age [yr]	MAI [m ³ ha ⁻¹ yr ⁻¹]	Height [m]	DBH [cm]
Red alder	210	25	8.5	20	19
Black cottonwood	260	25	10.4	26	27
Douglas-fir	594	70	8.5	28	30
Western hemlock	607	65	9.3	28	29
Sitka spruce	544	55	9.9	33	29
Western redcedar	519	100	5.2	28	25

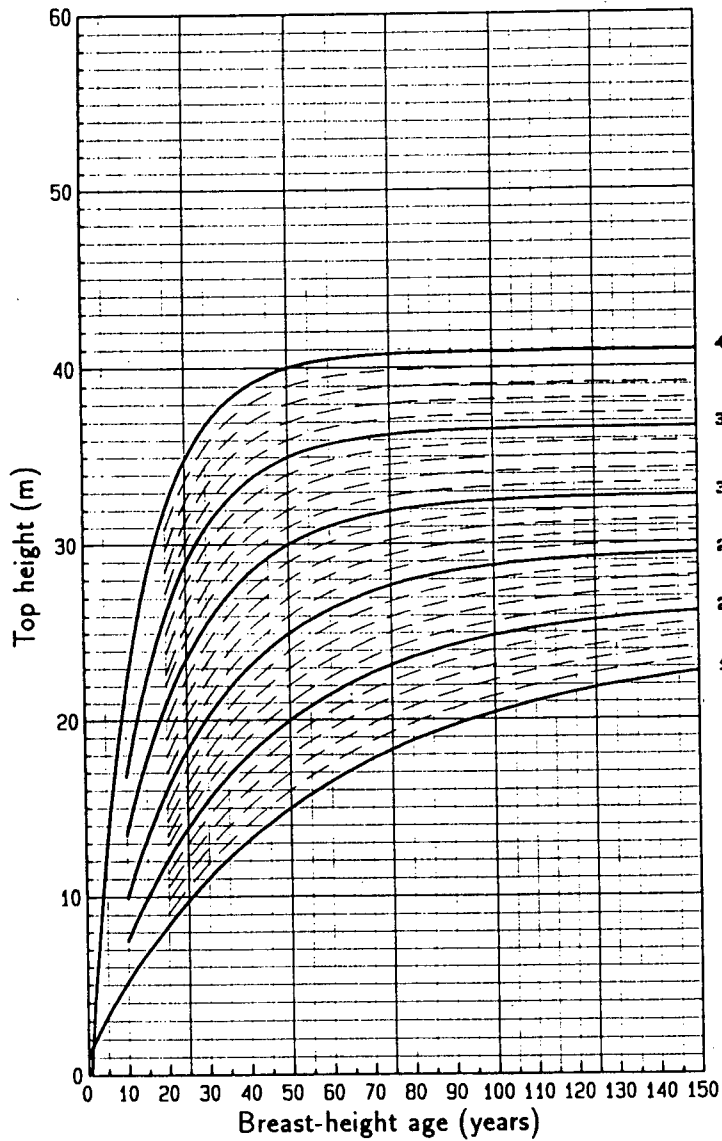
Table 2. 2. Yield of red alder at rotation at age for different site qualities in the Vancouver forest region (Peterson 1996).

Site	Objective	Yield [m ³ ha ⁻¹]	Age [yr]	MAI [m ³ ha ⁻¹ yr ⁻¹]	Height [m]	DBH [cm]
Poor	Max. MAI	204	40	5.1	18	19
Med.	Max. MAI	220	30	7.3	20	21
Fair	Max. MAI	211	20	10.6	19	20
Good	Max. MAI	228	15	15.2	21	22
Poor	Max. value	345	85	4.1	29	28
Med.	Max. value	350	60	5.9	30	29
Fair	Max. value	360	40	9.1	31	30
Good	Max. value	355	25	14.2	30	29

much different from the time Douglas-fir, hemlock, or Sitka spruce require to reach sawtimber dimensions (Table 2.1). However, growth rates in alder will respond more than conifer species to above average site conditions shortening sawtimber rotations to 25 years for good sites in the Vancouver forest region (Table 2.2.). Assuming that site quality factors for red alder and conifers are largely the same as indicated by the work of Harrington (1986) and Harrington and Courtin (1994), site index curves (Figure 2. 4.) imply that growth on poor sites is comparable to conifers. Rotation lengths for alder sawtimber are only reduced due to rapid juvenile growth under above average site conditions.

Relatively long rotations of 40 to 60 years in natural stands on median sites are mainly due to competition. Thinning will drastically increase growth rates and shorten rotation length. Zacharos (1980), Paltzat (1984), Harry et al. (1984), Hibbs (1987), Hibbs et al. (1989, 1995), and Puettmann et al. (1993) studied the response of red alder to different spacing and developed guidelines for tending red alder stands. Stands thinned within the first 20 years attained saw log size (30 cm) around age 30 or earlier, while it would take 45 years on average in unthinned natural stands. Knowe et al. (1997) and Knowe and Hibbs (1996) developed models to predict saw timber yield as a function of stand density and thinning. Their results indicate maximal value for sawtimber volume at rotations between 23 and 35 years. Rotation age for fiber production under controlled spacing could be around 10 years (Zavitkovski and Stevens 1972; DeBell et al. 1978; DeBell and Turpin 1983). These studies suggests that rotations of red alder are shorter than for any other species in the Pacific Northwest, except for biomass production systems with black cottonwood.

Coastal Red Alder



Coastal Douglas-fir

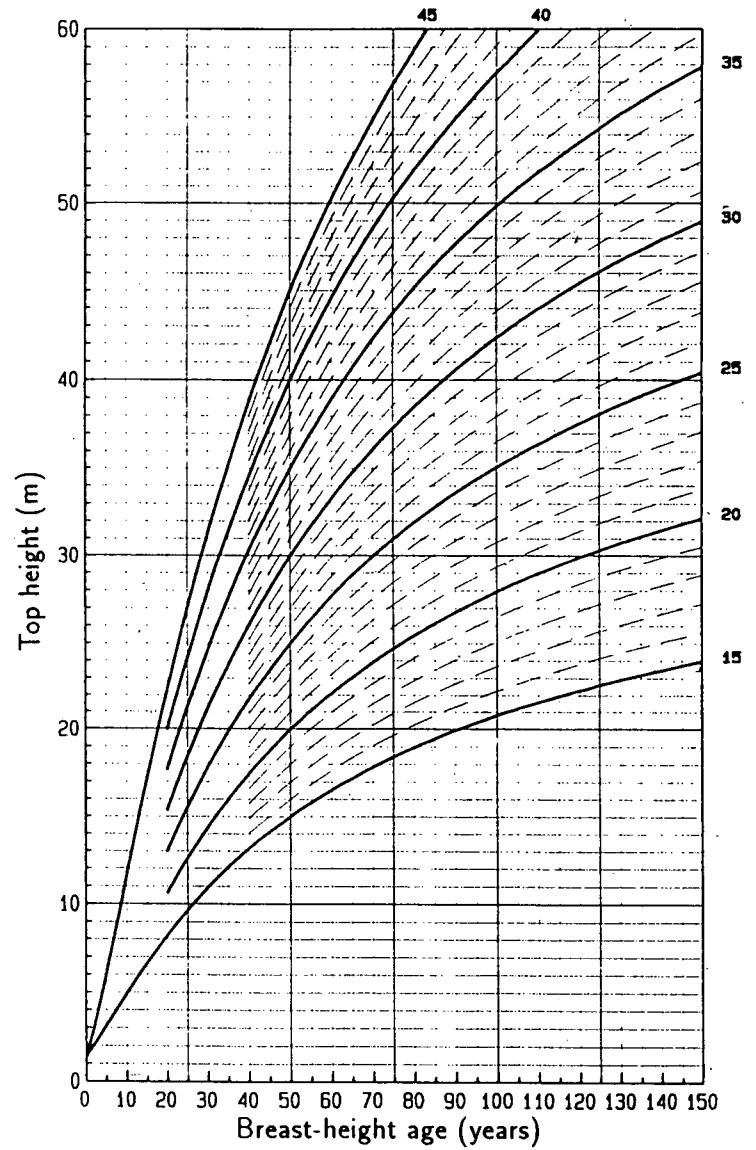


Figure 2. 4. Site index curves for red alder and Douglas-fir, the latter representative of most other conifers in coastal British Columbia (From: Thrower and Nussbaum 1991).

2. 2. 3. Resource utilization in British Columbia

About 14% of North America's red alder volume is found coastal British Columbia (Peterson 1996). Within British Columbia, the most significant volumes of red alder are in the Vancouver Forest Region, particularly in the area of the Georgia depression (Figure 2. 5.). In surveys conducted by Nielson (1977), McPherson (1980), and Massie (1990), volume in stands dominated by mature red alder in British Columbia were estimated at about 13 million m³, much of it on private lands (Figure 2. 6.). There were approximately 5 million ha of crownland and 4 million ha of private land, where red alder constitutes the main proportion of harvestable timber. Most of the northern resource (approximately 3 million m³) was on crown lands, while half of red alder in the region of the Georgia depression (approximately 10 million m³) was on private lands. The proportion of high quality stands of red alder is small throughout British Columbia. Only 10% of the stands could be harvested for quality sawtimber (Figure 2. 5.). Of these, a significant proportion occurs in riparian habitats which are off-limits for timber harvesting on crown lands.

Although the theoretical annual allowable cut for red alder was approximately 300,000 m³, only 10,000 to 70,000 m³ were harvested per year in the 1970's and 1980's (Peterson 1996). Only two companies in British Columbia held licenses to harvest up to 60,000 m³ of red alder each throughout the 1990's (Massie 1990). One company processed red alder into sawtimber and chips, another into veneer and chips. Alder sawtimber and veneer were sold green to the United States while chips were exported to Japan. The total harvest of hardwood logs in coastal British Columbia amounts to less than 0.1% of the harvested volume of conifers (Nilsson 1985, Simons 1993).

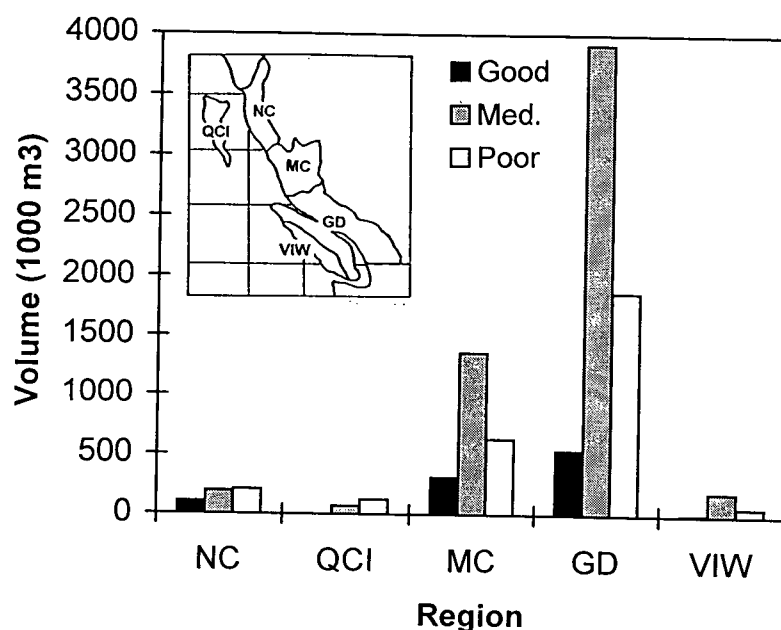


Figure 2. 5. Quality of stands in British Columbia by regions (data from Massie (1996) summarized by the following regions: NC, North Coast; MC, Mid Coast; GD, Georgia Depression; QCI, Queen Charlotte Islands; VIW, Vancouver Island Westcoast).

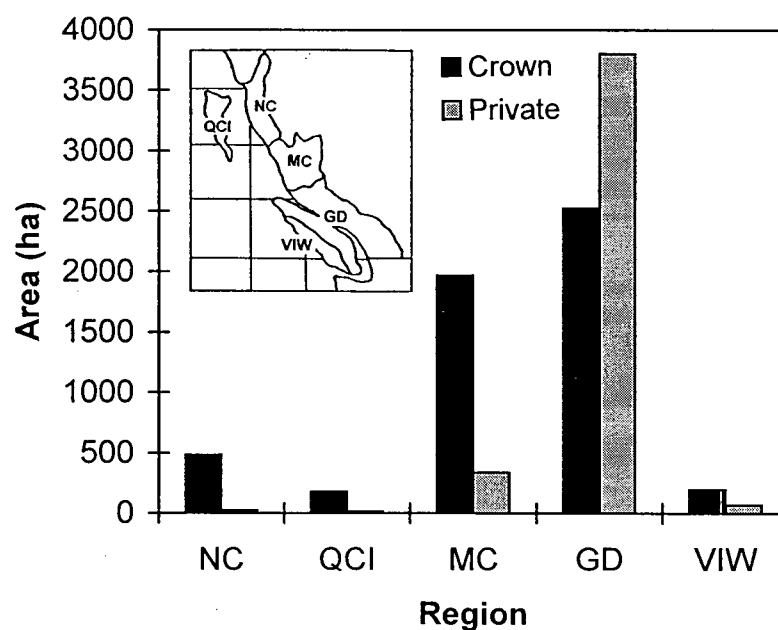


Figure 2. 6. Ownership of stands in British Columbia (data from Massie (1996) summarized by the following regions: NC, North Coast; MC, Mid Coast; GD, Georgia Depression; QCI, Queen Charlotte Islands; VIW, Vancouver Island Westcoast).

2. 2. 5. Implications for tree improvement

Red alder has always been a neglected resource in British Columbia, and although it has firmly established itself on international markets the species is still not used much in British Columbia. The reason is the low quality of the majority of existing stands, and the location of good stands in riparian habitats that are off-limits to harvesting. The low price of chips and pulp does not warrant investments necessary for harvesting medium and poor quality stands, and the low proportion of high quality saw logs in natural stands in British Columbia (unlike in Washington or Oregon) prevents their commercial harvest despite the market value of red alder products in the United States and overseas. If red alder is to become a significant forestry species in British Columbia, there is an obvious need to develop a forestry system aiming at high quality red alder saw logs production.

Growth and yield of red alder implies that a product equal or greater in value than any softwood currently managed in British Columbia can be produced in considerably shorter time. One major goal of a tree improvement program would be to shorten the rotation even further. In order to exploit the full early growth potential of red alder, it must be grown on fair to good sites (site index 27₅₀ or better). Contradicting the notion that alder should be grown on sites too poor for conifers, site index curves indicate that red alder loses its wide margin in profitability compared to softwoods on poor sites. Breeding populations should therefore consist of genotypes selected for above average site conditions.

It has been pointed out by Massie et al. (1994) and Daniels (1995) that a tree improvement program aiming at fiber production for red alder is unlikely to be economically viable. A biomass production system for red alder would have to compete with other short fiber species on world

markets, where strong competition exists through low cost silvicultural systems with fast growing species. Local competition also exists through efficient coppice systems with black cottonwood. Cottonwood grows slightly faster, aggressive tree improvement programs are already in place, and its pulp is more valuable than alder pulp.

A breeding program for red alder could focus instead on short rotation quality sawtimber production. Given the market demand for high-grade alder logs, tree improvement efforts should include quality-related traits such as stem form, sweep and lean, branch number, and size, epicormic branching, and wood properties. Cultural measures such as control of spacing at plantation establishment and thinning will also enhance growth rates and quality of stands. Assuming moderate genetic gains in growth and form from selection, rotations for high quality sawtimber production could be as low as 25 years, and this appears to be a reasonably profitable option for forestry in British Columbia.

2. 3. Genetic resource management

Whether the above breeding objectives can actually be realized depends on the genetic control of the traits involved. Also, genetic resource management at the level of regulating seed transfer will only be necessary if the genetic variation over the area of interest is substantial. In the following section I review what is known about red alder's variability in growth and adaptive traits. Then I will discuss implications for seed procurement and tree improvement in the context of approaches for applied genetics programs taken for sympatric conifer species in the Pacific Northwest and hardwoods elsewhere.

2. 3. 1. Genetic variability in red alder

Geographic variation in red alder was demonstrated by a small provenance test established in 1968 by the U. S. Forest Service in Washington. This trial includes 10 sources from Alaska to California, including a population from Idaho (Lester and DeBell 1989). A similar trial, also without family structure, was established with 15 sources in Britain in 1983 (Cannell et al. 1987). Also in 1983, a combined provenance progeny test with 120 half-sib families from four river drainages in Washington was laid out (Ager 1987). A second experiment using the same seed sources was established in France in 1984 (Hibbs et al. 1994). More recently in 1992, a provenance trial covering the natural range of the species in British Columbia with 68 sources and 316 half-sib families was established by the Ministry of Forests (Xie and Ying 1994). The review draws on results from these five common garden experiments, as well as on several progeny trials using seedlings.

Vegetative phenology

Red alder is one of the first deciduous trees to loose its leaves, the majority of leaves falling during October (Fowells 1965; Campbell and Franklin 1979). Ager (1987) and Ager et al. (1993) studied the genetic variation in red alder related to native climate. They evaluated a provenance/progeny trial of 30 trees x 2 half-sib families x 15 stands x 4 Washington provenances (total of 3600 trees; populations were sampled along 4 rivers from river mouth to highest elevation). Leaf abscission and bud break provided measures for growth rhythm. Overall performance was evaluated with respect to above ground biomass. Significant variation was observed for all traits at all levels of the sampling design. Variation within populations, however, was rather small, which was attributed to reduced effective population size in colonizing species. Bud break could be correlated with spring thermal sums, and leaf abscission with fall frost dates

of the source locations, suggesting that provenances regulate their growth rhythm based on different environmental cues.

In a similar trial for B. C. Provenances at Surrey, Xie et al. (1994) obtained comparable results. 65 Provenances x 5 families x 20 trees were evaluated for leaf abscission, bud break and growth at the end of the second growing season. Genetic variability was substantial in all traits both within and among provenances. Southern and low elevation provenances demonstrated earlier bud break, later leaf abscission and better growth rates.

Winter dormancy and frost hardiness of 15 red alder sources growing in Scotland were examined by Cannell et al. (1987). Detached shoots were regularly subjected to freezing tests throughout the year and also bud set and bud burst were recorded in weekly intervals during fall and spring. From their findings they conclude that hardening was triggered by shortening day length and not by fall frost. 70% of all variation of all measured traits were attributed to latitude. Hardening occurred about 2 days earlier for each degree latitude north, excluding the Idaho province. Dehardening and bud burst occurred rather simultaneously for all provenances.

Frost hardiness

Seedlings from 20 B. C. provenances x 5 families x 4 seedlings were evaluated by Sawada (1994) for frost hardiness in a laboratory experiment (freeze induced electrolyte leakage). Variation in frost hardiness was significantly different between provenances and families. Variation could be attributed to latitude, longitude and elevation. Latitude accounted for most of the variation among provenances (72 %) with the hardest provenances originating from the highest latitudes.

An 8-year-old provenance trial with 10 sources of red alder from Alaska, B. C., Washington, Oregon and Idaho was examined by DeBell et al. (1978). Severe frost damage on one planting site allowed evaluation of hardiness (Peeler and DeBell 1987). Frost hardiness and growth were inversely related. Alaska and Idaho provenances were hardiest, Washington and Oregon provenances grew fastest.

Drought resistance

Although red alder does not usually experience drought in its coastal habitats, some populations may have evolved to survive in climates with low summer rainfall. Shainski et al. (1994) reports stomatal control as a key feature that allows the species to grow on upland sites. In a provenance test with British Columbia sources Dang et al. (1994) measured ecophysiological parameters related to drought resistance, such as stomatal control, water use efficiency and transpiration rate. Water use efficiency and transpiration rate were significantly different at the provenance and at the family level. However they found very little stomatal control in British Columbia seed sources and concluded that none of the populations sampled are adapted to drought conditions.

Nitrogen fixation capacity

Genetic variation in nitrogen fixation capacity and biomass production was demonstrated by Monaco et al. (1981) among half-sib families from provenances in western Oregon. Ten seedlings x 2 families x 5 provenances were evaluated at age 5 months for N content (Kjeldahl), nitrogenase activity (acetylene reduction method), and total biomass. They found that provenances from poor sites had higher N fixation rates and performed better than provenances from good sites under greenhouse conditions with limited N supply. They also demonstrated that nitrogenase activity decreased with experimental increase of available nitrogen over all provenances and families.

Sensitivity to waterlogging

In a provenance trial on partly waterlogged soils, Hook et al. (1987) showed, that height growth can be strongly affected by water logging in some families but not in others. The most sensitive families showed more than 50 % reduction in height as the water table approaches the surface, while the most tolerant families showed no significant changes. Water logging tolerance could not be clearly related to site conditions of the seed source. Hook et al. (1987) suggests that nodulation of red alder roots could be reduced by soil water logging or by decreasing aeration in general. Family variation was not investigated, but it seems possible that reduced growth from waterlogging is partially due to decreased nitrogen fixation capacity. A study with seedlings, however, suggested that tolerance to water-logging depends mainly on the capability to develop adventitious roots, that grew on top of the saturated soil surface (Harrington 1994). This may be an important adaptive trait on flood plain sites.

Growth traits

A large proportion of variability among provenances in growth traits is determined by the length of the growing season. In the provenance test established by Ager, Washington sources from temperate coastal climate with longer growing seasons performed best regarding above ground biomass production (Ager et al. 1993). Low elevation coastal sources also performed best in the provenance trial with British Columbia seed sources (Xie et al. 1994). In the common garden experiments covering the entire range of the species, Oregon and Washington sources grew better than more southern or northern provenances. Outlying populations in Idaho and Alaska had the lowest growth rates.

Based on material from a thinning treatment in Ager's trial, Hook et al. (1990) investigated variation in growth traits and biomass partitioning among 36 half-sib families from Washington

sources below 300 m elevation. They estimated heritabilities ranging from 0 to 0.39 for growth traits like height, diameter and biomass. Heritabilities for dry weight partitioning were rather high ranging from 0.39 to 0.63. However, when this study was repeated four years later, traits for biomass partitioning were also found to be so low that selection would not be warranted (Ager and Stettler 1994). Standard errors of the estimates of genetic parameters are not provided in either study, but the relatively small sample size (a total of 360 trees) suggests that they might be large.

In an investigation of wood specific gravity, Harrington and DeBell (1980) did not find significant differences among provenances. Another study conducted in France by Radi and Hibbs (cited in Ager and Stettler 1994) confirms that differences in wood specific gravity are small and not statistically significant.

2. 3. 2. Seed procurement

The choice of seed sources for reforestation is a critical decision to ensure a successful crop. Using inappropriate seed sources can result in maladapted tree populations low in vigor and prone to pests and injury due to climatic abnormalities. Seed zones and seed transfer guidelines are essential tools to minimize the risks of maladaptation through moving seed or vegetative material from its source to another location. For coastal British Columbia, the Ministry of Forests delineates seed planning zones that are based on biogeoclimatic subzones and variants. Within a seed planning zone, seed transfer is further restricted to varying degrees for different species based on results from provenance and progeny tests when available, or observations of general patterns of adaptive genetic variation (Ministry of Forests 1995). Seed transfer along the Pacific

coast of the United States is similarly guided by maps that partition forest regions into areas homogeneous in physiography and forest type. Seed zone boundaries were initially established by consensus of several committees and researchers without information on whether the seed zones are related to patterns of adaptive variation in forest trees (Campbell 1991).

These approaches implicitly assume that local sources are optimal, following from the expectation that natural selection has resulted in trees that are well adapted within their area of origin but not necessarily in other regions. Local optimality is subject to considerable debate, and local tree populations have been shown theoretically and experimentally to be not necessarily the optimum seed source (Namkoong 1969; Mangold and Libby 1978; Matyas 1990). Field testing has shown that for some species when seedlots are moved north or up in elevation, they tend to be more productive than the local sources. Transferred southern and lower elevation sources utilize an extended growing season, while northern and high elevation provenances are unable to take advantage of the favorable growing conditions when moved south or down. Therefore, original seed zones and seed transfer guidelines are updated when such information becomes available for a species. Further, provenances proven superior in comprehensive field tests, with capabilities to grow faster or tolerate pests better than other seed sources, have greater transfer allowances than regular seed (Ministry of Forests 1995).

For coastal British Columbia, the Ministry of Forests delineates three seed planning zones: Maritime, Georgia Lowland, and Submaritime (Lester et al. 1990). The Maritime and Submaritime zone are bands of approximately 100 km width that stretch along the entire coast of British Columbia. The Maritime zone further includes Vancouver Island and the Queen Charlotte Islands. Movement of seed sources is usually restricted to 3° latitude or 300m elevation in the Maritime zone and to 1.5° latitude or 200m elevation for the Submaritime zone, but may differ

for particular species. For some species, specific restrictions also exist for movement between island and mainland region. Species with narrow transfer limits have been proven to be more sensitive to change in environmental conditions, while species with wider transfer limits exhibit less geographic variation or a greater environmental tolerance. These rules are considered conservative transfer guidelines given information on optimality and genetic variation from provenance trials (Lester et al. 1990). Red alder's natural range is restricted to these coastal seed planning zones. In the following I review the provenance research for conifers with a similar distribution as red alder to establish what magnitude of clinal variation in growth and adaptive traits is related to conservative transfer rules.

Sitka spruce is among the species sufficiently tested to recommend a north and upward transfer of up to 4° latitude or 300m, while south or downward movement is restricted to 1° latitude or 200m (Ministry of Forests 1995). Falkenhagen (1977) found that a 1° latitude southward move results in approximately 5% 2-year height reduction over local sources. In a European test, Burley (1966) found 3.3% height reduction for 1-year height and bud set to be 4 days earlier for a 1° latitude southward move. Campbell and Sorensen (1978) evaluated coastal Douglas-fir provenances over elevational gradients at different distances from the coast. For this species the Ministry of Forests (1995) recommends transfer limits of 350 m for both, Maritime and Submaritime zones. For provenances from 200 km inland (Submaritime) Campbell and Sorensen (1978) found 14% reduction in 2-year height and 3.5 days earlier bud set for a 350 m downward move, while there were no trends over elevational clines on the coast. Western Hemlock was investigated by Kuser and Ching (1980). A recommended maximal transfer of 3° latitude south in this species (Ministry of Forests 1995) corresponded to 12 days earlier bud break, 4.5 days earlier bud set, 12 percentage points less survival than the local source. Meagher (1976) found a 10% decrease in height over the recommended maximum of 300 m elevation transfer. Many more

references provide correlation coefficients of quantitative traits with geographic variables but no regression coefficients. However, it appears that about 10% reduction in growth or survival, and about 4 days shift in phenological traits are generally accepted as a consequence of seed transfer.

The scarce test information available for red alder suggests that there is enough clinal variation in this species to warrant similar transfer guidelines as for conifers. Hibbs and Ager (1989) proposed that seed transfer guidelines and seed zones for Douglas-fir should serve as provisional guidelines for red alder. Ager's et al. (1993) study focused mainly on elevational gradients and the magnitude and patterns of geographic diversity in red alder are comparable to those of conifers managed in the Northwest. In three out of four watershed studied, a 10% decline in growth was approximately equivalent to an elevation change of 200 m. A 4 day shift in the onset of frost hardness occurred every 2° of latitude (Cannell et al. 1987).

2. 3. 3. Tree improvement

Essential elements of a tree improvement program are genetic testing, selection of genotypes, assembling of breeding and production populations, and production of improved planting stock. There are a number of choices for each for each of these elements, and their particular combination makes up the breeding strategy for a species. Selection methods may be simple techniques or advanced selection indices and best linear unbiased prediction (BLUP) methodologies. Mating between selected genotypes may be unrestricted or limited to particular crosses, using single or multiple breeding populations of various size, and various mating designs. Production of planting stock may be through seedlings or vegetative propagation, or a

combination of both. The optimum breeding strategy will depend on biology of the species, the genetic variability in the traits of interest, the breeding objectives and the resources available.

Hardwood tree improvement in the Pacific Northwest has focused on hybrids of the native black cottonwood (*Populus trichocarpa* Torr. & Gray) with *P. deltoides* Bartr. ex Marsh., *P. maximowiczii* Henry, and more recently with *P. nigra* L. These hybrids are now being grown commercially for fiber production at high densities (spacing of 2 x 3 m) and harvested after 6-7 years. Improvement programs are pursued by individual companies and cooperatives and have focused on genetic testing of hybrids and clonal propagation of superior genotypes. Selection criteria were volume growth and disease resistance. Improvement in growth of poplar planting stock is largely attributable to selection of parents for hybrid combinations rather than selection within a hybrid population. Current research focuses on molecular genetics and genetic engineering of poplar hybrids (Heilman et al. 1995). Similarly advanced tree improvement programs with the objective of fiber production for poplar hybrids (*Populus* spp.), birches (*Betula* spp.), and willow (*Salix* spp.) exist in Europe (Eriksson et al. 1991).

Tree improvement in hardwoods with the goal of timber and veneer production does not exist in the Pacific Northwest, but there are a number of programs for oak species in other regions of the United States (Steiner 1993). Because of the slow growth of oak, tree improvement focuses largely on plus-tree selection in natural stands and establishment of untested orchards. Genetic testing is done in only about half of the programs. Other hardwoods that are under intensive management comprise aspen (*Populus tremuloides* Michx.), sycamore (*Platanus occidentalis* L.), sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), and green ash (*Fraxinus pennsylvanica* Marsh.). These hardwood tree improvement programs are all relatively recently initiated, involve plus tree selection in natural stands, progeny testing, and

seed orchard establishment (Byram et al. 1997). In Europe, genetic resources management for valuable timber species focus on beech (*Fagus sylvatica* L.), maples (*Acer platanoides* L. and *Acer pseudoplatanus* L.), elms (*Ulmus* spp.), ashes (*Fraxinus* spp.), chestnut (*Castanea sativa* Mill.), walnut (*Juglans regia* L.), and oaks (*Quercus* spp.). All of these programs are largely concerned with gene conservation, rather than genetic tree improvement and focus on collections in wild stands and study of genetic differentiation using marker techniques (Turok 1997).

There is little detail published on breeding strategies for hardwoods with comparable objectives and biological constraints as for red alder. Apart from the hybrid poplar programs, existing hardwood tree improvement efforts appear to be fairly standard improvement programs following the same basic strategy of plus tree selection, orchard establishment with a single population for a defined geographic region and sometimes progeny testing.

2. 3. 4. Options for red alder

Stettler (1978) envisioned three potential objectives for a red alder breeding program. (1) Short rotation fiber production, (2) normal rotation log production and (3) improved properties for site amelioration. I have shown that pursuit of objectives (1) and (2) would require genotypes tailored for relatively productive sites, contrary to the notion that preferred planting sites for red alder are waterlogged habitats and sites impoverished in nitrogen. The main difference between objective (3) versus (1) and (2) for a tree breeding program would be that genotypes optimally suited for site amelioration would aim at trees adapted to special sites.

With respect to objective (3) Daniels (1995) argues that breeding for increased nitrogen efficiency would require a considerable research effort into the interaction of host and endosymbiont. He concludes that this is not an economically feasible option for a commercial tree breeding cooperative. Understanding the genetics of host and endosymbiont interactions, however, may not be necessary. *Frankia* is not host specific, nodulates with many species resulting in similar fixation rates, and it is reasonable to expect no interactions with the host genotype (Huss-Danell 1991). Further, *Frankia* can live independently as a saprophyte (Li et al. 1997), and its resulting ubiquity probably makes inoculation of a tree by a particular strain impossible. It was shown that nitrogen production is always highly correlated with overall growth rates of red alder. Therefore, simply selecting for performance on impoverished sites would probably achieve maximal soil amelioration without understanding the genetics or the mechanism of cause and effect for increased growth and fixation rates. If large scale reclamation of a particular type of site is required, simple selection for growth traits under these site conditions would be effective. Breeding for genotypes that perform well under generally poor site conditions will not result in an economic advantage over planting conifers. Without a particular special site in mind, I do not see the need to pursue objective (3).

Objective (2) appears to be the economically most desirable option for a tree improvement program with red alder in British Columbia, since high quality saw logs of red alder are in short supply and command premium prices in both U. S. and overseas markets. Without further genetic testing, however, it is difficult to say whether those breeding objectives should be pursued, and there is no way to predict gains from selection in relevant growth and form traits. Daniels (1995) concluded that there is little opportunity for genetic improvement for growth and form traits within populations based on the limited within-population variability found by Ager and Stettler (1994). They suspected that in red alder, being an aggressive colonizer, intensive selection for

height growth could have resulted in reduced variability in growth traits. It has been stated that red alder is morphologically remarkably uniform throughout its range (DeBell and Wilson 1978). Stem form, branchiness, branch angle, leave size and leave shape are all considered homogeneous in populations from California to Alaska, including outlying populations in Idaho. Presumably, intense natural selection in dense even aged stands has reduced the genetic variability in biomass partitioning for less than optimal combinations of stem, crown, and other morphological traits.

Nonetheless, substantial among-population variance in red alder growth and adaptive traits will require some form of genetic management. It also includes the opportunity for genetic improvement based on provenance selection (Hall and Maynard 1979), although better growing provenances that utilize a longer period of the growing season may be more at risk to spring or fall frost damage. The question of optimal adaptation to local environments and the genetic correlations among growth traits and adaptive traits need to be examined to derive a suitable breeding strategy for red alder that minimizes the risk of maladaptation while keeping the number of breeding populations manageable. A criterion for the definition of breeding zones would be areas in which there are no rank changes in performance of genotypes among environments above some accepted level (equivalent to no or little genotype \times environment interaction for a sample of populations and sites within a breeding zone). These regions should ideally be defined on the basis of tests evaluating several traits, and an understanding the functional relations among these traits.

2. 4. References

- Ager, A. A. 1987. Genetic variation in red alder in relation to climate and geography of the Pacific Northwest. Ph. D. Dissertation, University of Washington, Seattle.
- Ager, A. A., Heilman, P. E., and Stettler, R. F. 1993. Genetic variation in red alder (*Alnus rubra*) in relation to native climate and geography. Canadian Journal of Forest Research 23: 1930-1939.
- Ager, A. A. and Stettler, R. F. 1994. Genetics of red alder and its implication for future management. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 92-105.
- Ager, A. A., Tanaka, Y. and McGrath, J. 1994. Biology, ecology, and utilization of red alder seed. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 159-169.
- Ahrens, G. R. 1994. Seedling quality and nursery practices for red alder. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 170-185.
- Ahrens, G. R., Dobkowski, A., and Hibbs, D. E. 1992. Red alder: guidelines for successful regeneration. Special Publication No. 24. Forest Research Laboratory, Oregon State University. Corvallis, Oregon.
- Allen, E. 1993. Decay in living red alder trees. FRDA Research Memo No. 216. B. C. Ministry of Forests, Victoria, British Columbia.
- Atkinson, W. A. and Hamilton, W. I. 1978. The value of red alder as a source of nitrogen in Douglas-fir/alder mixed stands. In Briggs, D. G., DeBell, D. S., Atkinson, W. A., eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 335-351.
- Atterbury, T. 1978. Alder characteristics as they affect utilization. In Briggs, D. G., DeBell, D. S., Atkinson, W. A., eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 71-82.
- Bancroft, B. G., Butt, G., and Lousier, J. D. 1990. Red alder seed tree control in coastal British Columbia: a review. For. Can. and B. C. Ministry of Forests, FRDA Report No. 159, Victoria, British Columbia.
- Berry, A. M. and Torrey, J. G. 1985. Seed germination, seedling inoculation and establishment of *Alnus* spp. in containers in greenhouse trials. Plant & Soil 87: 161-173.

Bormann, B. T. 1983. Ecological implications of phytochrome-mediated seed germination in red alder. *For. Sci.* 29: 734-738.

Bormann, B. T. 1985. Early wide spacing in red alder (*Alnus rubra* Bong.): effects on stem form and stem growth. Research Note PNW-423, Pacific Northwest Forest and Range Experiment Station, U. S. Department of Agriculture, Forest Service.

Bormann, B. T., Cromack, K., and Russell W. O. 1994. Influences of red alder on soils and long-term ecosystem productivity. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 47-56.

Bousquet, J., Cheliak, W. M., and Lalonde, M. 1988. Allozyme variation within and among populations of speckled alder (*Alnus rugosa*) and relationships with green alder (*A. crispa*), *Am. J. Bot.* 75: 1678-1686,

Bousquet, J., Cheliak, W. M., Wang, J., and Lalonde, M. 1990. Genetic divergence and introgressive hybridization between *Alnus sinuata* and *A. crispa* (*Betulaceae*). *Pl. Syst. Evol.* 170: 107-124.

Bousquet, J. and Lalonde, M. 1991. The population genetics of alder: an overview. In S. Fineschi, M. E. Malvolti, F. Cannata, and H. H. Hattemer. *Biochemical markers in the population genetics of forest trees*. SPB Academic Publishing, The Hague, Netherlands, pp. 105-112.

Brewbaker, J. L. 1990. Nitrogen fixing trees. In D. Werner and P. Müller, eds. *Fast Growing Trees and Nitrogen Fixing Trees*. G. Fischer Verlag, Stuttgart, New York, pp. 253-261.

Briggs, D. G., DeBell, D. S., Atkinson, W. A., eds. 1979. Utilization and management of alder: Proceedings of a symposium, 1977 April 25-27, Ocean Shores, WA. Gen. Tech. Rep. PNW-70. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.

Burley, J. 1966. Genetic variation in seedling development of Sitka spruce, *Picea sitchensis* (Bong.) Carr. *Forestry* 39: 69-84.

Byram, T. D., Bridgwater, F. E., Gooding, G. D., and Lowe, W. J. 1997. Forty-fifth progress report of the Cooperative Forest Tree Improvement Program. Texas Forest Service. Circular No. 297, Texas A&M University, College Station, Texas.

Cannell, M. G. R., Murray, M. B. and Shepard, L. J. 1987. Frost hardiness of red alder (*Alnus rubra*) provenances in Britain. *Forestry* 60: 57-67.

- Campbell, R. K. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. *For. Sci.* 37: 973-986.
- Campbell, A. G. and Ching, K. K. 1980. Genetic differences in red alder populations along an elevational transect. Forest Research Laboratory, Research Note 64, Oregon State University, Corvallis, Oregon.
- Campbell, A. G. and Franklin, J. F. 1979. Riparian vegetation in Oregon's western Cascade Mountains: composition, biomass, and autumn phenology. U. S./International Biological Program, Ecosystem Analysis Studies, Coniferous Forest Biome Bull. No. 14. University of Washington, Seattle, Washington.
- Campbell, A. G. and Sorensen, F. C. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. *Theor. Appl. Genet.* 51: 233-246.
- Chen J., Karchesy, J. J., and Gonzalez-Laredo, R. F. 1998. Phenolic diarylheptenones from *Alnus rubra* bark. *Planta Medica* 64: 74-75.
- Cole, D. W., Compton, J. E., Edmonds, R. L., Homann, P. S., and Miegroet, H. van. 1995. Comparison of carbon accumulation in Douglas fir and red alder forests. In McFee, W. W. Kelly, J. M., eds. *Carbon Forms and Functions in Forest Soils*. Soil Science Society of America Inc., Madison, USA, pp. 527-546.
- Comeau, P. G., Harper, G. J., Biring, B. S., and Thomas K. D. 1996. Field studies of red alder-conifer mixtures. In P. G. Comeau and K. D. Thomas, eds. *Proc. Designing Mixedwood Experiments Workshop*, Mar. 2, 1995, Richmond, British Columbia, Work. Pap. No. 20.
- Comeau, P. G., Harper, G. J., and D'Anjou, B. 1995 Effects of red alder on stand dynamics and nitrogen availability. B. C. Ministry of Forests and Canadian Forest Service, Victoria. FRDA Memo 223.
- Comeau, P. and Sachs, D. 1992. Simulation of the consequences of red alder management on the growth of Douglas-fir using FORCYTE-11. B. C. Ministry of Forests, FRDA Report 187. Victoria, British Columbia.
- Compton, J. E., Cole, D. W., and Homann, P. S. 1997. Leaf element concentrations and soil properties in first- and second-rotation stands of red alder (*Alnus rubra*). *Can. J. For. Res.* 27: 662-666.
- Crannell, W. K., Tanaka, Y., and Myrold, D. D. 1994. Calcium and pH interaction on root nodulation of nursery-grown red alder (*Alnus rubra* Bong.) seedlings by *Frankia*. *Soil Biol. Biochem.* 26: 607-614.

- Cros, E. T. du, Auclair, D., Bouvarel, L., Kremer, A., Slak, M. F., and Dumas, C. 1989. Genetic improvement and modified conventional culture of forest trees for short term biomass production. Fifth intermediate report. Energy from biomass 4. Proceedings of the third contractors' meeting, Paestum, 25-27 May 1988. Elsevier Applied Science Publishers, London, pp. 47-50.
- Dale, V. H. 1989. Wind dispersed seeds and plant recovery on the Mount St. Helens debris avalanche. *Can. J. Bot.* 67: 1434-1441.
- Dang, Q. L., Xie, C. Y., Ying, C. C. and Guy, R. D. 1994. Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.). *Can. J. For. Res.* 24: 2150-2156
- Daniels, J. D. 1995. Managing red alder genetic resources: options for cooperative tree improvement. Unpublished manuscript prepared for Oregon Department of Forestry and U. S. Department of Agriculture, Forest Service, State and Private Division.
- DeBell, D. S. 1979. Future potential for use of symbiotic nitrogen fixation in forest management. In Gordon, J. C., Wheeler, C. T., Perry, D. A., eds. Symbiotic nitrogen fixation in the management of temperate forests: Proceedings of a workshop, 1979 April 2-5, Corvallis, Oregon. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, pp. 451-466.
- DeBell, D. S., Strand, R. F., and Reukema, D. L. 1978. Short-rotation production of red alder: some options for future forest management. In Briggs, D. G., DeBell, D. S., Atkinson, W. A., eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 231-244.
- DeBell, D. S. and Turpin, T. C. 1983. Red Alder. In Burns, R. M, eds. Silvicultural systems for the major forest types of the United States. 1 ed. Agricultural Handbook No. 445. U. S. Department of Agriculture, Washington DC, pp. 26-28.
- DeBell, D. S. and Wilson, B. C. 1978. Natural variation in red alder. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon. pp. 209-222.
- Dorworth, C. E. 1995. Biological control of red alder (*Alnus rubra*) with the fungus *Nectria ditissima*. *Weed Technology* 9: 243-248.
- Dorworth, C. E., Macey, D. E., Sieber, T. N., and Woods, T. A. D. 1996. Biological control of red alder (*Alnus rubra*) with indigenous pathogenic *Ascomycotina*. *Can. J. Plant Pathol.* 18: 315-324.

Elliott, D. M. and Tailor I. E. P. 1981a. The importance of fertility and physical characteristics of soil in early development of red alder seedlings grown under controlled environmental conditions. *Can. J. For. Res.* 11: 522-529.

Elliott, D. M. and Tailor I. E. P. 1981b. Germination of red alder seed from several locations in its natural range. *Can. J. For. Res.* 11: 517-521.

Erstad, A. 1989. American alders for shelterbelts. *Gartneryrket* 79: 22-23.

Eriksson, G., Jonsson, A., Beuker, E., Werner, M., Karlsson, B., Rousi, M., Vihera-Aarnio, A., Rynanen, L., John, A., Salonen, M., and Kukkonen, H. 1991 Breeding of broad-leaved trees and micropropagation of forest trees. Proceedings of the Nordic Group for Tree Breeding in Finland 19.-21.9.1989. Metsanjalostussaatio, Helsinki, Finland.

Falkenhagen, E. R. 1977. Genetic variation in 38 provenances of Sitka spruce. *Silv. Genet.* 26: 67-75.

Figueroa, P. F. 1991. Ground applied herbicide methods for red alder control: herbicide efficacy, labor costs, and treatment method efficiency. Proceedings of the Western Society of Weed Science, Seattle, Washington, USA, 12-14 March 1991. *Western Society of Weed Science* 44: 53-68.

Fowells, H. A., ed. 1965. *Silvics of forest trees of the United States*. Agric. Handb. 271. U. S. Department of Agriculture, Forest Service. Washington DC.

Franklin, J. F. 1979. Vegetation of the Douglas-fir region. In Heilman, P. E., Anderson, H. W., Baumgartner, D. M., eds. *Forest soils of the Douglas-fir region*. Washington State University, Cooperative Extension Service, Pullman, Washington, pp. 93-112.

Franklin, J. F. and Pechanec, A. A. 1968. Comparison of vegetation in adjacent alder, conifer, and mixed alder-conifer communities. I. Understory vegetation and stand structure. In Trappe, J. M., Franklin, J. F., Tarrant, R. F., Hansen, G. M., eds. *Biology of alder: Proceedings of a symposium: 40th annual meeting of the Northwest Scientific Association, April 14-15, 1967, Pullman, Washington*. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, pp. 37-43.

Furrow, J. J. 1979. The systematics of the American species of *Alnus* (Betulaceae) Part 1. *Rhodora* 81: 1-121.

Giardina, C. P., Huffman, S., Binkley, D., and Caldwell, B. A. 1995. Alders increase soil phosphorus availability in a Douglas-fir plantation. *Can. J. For. Res.* 25: 1652-1657.

- Green, R. N. and Klinka, K. 1994. A field guide to site identification and interpretation for the Vancouver Forest Region. British Columbia Land Management Handbook No. 28. Ministry of Forests, Victoria, British Columbia.
- Haeussler, S. and Coates, D. 1986. Autecological characteristics of selected species that compete with conifers in British Columbia: a literature review. Land Management Report No. 33. B. C. Ministry of Forests, Information Services Branch. Victoria, British Columbia.
- Haeussler, S. and Tappeiner, J. C., II. 1993. Effect of the light environment on seed germination of red alder (*Alnus rubra*). Can. J. For. Res. 23: 1487-1491.
- Haeussler, S., Tappeiner, J. C., II., and Greber, B. J. 1995. Germination, survival, and early growth of red alder seedlings in the central Coast Range of Oregon. Can. J. For. Res. 25: 1639-1651.
- Hall, F. C. 1984. Ecoclass coding system for the Pacific Northwest plant associations. R6 Ecol 173-1984. Portland, OR: U. S. Department of Agriculture, Forest Service, Pacific Northwest Region. 83 p.
- Hall, R. B. and Maynard, C. A. 1979. Considerations in the genetic improvement of alder. In J. C. Gordon, C. T. Wheeler and D. A. Perry, eds. Symbiotic Nitrogen Fixation in the Management of Temperate Forests. Oregon State University, Corvallis, Oregon, pp. 322-344.
- Hanley, T. A. and Hoel, T. 1996. Species composition of old-growth and riparian Sitka spruce - western hemlock forests in southeastern Alaska. Can. J. For. Res. 26: 1703-1708.
- Harrington, C. A. 1990. *Alnus rubra* Bong. In R. M. Burns and B. H. Honkala, eds. Silvics of North America. Vol. 2. Hardwoods. U. S. Department of Agriculture, Handbook 654. Washington DC, pp. 116-123.
- Harrington, C. A. 1986. A method for site quality evaluation for red alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-192.
- Harrington, C. A. 1984. Factors influencing initial sprouting of red alder. Can. J. For. Res. 14: 357-361.
- Harrington, C. A. and DeBell, D. S. 1980. Variation in specific gravity of red alder (*Alnus rubra* Bong.). Can. J. For. Res. 10: 293-299.
- Harrington, C. A. and Courtin, P. J. 1994. Evaluation of site quality for red alder. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 141-158.

- Harrington C. A. and Curtis, R. O. 1986. Height growth and site index curves for red alder. Pacific Northwest Research Station. Research Paper PNW-358.
- Harrington, C. A., Zasada, J. C. and Allen, E. A. 1994. Biology of red Alder (*Alnus rubra* Bong.) In *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 3-22.
- Harry, J., Smith, G. and Todd, K. 1984. Red alder has increased tree sizes but reduced total yields six years after spacing. Special Publication VIF 1888, University of British Columbia, Vancouver, British Columbia.
- Hatalcik, J. 1988. General overview of the biological and financial value of British Columbia's red alder. Bachelor thesis, University of British Columbia, Vancouver, British Columbia.
- Heilman, P. E. 1990a. Growth and N status of *Populus* in mixture with red alder on recent volcanic mudflow from Mount Saint Helens. *Can. J. For. Res.* 20: 84-90.
- Heilman, P. E. 1990b. Growth of Douglas fir and red alder on coal spoils in western Washington. *Soil Sci. Soc. Am. J.* 54: 522-527.
- Heilman, P. E., Stettler, R. F., Hanley, D. P., and Carkner, R. W. 1995. High yield hybrid poplar plantations in the Pacific Northwest. Pacific Northwest Cooperative Extension Publication No. PNW-356, Washington State University Cooperative Extension, Pullman, Washington.
- Hibbs, D. E. 1987. The self-thinning rule and alder management. *For. Ecol. Manag.* 19: 273-281.
- Hibbs, D. E. and Ager, A. A. 1989. Red alder: guidelines for seed collection, handling and storage. Forest Research Laboratory, Special Publication No. 18. Oregon State University, Corvallis, Oregon.
- Hibbs, D. E., Bouvaral, L., and Cros, E. T. du. 1994. Performance of red alder sources in France. *Can. J. For. Res.* 24: 1008-1014.
- Hibbs, D. E., DeBell, D. S., and Tarrant, R. F., eds. 1994. *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon.
- Hibbs, D. E., Emmingham, W. H., and Bondi, M. 1989. Thinning red alder: effects of method and spacing. *For. Sci.* 35: 16-29.
- Hibbs, D. E., Emmingham, W. H., and Bondi, M. C. 1995. Responses of red alder to thinning. *West. J. Appl. For.* 10: 17-23.

- Holstein, G. 1984. California riparian forests: deciduous islands in an evergreen sea. In Warner, R. E., Hendrix, K. M., eds. California riparian systems: Ecology, conservation, and productive management: Proceedings of a conference, 1981 September 17-19, Davis, California. University of California Press, Berkeley, California, pp. 2-22.
- Hook, D. D., DeBell, D. S., Ager, A. A., and Johnson, D. 1990. Dry weight partitioning among 36 open-pollinated red alder families. *Biomass* 21: 11-25.
- Hook, D. H., Murray, M. D., DeBell, D. S., and Wilson, B. C. 1987. Variation in Growth of red alder families in relation to shallow water tables. *For. Sci.* 33: 224-229.
- Huss-Danell, K. 1991. Influence of host (*Alnus and Myrica*) genotype on infectivity, N fixation, spore formation and hydrogenase activity in *Frankia*. *New Phytol.* 1991. 119: 121-127.
- Johnson, F. D. 1968a. Disjunct populations of red alder in Idaho. In Trappe, J. M., Franklin, J. F., Tarrant, R. F., Hansen, G. M., eds. Biology of alder. April 14-15, 1967, Pullman, Washington. Northwest Scientific Association 40th Annual Meeting. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, pp. 1-8.
- Johnson, F. D. 1968b. Taxonomy and distribution of northwestern alders. In Trappe, J. M., Franklin, J. F., Tarrant, R. F., Hansen, G. M., ed. Biology of alder. April 14-15, 1967, Pullman, Washington. Northwest Scientific Association 40th Annual Meeting. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, pp. 9-22.
- Johnson, H. M. 1917. *Alnus oregona*: its value as a forest type on the Sinuslaw National Forest. *J. For.* 15: 981-987.
- Johnson, H. M., Hanzlik, E. J., and Gibbons, W. H. 1926. Red alder of the Pacific Northwest: its utilization, with notes on growth and management. Bulletin No. 1437, U. S. Department of Agriculture, Washington DC.
- Kenady, R. M. 1978. Regeneration of red alder. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 183-191.
- Knowe, S. A. and Hibbs, D. E. 1996. Stand structure and dynamics of young red alder as affected by planting density. *For. Ecol. Manag.* 82: 69-85.
- Knowe, S. A., Ahrens, G. R., and DeBell, D. S. 1997. Comparison of diameter-distribution-prediction, stand-table-projection, and individual-tree-growth modeling approaches for young red alder plantations. *For. Eco. Manag.* 98: 49-60.

Knowe, S. A., Cole, E. C., and Newton, M. 1995. Response surface analysis of control of red alder and vine maple with glyphosate-imazapyr and triclopyr-imazapyr. *West. J. Appl. For.* 10: 127-132.

Kuser, J. E. and Cing, K. K. 1980. Provenance variation in phenology and cold hardiness of western hemlock seedlings. *For. Sci.* 26: 463-470.

Leney, L., Jackson, A., and Erickson, H. D. 1978. Properties of red alder (*Alnus rubra* Bong.) and its comparison to other hardwoods. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. *Utilization and Management of Alder*. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 25-33.

Lester, D. T., and DeBell, D. S. 1989. Geographic variation in red alder. U. S. Department of Agriculture, Forest Service, Res. Pap. PNW-409.

Lester, D. T., Ying, C. C., and Konishi, J. D. 1990. Genetic Control and Improvement of Planting Stock. In Lavender, D. P., Parish, R., Johnson, C. M., Montgomery, G., Vyse, A., Willis, R. A., and Winston, D., eds. *Regenerating British Columbia's forests*, University of British Columbia Press, Vancouver, British Columbia, pp. 180-192.

Li, C. Y., Crawford, R. H., and Chang T. T. 1997. *Frankia* in decaying fallen trees devoid of actinorhizal hosts and soil. *Microbiol. Res.* 152: 167-169.

Little, G. R. 1978. Supply of red alder stumpage, its quantity and quality, and trends in alder stumpage prices and product markets for the State of Washington. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. *Utilization and Management of Alder*. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 9-23.

Mangold, R. D. and Libby, W. J. 1978. A model for reforestation with optimal and suboptimal tree populations *Silv. Genet.* 27: 66-68.

Markham, J. H. 1996. A field test of the degree of coevolution between red alder and *Frankia* populations. Ph. D. thesis, University of British Columbia, Vancouver, British Columbia

Markham, J. H. and Chanway C. P. 1998. Response of red alder (*Alnus rubra*) seedlings to a woolly alder sawfly (*Eriocampa ovata*) outbreak. *Can. J. For. Res.* 28: 591-595.

Martin, A. C., Zim, H. S., and Nelson, A. L. 1951. *American wildlife and plants*. McGraw-Hill Book Company Inc, New York.

Massie, M. R. C. 1990. Current biomass status of red alder in coastal British Columbia. FRDA Report (Victoria, British Columbia). FRDA Report 115, Research Branch, BC Ministry of Forests and Lands, Victoria, British Columbia.

Massie, M. R. C., Peterson, E. B., Peterson, N. M., and Enns, K. A. 1994. An assessment of the strategic importance of the hardwood resource in British Columbia. FRDA Report No. 221, B. C. Ministry of Forests and Lands, Victoria, British Columbia.

Matyas, C. 1990. Adaptation lag: a general feature of natural populations. Proceedings Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties Sep. 02-05, 06, 12 and 14., 1990, Olympia, Washington.

McComb, W. C. 1994. Red alder: interactions with wildlife. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 131-140.

McCutcheon, A. R., Ellis, S. M., Hancock, R. E. W., and Towers, G. H. N. 1992. Antibiotic screening of medicinal plants of the British Columbian native peoples. *J. Ethnopharm.* 37: 213-223.

McCutcheon, A. R., Ellis, S. M., Hancock, R. E. W., and Towers, G. H. N. 1994. Antifungal screening of medicinal plants of British Columbian native peoples. *J. Ethnopharm.* 44: 157-169.

McCutcheon, A. R., Stokes, R. W., Thorson, L. M., Ellis, S. M., Hancock, R. E. W., and Towers, G. H. N. 1997. Anti-mycobacterial screening of British Columbian medicinal plants. *Int. J. Pharmacog.* 35: 77-83.

McIver, H. W. 1991. Red alder: a broadleaved species for central Scotland. *Scottish Forestry* 45: 95-105.

Meagher, M. D. 1976. Studies of variation in hemlock (*Tsuga*) populations and individuals from southern British Columbia. Ph. D. Dissertation, University of British Columbia, Vancouver.

Miller, R. E. and Murray, M. D. 1978. The effects of red alder on growth of Douglas-fir. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. *Utilization and Management of Alder*. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 283-306.

Miller, R. E. and Murray, M. D. 1979. Fertilizer versus red alder for adding nitrogen to Douglas-fir forests of the Pacific Northwest. In Gordon, J. C., Wheeler, C. T., Perry, D. A., eds. *Symbiotic nitrogen fixation in the management of temperate forests: Proceedings of a workshop, April 2-5, 1979, Corvallis, Oregon*. Oregon State University, Forest Research Laboratory, Corvallis, Oregon, pp. 356-373.

Miller, R. E., Reukema, D. L., and Max, T. A. 1993. Size of Douglas-fir trees in relation to distance from a mixed red alder - Douglas-fir stand. *Can. J. For. Res.* 23: 2413-2418.

- Ministry of Forest. 1995. Seed and vegetative material guidebook. British Columbia Forest Service, Victoria, British Columbia.
- Mitchell, K. J. 1988. Site index curves and tables for British Columbia: coastal species. B. C. Ministry of Forests Research Branch, FRDA Report No 37, Victoria, British Columbia
- Moffat, A. J., Roberts, C. J., and McNeill, J. D. 1989. The use of nitrogen-fixing plants in forest reclamation. Research Information Note No. 158. Forestry Commission Research Division. United Kingdom.
- Monaco, P. A., Ching, T. M., and Ching, K. K. 1980. Rooting of *Alnus rubra* cuttings. Tree Planter's Notes. 31(3): 22-24.
- Monaco, P. A., Ching, T. M., and Ching, K. K. 1981. Variation of *Alnus rubra* for nitrogen fixation capacity and biomass production. Silv. Genet. 30: 46-50.
- Namkoong, G. 1969. Nonoptimality of local races. Proceedings of the 10th Southern Conference on Forest Tree Improvement, Texas A&M University, College Station. pp. 149-153.
- Nelson, E. E., Hansen, E. M., Li, C. Y. and Trappe, J. M. 1978. The role of red alder in reducing losses from laminated root rot. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon, pp. 273-282.
- Newton, M. and Cole, E. C. 1994. Stand development and successional implications: pure and mixed stands. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 106-115.
- Nielson, R. W. 1977. Red alder utilization in British Columbia. Canadian Forest Service. Report VP-X-164.
- Nilsson, S. 1985. An analysis of the British Columbia forest sector around the year 2000. Volume II: data used in the baseline analysis. Forest Economics and Policy Analysis Project, Information Report 85-2, Vancouver, British Columbia.
- Oregon Department of Forestry. 1999. On-line. Log price information of Forest Management Division, Salem. Available: <http://www.odf.state.or.us/TMBRMGT/LOGPPAGE.HTM>. 5 April 1999.
- Owens, J. N. and Blake, M. D. 1985. Forest tree seed production. Forestry Canada Information report PI-X-53.

- Palzat, R. 1984. Performance of red alder in Nelder plot designs at age 7 at the University of British Columbia research forest. Bachelor thesis, University of British Columbia, Vancouver, British Columbia.
- Peeler, K. C. and DeBell, D. S. 1987. Variation in damage from growing season frosts among open pollinated families of red alder. U. S. Department of Agriculture, Forest Service, Res. Note PNW 464.
- Perinet, P. and Tremblay, F. M. 1987. Commercial micropropagation of five *Alnus* species. New For. 1: 225-230.
- Peterson, E. B. 1996. Red Alder managers' handbook for British Columbia FRDA-II Report No. 240, Research Branch, BC Ministry of Forests and Lands, Victoria, British Columbia.
- Plank, M. E. and Willits, S. 1994. Wood quality, product yield, and economic potential. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 243-247.
- Plank, M. E., Snellgrove, T. A., and Willits, S. 1990. Product values dispel 'weed species' myth of red alder. For. Prod. J. 40: 23-28.
- Puettmann, K. J., DeBell, D. S., and Hibbs, D. E. 1993. Density management guide for red alder. Research Contribution No. 2. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.
- Radwan, M. A. and DeBell, D. S. 1988. Nutrient relations in coppiced black cottonwood and red alder. Plant & Soil 106: 171-177.
- Radwan, M. A. and DeBell, D. S. 1981. Germination of red alder seed. Research Note PNW-370. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon.
- Radwan, M. A., Max, T. A., and Johnson, D. W. 1989. Softwood cuttings for propagation of red alder. New For. 3: 21-30.
- Radwan, M. A., Tanaka, Y., and Dobkowski, A., and Fangen, W. 1992. Production and assessment of red alder planting stock U. S. Department of Agriculture, Forest Service, Res. Pap. PNW-450.
- Resch, H. 1988. Red alder: opportunities for better utilization of a resource. Special Publication 16, Oregon State University, College of Forestry, Forest Research Lab, Corvallis, Oregon.

Sawada, S. 1994. Geographic variation in frost hardiness of red alder seedlings from twenty B. C. Provenances sampled on October 24, 1994, Unpublished project report.

Saxena, G., Farmer, S., Hancock, R. E. W., and Towers, G. H. N. 1995. Antimicrobial compounds from *Alnus rubra*. International Journal of Pharmacognosy 33: 33-36.

Shainsky, L. J., Yoder, B. J., Harrington, T. B., and Chan, S. S. N. 1994. Physiological characteristics of red alder: water relations and photosynthesis. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon, pp. 73-91.

Sheppard, L. J., Hooker, J. E., Wheeler, C. T., and Smith, R. I. 1988. Glasshouse evaluation of the growth of *Alnus rubra* and *Alnus glutinosa* on peat and acid brown earth soils when inoculated with four sources of *Frankia*. Plant & Soil 110: 187-198

Sieber, T. E., Sieber-Canavesi, F., and Dorworth, C. E. 1990. Identification of key pathogens of major coastal forest weeds. FRDA Report No. 113, Research Branch, BC Ministry of Forests and Lands, Victoria, British Columbia.

Simons, H. A. 1993. Historical and future log, lumber, and chip prices in British Columbia. FRDA Report No. 207, Research Branch, BC Ministry of Forests and Lands, Victoria, British Columbia.

Smith, J. H. G. 1968. Growth and yield of red alder in British Columbia. In Trappe, J. M., Franklin, J. F., Tarrant, R. F., Hansen, G. M, eds. Biology of Alder. April 14-15, 1968, Pullman, Washington. Northwest Scientific Association 40th Annual Meeting. U. S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station, Portland, Oregon, pp. 273-286.

Steiner, K. C. 1993. Genetic improvement of oaks in North America. Annales des Sciences Forestieres 50: Suppl.1, 359s-367s.

Stettler, T. F. 1978. Biological aspects of red alder pertinent to potential breeding programs. In D. G. Briggs, D. S. DeBell and W. A. Atkinson, eds. Utilization and Management of Alder. U. S. Department of Agriculture, Forest Service, Gen. Tech. Rep. PNW-70, Portland, Oregon. pp. 209-222.

Stowers, M. D. and Smith, J. E. 1985. Inoculation and production of container-grown red alder seedlings. Plant & Soil 87:135-160.

Swanston, C. W. and Myrold, D. D. 1997. Incorporation of nitrogen from decomposing red alder leaves into plants and soil of a recent clearcut in Oregon. Can. J. For. Res. 27: 9, 1496-1502.

- Tanaka, Y., Brotherton, P., Hostetter, S., Chapman, D., Dyce, S., Belanger, J., Johnson, B., and Duke, S. 1997. The operational planting stock quality testing program at Weyerhaeuser. *New For.* 13: 423-437.
- Tarrant, R. F., Hibbs, D. E., and DeBell, D. S. 1994. Red alder and the Pacific Northwest. In D. E. Hibbs, D. S. DeBell and R. F. Tarrant, eds. *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. ix-xii.
- Thrower, J. S. and Nussbaum, A. F. 1991. Site index curves and tables for British Columbia: coastal species. B. C. Ministry of Forests, Land Management Handbook, Victoria, British Columbia.
- Turok, J. 1997. International collaboration on the conservation of forest genetic resources in Europe. IUFRO (International Union of Forestry Research Organizations) Secretariat, Wien, Austria, World Series 6: 149-158.
- Wall, R. E. 1994. Biological control of red alder using stem treatments with the fungus *Chondrostereum purpureum*. *Can. J. For. Res.* 24: 1527-1530.
- Werner, D. 1992. *Symbiosis of Plants and Microbes*. Chapman & Hall, London.
- Wheeler, C. T. 1991. Symbiotic nitrogen fixation. In A. S. Raghavendra, ed. *Physiology of trees*. John Wiley & Sons Inc, New York, pp. 111-135.
- Wheeler, C. T., Hollingsworth, M. K., Hooker, J. E., McNeill, J. D., Mason, W. L., Moffat, A. J., and Sheppard, L. J. 1991. The effect of inoculation with either cultured *Frankia* or crushed nodules on nodulation and growth of *Alnus rubra* and *Alnus glutinosa* seedlings in forest nurseries. *For. Ecol. Manag.* 43: 153-166.
- Wheeler, C. T., Hooker, J. E., Crowe, A., and Berrie, A. M. M. 1986. The improvement and utilization in forestry of nitrogen fixation by actinorhizal plants with special reference to *Alnus* in Scotland. *Plant & Soil* 90: 393-406.
- Willits, S., Snellgrove, T. A., and Plank, M. E. 1990. Lean in red alder: its effects on product volume and quality. *Forest Products Journal* 40: 31-34.
- Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. *Can. J. Fish. Aquat. Sci.* 54: 1259-1269.
- Worthington, N. P., Ruth, R. H., and Matson, E. E. 1962. Red alder: Its management and utilization. Miscellaneous Publication No. 881. U. S. Department of Agriculture, Forest Service. Washington DC.

- Xie, C. Y., and Ying, C. 1994. Genetic variability and performance of red alder. Proc. Ecol. Manage. of B. C. Hardwoods. Dec. 1 and 2 1993, Richmond, British Columbia.
- Zacharatos, T. 1980. Effect of thinning on 4 and 10 year old red alder. Bachelor thesis, University of British Columbia, Vancouver, British Columbia.
- Zavitkovski, J. and Stevens, R. D. 1972. Primary productivity of red alder ecosystems. Ecol. 53: 235-242.
- Zou X. M., Binkley, D., and Caldwell, B. A. 1995. Effects of dinitrogen-fixing trees on phosphorus biogeochemical cycling in contrasting forests. Soil Sci. Soc. Am. J. 59: 1452-1458.
- Zwolinski, J. B. 1988. Three-year results from provenance trials of *Alnus formosana*, *A. rubra*, *Calocedrus formosana*, *Cunninghamia lanceolata* and *Taiwania cryptomerioides*. South Afr. For. J. 146: 34-37.

Chapter 3.

Multivariate analysis of allozymic and quantitative trait variation in *Alnus rubra*: geographic patterns and evolutionary implications.

3. 1. Abstract

Frequency data from six polymorphic allozyme loci and measurements of six quantitative traits were used to examine geographic differentiation among 65 British Columbia provenances of red alder (*Alnus rubra* Bong.). Principal component analysis showed that variation in quantitative traits can be reduced to two underlying dimensions, one representing general vigor including the timing of termination of the growing period, the other being the start of the growing period. Canonical correlation analysis among quantitative traits, allozyme frequencies, and geographic variables revealed complex associations of quantitative traits with the latitude, distance to the coast, and elevation of the seed source. There were no significant correlations among allozyme frequencies and quantitative traits, but the frequency of the most common allele at most loci decreased with latitude. Further, cluster analysis based on Nei's genetic distance revealed a strong differentiation among island and mainland provenances at one allozyme locus. This differentiation can be interpreted as a result of migration from two different refugia since the last glaciation. The island populations presumably originate solely from isolated coastal refugia west of the Cordilleran ice sheet, while mainland populations were also recruited from areas south of the ice.

3. 2. Introduction

Red alder is among the most abundant hardwood species in the Pacific Northwest. Its natural range extends from California (32°N) to Alaska (68°N) within 300 km from the Pacific Ocean, with the exception of small outlying populations in Idaho. In recent decades red alder has attracted considerable attention as a potential reforestation species because of its fast growth and its ability to symbiotically fix nitrogen (Hibbs et al. 1994). The population genetics of this species, however, are relatively poorly studied compared to that of conifers with commercial value. Species with a comparable range in the Pacific Northwest that are quite variable in morphological characteristics and physiological traits generally show medium to high levels of variation in allozymes, e.g. *Picea sitchensis* (Yeh and El-Kassaby 1980), *Pseudotsuga menziesii* (Yeh and O'Malley 1980), *Pinus contorta* (Wheeler and Gurries 1982), or *Alnus sinuata* (Bousquet et al. 1990), while species that are morphologically more uniform such as *Thuja plicata* have been found to be predominantly monomorphic at allozyme loci (Yeh 1978). While red alder is morphologically remarkably uniform throughout its range, there is considerable genetic variation in adaptive traits. Range wide provenance trials have demonstrated clinal variation over the wide latitudinal distribution of the species (DeBell and Wilson 1978; Canell et al. 1987; Ager and Stettler 1994). This study investigates approximately one third of the species' natural range in greater detail than the previous trials. In British Columbia (48°N to 56°N) red alder occurs over a wide range of climatic conditions and the purpose of this study is to investigate presumed genetic differentiation of red alder provenances in adaptive and growth traits along environmental gradients. Furthermore, geographic patterns in allozyme frequencies are investigated, and will be interpreted with respect to evolutionary history since the last glaciation. Multivariate and averaging techniques are used to detect ecotypic variation in

morphological and allele frequency data, while correlation techniques are employed to examine clinal variation along geographic variables. This study is restricted to the investigation of geographic patterns in morphological traits and allozyme frequencies. Partitioning of variance components for morphological data is provided elsewhere (Xie and Ying 1994), and a general analysis of allozyme frequency data with respect to diversity and population structure is provided by El-Kassaby et al. (1998).

3. 3. Materials and Methods

3. 3. 1. Study area and plant material

Data were obtained from a provenance trial established by the Ministry of Forests in 1992 south of Vancouver, British Columbia. The locations of the 65 B. C. provenances studied and the planting site of the provenance trial are shown in Figure 3. 1. The total area covered was arbitrarily subdivided into six regions: Vancouver Island Westcoast, Vancouver Island Eastcoast, Queen Charlotte Islands, Mainland 49-51°N, Mainland 51°-53°N, and Mainland 53°-55°N latitude. The areas are represented by symbols throughout the text to better visualize geographic differentiation. 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 orientation of the 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.

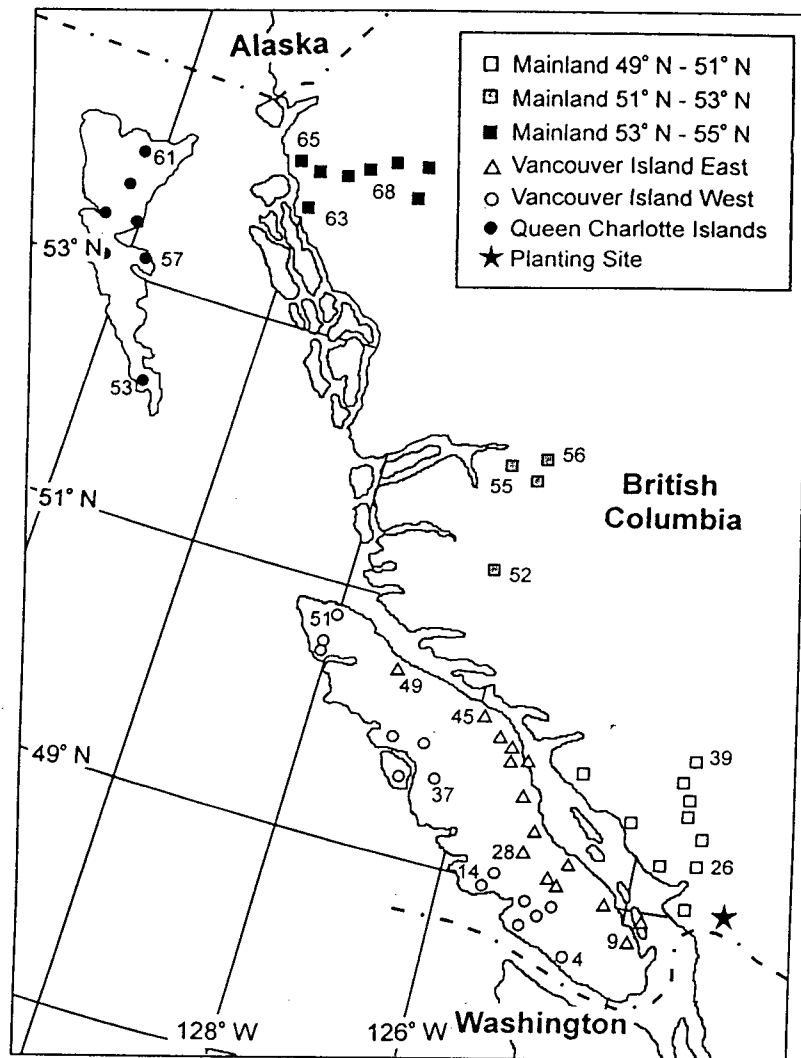


Figure 3. 1. Location of provenances and planting site for B. C. red alder provenance trial. Symbols represent regions, and numbers refer to provenances assayed for allozyme frequencies.

3. 3. 2. Data collection

Trees of all provenances included in the field trial were evaluated in 1996 at the end of the fourth growing season. Height, diameter at breast height and total above ground dry weight, as well as the number of flower clusters per tree were recorded. Abscission of the top five leaves and bud break of the top five buds was recorded in weekly intervals at the end of the first growing season and the beginning of the second growing season. The average day of bud break and the average date of leaf abscission were calculated as weighted averages for individual trees from these repeated measurements. Analysis in this study is based on mean values of measurements from 100 trees for each of the 65 provenances except for above ground dry weight, where only 20 trees were destructively sampled.

Allozyme polymorphisms, using horizontal starch gel electrophoresis, were evaluated for approximately 80 trees for each of 19 provenances. These provenances were selected to represent the entire range of red alder in British Columbia. Proteins were extracted from newly developed vegetative bud primordia collected in October according to Cheliak and Pitel (1984).

Electrophoresis was conducted on 11% horizontal starch gels using lithium-borate buffer (Ridgeway et al. 1970) or morpholine-citrate buffer (Clayton and Tretiak 1972). The staining methods used followed those of Conkle et al. (1982). A locus was included in this study if the most common allele had a frequency of less than 95%, namely aconitase (ACO, EC 4.2.1.3), alcohol dehydrogenase (ADH, EC 1.1.1.1), glutamate dehydrogenase (GDH, EC 1.4.1.3.), and uridine-5'-diphosphoglucose dehydrogenase (UGP, EC 1.1.1.22), which were single locus enzyme systems. Further, the more cathodally migrating locus of two aspartate aminotransferase (AAT, EC 2.6.1.1) loci and the intermediately migrating locus of three malate dehydrogenase (MDH, EC 1.1.1.37) loci were included.

3. 3. 3. Statistical analysis

As a means to compare patterns of similarity among provenances based on the morphological and allozyme data sets, and to identify groups of genetically similar provenances, cluster analysis was applied to both data sets separately. Only the 19 provenances for which both allozymic and quantitative data were available were included. The unbiased genetic distances D_N among provenances according to Nei (1978) were generated from allele frequency data. As an analogous measure, a matrix of Mahalanobis distances D_M among provenances was calculated from normalized data for quantitative traits (Dillon and Goldstein 1984). Based on these distance measures, dendrograms were constructed to better visualize allozymic and morphological differentiation among provenances. The unweighted group average method (UPGMA) was used to construct dendrograms (Sneath and Sokal 1973). Another descriptive tool, principal component analysis, was applied to quantitative data including all 65 provenances. Orthogonal variates, which are linear combinations of the original variables that best account for the total variance in the data set, were extracted from correlation matrices. Only principal components with Eigenvalues greater than one were retained. The first two variates were plotted against each other to highlight different dimensions in the original data set. Calculations were made using the CLUSTER procedure and the PRINCOMP procedure of the SAS statistical software package (SAS Institute Inc. 1988). The IML procedure was used to generate distance matrices.

In addition to the descriptive multivariate techniques above, canonical correlation analysis and canonical redundancy analysis were used to investigate relations among geographic variables, morphological variables and allozyme frequencies. Canonical correlation analysis generates pairs of linear combinations from two sets of original variables so that the correlation is maximal among the two variates (Dillon and Goldstein 1984). Because the number of variables (alleles)

was large relative to the number of samples (provenances), only the most frequent allele of each locus was used in the analysis. Since the frequency of the other alleles at the same locus are not independent, little information was lost and the statistical power was enhanced for canonical analysis by lowering the degrees of freedom in the numerator (Gittins 1985). Canonical redundancy analysis was used to determine what proportion of the variation in one original data set, e.g. morphological variables, can be accounted for by a canonical variate of another data set, e.g. geographic variables (Cooley and Lohnes 1977). Calculations were made with the CANCELL procedure of the SAS statistical software package (SAS Institute Inc. 1988).

3. 4. Results

3. 4. 1. Population differentiation

The dendrograms produced by UPGMA clustering technique based on Nei's genetic distance for allozyme allele frequencies, and on Mahalanobis distance for quantitative measurements are shown in Figure 3. 2. and 3. 3., respectively. Using allele frequency data, the provenances cluster into two groups of provenances: island and mainland. The average genetic distance between island and mainland provenances is 0.0149, considerably larger than differences within these regions, averaging 0.0029. Provenances from the Queen Charlotte Islands and from Vancouver Island cluster closely together, although they are separated by a large geographic distance. Only one locus, AAT, is responsible for the differentiation of island and mainland provenances. Table 3. 1. shows that AAT is fixed or nearly fixed in island provenances, while it is segregating in mainland provenances. When this locus is removed from the cluster analysis, no separation

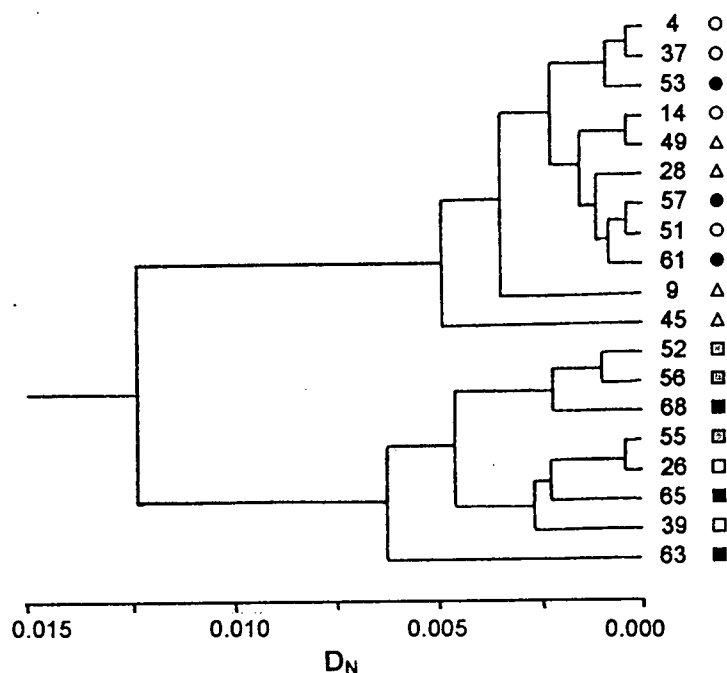


Figure 3. 2. Dendrogram of 19 B. C. red alder provenances using UPGMA clustering technique for Nei's unbiased genetic distance. Symbols refer to regions specified in Figure 1.

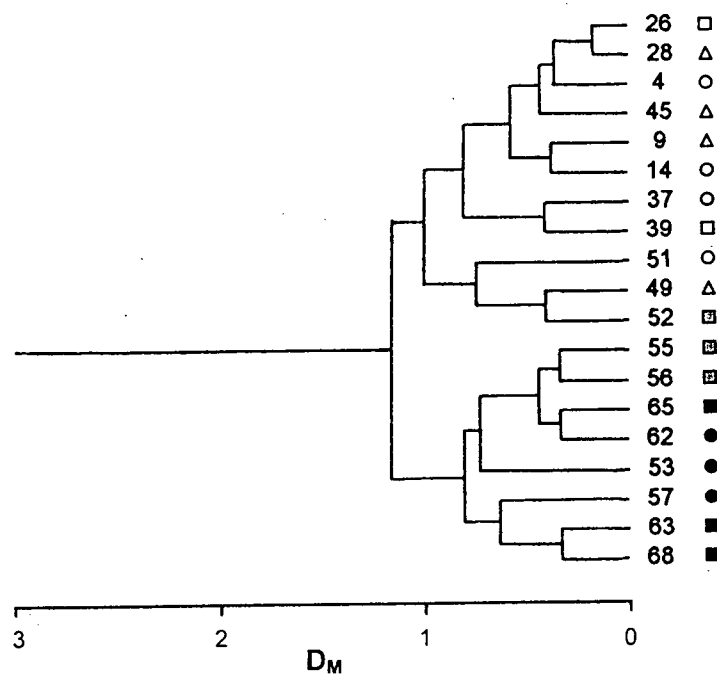


Figure 3. 3. Dendrogram of 19 B. C. red alder provenances using UPGMA clustering technique for Mahalanobis distances derived from quantitative traits. Symbols refer to regions specified in Figure 1.

Table 3. 1. Allele frequencies for 19 red alder populations from British Columbia
Monomorphic loci and the least frequent allele of each polymorphic locus are omitted

Population Number	ACO Allele 1	ADH			AAT Allele 1	GDH		MDH		UGPD Allele 1
		Allele 1	Allele 2	Allele 3		Allele 1	Allele 2	Allele 1	Allele 2	
<u>Mainland 53°-55°N</u>										
63	0.73	0.37	0.25	0.21	0.59	0.54	0.33	0.78	0.22	0.76
65	0.84	0.60	0.17	0.10	0.71	0.72	0.22	0.91	0.08	0.85
68	0.80	0.51	0.20	0.20	0.29	0.70	0.26	0.84	0.16	0.90
<u>Mainland 51°-53°N</u>										
52	0.75	0.66	0.11	0.14	0.40	0.77	0.17	0.83	0.10	0.86
55	0.81	0.53	0.27	0.13	0.46	0.68	0.28	0.87	0.11	0.78
56	0.80	0.67	0.13	0.12	0.37	0.79	0.12	0.86	0.10	0.88
<u>Mainland 49°-51°N</u>										
26	0.83	0.69	0.13	0.13	0.59	0.67	0.25	0.91	0.07	0.88
39	0.79	0.58	0.19	0.13	0.69	0.79	0.17	0.76	0.24	0.91
<u>Vancouver Island East</u>										
9	0.64	0.81	0.06	0.06	1.00	0.94	0.03	0.92	0.08	0.92
28	0.71	0.65	0.19	0.11	0.99	0.72	0.25	0.85	0.12	0.85
45	0.72	0.42	0.10	0.25	0.99	0.56	0.30	0.74	0.20	0.87
49	0.71	0.72	0.15	0.05	0.99	0.71	0.22	0.92	0.05	0.85
<u>Vancouver Island West</u>										
4	0.90	0.70	0.15	0.07	1.00	0.77	0.20	0.92	0.05	0.91
14	0.68	0.73	0.15	0.03	1.00	0.80	0.20	0.90	0.10	0.83
37	0.93	0.67	0.13	0.10	1.00	0.76	0.15	0.88	0.12	0.91
51	0.73	0.55	0.15	0.17	0.99	0.72	0.17	0.81	0.15	0.93
<u>Queen Charlotte Islands</u>										
53	0.84	0.69	0.18	0.09	0.90	0.77	0.16	0.92	0.07	0.86
57	0.76	0.61	0.21	0.13	1.00	0.80	0.14	0.89	0.11	0.89
61	0.73	0.58	0.14	0.15	0.99	0.68	0.26	0.83	0.17	0.88

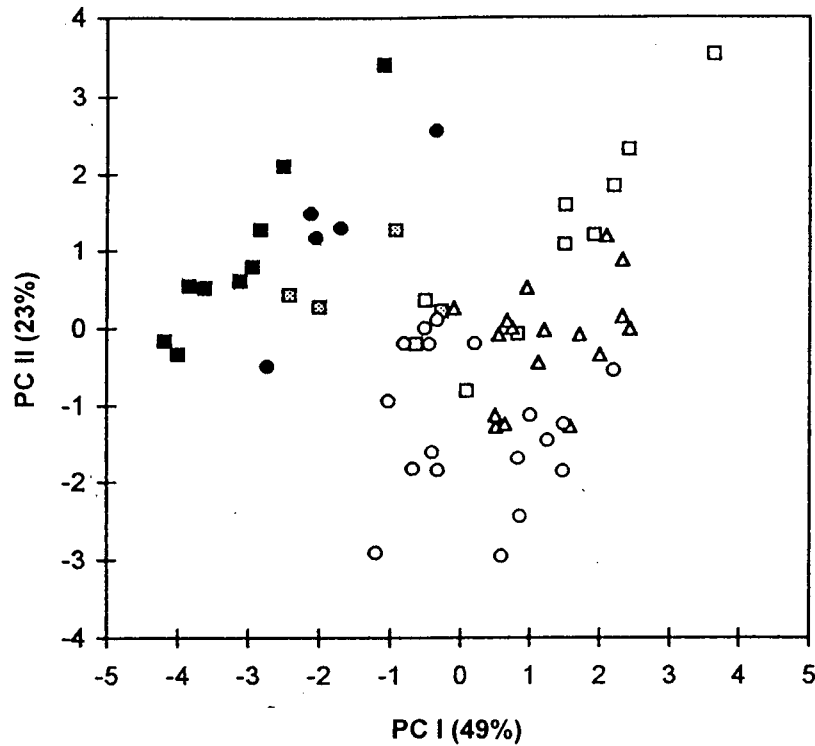


Figure 3. 4. Plot of the first two principal components for 65 B. C. red alder provenances based on 6 quantitative traits. Symbols refer to regions specified in Figure 1.

Table 3. 2. Component loadings of the first two principal components for six quantitative traits.

Trait	Eigenvectors	
	PC 1	PC2
Height	0.47	0.02
Diameter at breast height	0.44	0.11
Dry Weight	0.51	0.13
Date of bud break	-0.01	-0.81
Date of leaf abscission	0.41	-0.50
Number of flowers	0.38	0.22

among island and mainland provenances was detected. In contrast, distances based on quantitative data are larger between northern and southern provenances than within these groups. Mainland and island provenances from comparable latitudes are not distinct from each other.

The principal component analysis identified two variates with Eigenvalues greater than 1.0 which accounted for 72.3% of the variation in 6 quantitative traits. The first variate is interpreted as representing all variables except bud break in roughly equal proportions, while the second variate represents primarily phenology, including the date of bud break and leaf abscission (Table 3. 2.). Figure 3. 4. shows a plot of the 65 provenances over the two composite variates. Regional differences are expressed by both variates. Latitudinal differences are apparent mostly from the right to the left representing the first principal component, with dark symbols representing provenances from further north and light symbols provenances from the south. Clinal differences with distance from the coast are represented by the second principal component, separating the provenances of the three regions Westcoast Vancouver Island, Eastcoast Vancouver Island, and Mainland 49-51°N.

3. 4. 2. Simple correlations among variables

Table 3. 3. shows simple correlations among variables and Table 3. 4. shows summary statistics for quantitative traits and regression coefficients from simple linear regression analysis of each quantitative trait with latitude, distance to the coast and altitude. For simple correlations among quantitative traits it is notable that all growth traits are significantly correlated with the date of leaf abscission but not with the date of bud break (although date of leaf abscission and bud break are relatively weakly correlated). After sequential Bonferroni adjustment for simultaneous

Table 3. 3. Simple correlations among quantitative traits and geographic variables based on population means.

Trait	HT	DIA	TDW	BUD	LAB	FLW	LAT	DIST	ALT
HT	-	0.58 *	0.70 *	-0.12	0.50 *	0.31 *	-0.27	0.11	-0.15
DIA		-	0.55 *	-0.05	0.56 *	0.37 *	-0.46 *	0.35 *	0.29 *
TDW			-	-0.10	0.59 *	0.59 *	-0.44 *	0.43 *	-0.02
BUD				-	0.44 *	-0.19	-0.63 *	-0.18	0.07
LAB					-	0.39 *	-0.80 *	0.24	0.06
FLW						-	-0.28	0.53 *	0.09

Note: * Indicates a significant r-value at $p < 0.05$ after sequential Bonferroni adjustment (Rice 1989) for quantitative traits ($k=15$) and for correlations among geographic and quantitative traits ($k=18$). ALT, Altitude; DIST, Distance to the coast; LAT, Latitude; HT, Height; DIA, Diameter at breast height; TDW, Total above ground dry weight; BUD, Date of bud break; LAB, Date of leaf abscission; FLW, Number of flowers per tree;

Table 3. 4. Summary statistics and regression coefficients for quantitative traits based on population means.

Trait (unit)	Mean (Stdev)	Min	Max	Regression Coefficients		
				D/LAT	D/DIST	D/ALT
Height (m)	4.89 (0.26)	4.11	5.65	n.s.	n.s.	n.s.
Diameter at breast height (cm)	2.95 (1.11)	2.26	3.84	-0.3	-0.35	0.06
Dry Weight (kg)	1.24 (0.22)	0.93	1.64	-0.1	-0.08	n.s.
Date of bud break (day)	84 (2.57)	78	89	-1	n.s.	n.s.
Date of leaf abscission (day)	329 (5.09)	317	335	-2.1	n.s.	n.s.
Number of flowers	3.2 (1.54)	0.8	8.4	n.s.	-1.22	n.s.

Note: Min, smallest population mean; Max, largest population mean; Stdev, Standard deviation; D/LAT change in trait if provenance transferred 1° latitude south; D/DIST, change in trait if provenance transferred 100 km inland; D/ALT, change in trait if provenance transferred 100m to lower elevation; n.s., coefficient not significantly different from 0 at $p < 0.05$ after sequential Bonferroni adjustment (Rice 1989).

inference (Rice 1989), allozyme frequencies are not significantly correlated with quantitative traits or geographic variables (data not shown). The planting site is located at a southeast, low elevation position of the sampled range. Therefore, geographic variables of provenances represent the effects of a transfer from a certain location to this planting site on quantitative traits. Diameter and total above ground dry weight decrease on the average by 9% and 6% over the local source, respectively, for every degree latitude a provenance is transferred south to the planting site. Bud break occurs approximately one day later and leaf abscission two days later per degree latitude transfer to the south. Transferring provenances from the coast further inland results in decreased diameter and biomass production and a lower number of flowers. The effect of elevation is not significant for most traits. Only diameter changes significantly with elevation, increasing by 6 mm for every 100 m a provenance is transferred from a higher elevation to the planting site.

3. 4. 3. Canonical correlation and redundancy analysis

The canonical structure is summarized in Table 3. 5., providing the correlation of the original variables with their canonical variates. Tests for significance of correlations among canonical variates are shown in Table 3. 6. The first three rows of Table 3. 5. and 3. 6. investigate the relationships of growth and adaptive traits with the geographic origin of the provenance. The three canonical correlations are 0.90, 0.62, and 0.46, all significantly different from zero. The first pair of canonical variables demonstrates mainly the effect of latitude, since latitude has the highest correlation with its canonical variable (Table 3. 5.). It can be seen that trees from lower latitudes grow larger in height and diameter, break bud later and abscise leaves later than provenances transferred to the planting site from further north. The second canonical pair

Table 3. 5. Correlations between original variables and their canonical variates.

Pair	Variable Set 1						Variable Set 2					
	HT	DIA	TDW	BUD	LAB	FLW		LAT	DIST	ALT		
1	0.34 *	0.47 *	0.52 *	0.71 *	0.92 *	0.32 *		-0.98 *	0.21	-0.19		
2	0.03	0.46 *	0.50 *	-0.50 *	0.09	0.75 *		-0.06	0.98 *	-0.14		
3	-0.46 *	0.31 *	-0.50 *	0.28 *	-0.15	-0.32 *		-0.19	0.41	0.91 *		
	ACO	ADH	ATT	GDH	MDH	UGP		LAT	DIST	ALT		
4	0.11	0.66 *	0.85 *	0.46 *	0.57 *	0.29		-0.75 *	-0.52 *	0.28		
5	0.02	0.17	-0.04	0.14	-0.39	0.49 *		-0.56 *	0.83 *	0.62 *		
6	0.73 *	-0.43	-0.02	-0.20	-0.28	0.20		0.34	-0.13	0.72 *		
	HT	DIA	TDW	BUD	LAB	FLW	ACO	ADH	ATT	GDH	MDH	UGP
7	0.29	0.29	0.84 *	0.79 *	0.55 *	0.18	-0.39	0.63 *	0.44 *	0.41 *	0.18	0.55 *
8	0.00	-0.13	-0.32	0.00	0.24	-0.41	0.20	0.00	0.36	-0.51 *	0.35	-0.38
9	-0.06	0.24	-0.12	-0.34	-0.65 *	-0.09	0.04	-0.56 *	-0.17	-0.51 *	-0.47 *	0.35

Note: * Indicates a significant r-value at $p < 0.05$; ALT, Altitude; DIST, Distance to coast; LAT, Latitude; HT, Height; DIA, Diameter at breast height; TDW, Total above ground dry weight; BUD, Date of bud break; LAB, Date of leaf abscission; FLW, Number of flowers per tree; ACO, ADH, ATT, GDH, MDH, UGP, Frequency of most common allele at isozyme loci.

Table 3. 6. Correlation analysis of the relationship between pairs of canonical variables

Pair	Coef	Sterr	F	dfn	dfd	p>F
1	0.90	0.02	11.6	18	156	0.001
2	0.62	0.08	4.8	10	112	0.001
3	0.46	0.10	3.7	4	57	0.009
4	0.81	0.08	2.3	18	29	0.024
5	0.74	0.11	2.2	10	22	0.057
6	0.66	0.13	2.4	4	12	0.104
7	0.89	0.05	1.4	36	34	0.189
8	0.83	0.07	1.1	25	31	0.405
9	0.67	0.13	0.8	16	28	0.671

Note: Coef, Canonical correlation coefficient; Sterr, Standard error; F, F-value approximation; df, Degrees of freedom (nominator/denominator); p>F, probability of greater F-values.

represents the effect of distance to the coast. Provenances from further inland utilize a longer growing season at the planting site and grow larger in diameter and height compared to those provenances transferred from more coastal areas. The third pair represents the effect of altitude and to some degree the distance from the coast. Provenances from higher elevation further inland grow shorter in height and larger in diameter (more taper), with an overall reduced biomass production. At the planting site they exhibit a reduced growing season with a late date of bud break and an early date of leaf abscission. Canonical redundancy analysis shows that the three canonical variates, representing the effects of latitude, distance to the coast and altitude, account for 22, 10 and 5% of the total variation in the quantitative data respectively.

Geographic trends of allozyme frequencies are investigated in rows four to six of Table 3. 5. and 3. 6. The first linear combinations of allozyme and geographic variables are significantly correlated. The frequency of the most common allele increases at all loci with decreasing latitude and distance from the coast. This increase is significant for ADH, AAT, GDH, MDH but not for UGP and ACO. This implies that the overall expected heterozygosity increases with latitude and distance to the coast, which can be seen in Figure 3. 5., where the expected heterozygosity is plotted over latitude. Coastal provenances and inland provenances are represented by the usual symbols. The correlation of the second pair of canonical variates is "almost significant" at $p < 0.05$, indicating that the frequency of the most common allele at the locus UGP increases with distance from the coast. The three canonical variates account for 29%, 3%, and 1% of the total variation in allele frequencies.

Rows seven to nine of Table 3. 5. and 3. 6. represent associations of allozyme data with quantitative traits. The coefficients themselves are rather high with approximately 0.8 for the first canonical pair and 0.6 for the second pair of each comparison. Although none of the canonical coefficients are statistically significant, there appears to be a trend that for large trees which

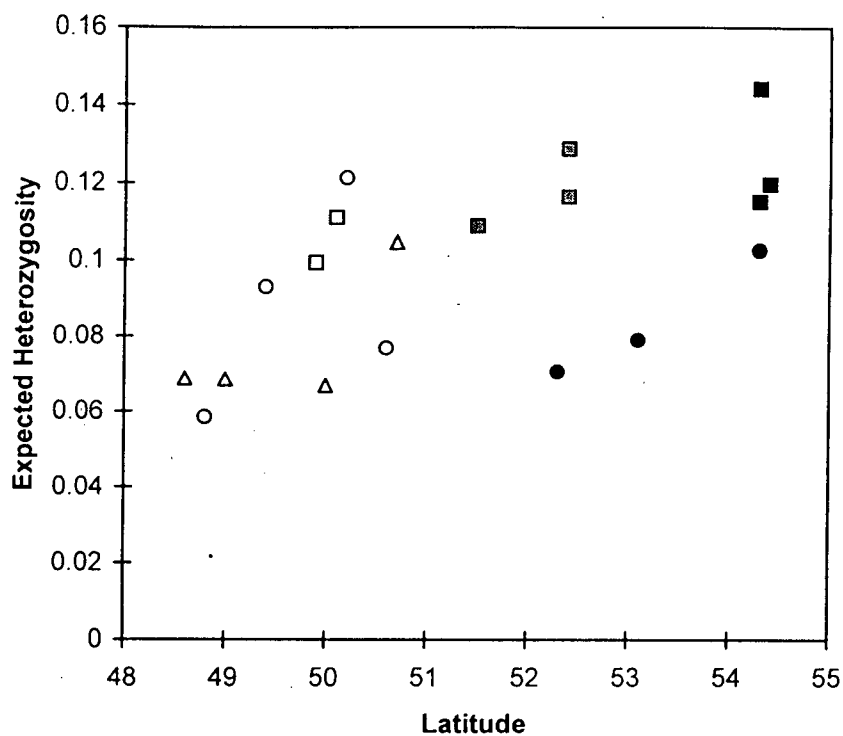


Figure 3. 5. Expected heterozygosities for 19 B. C. red alder provenances plotted as a function of latitude. Symbols refer to regions specified in Figure 1.

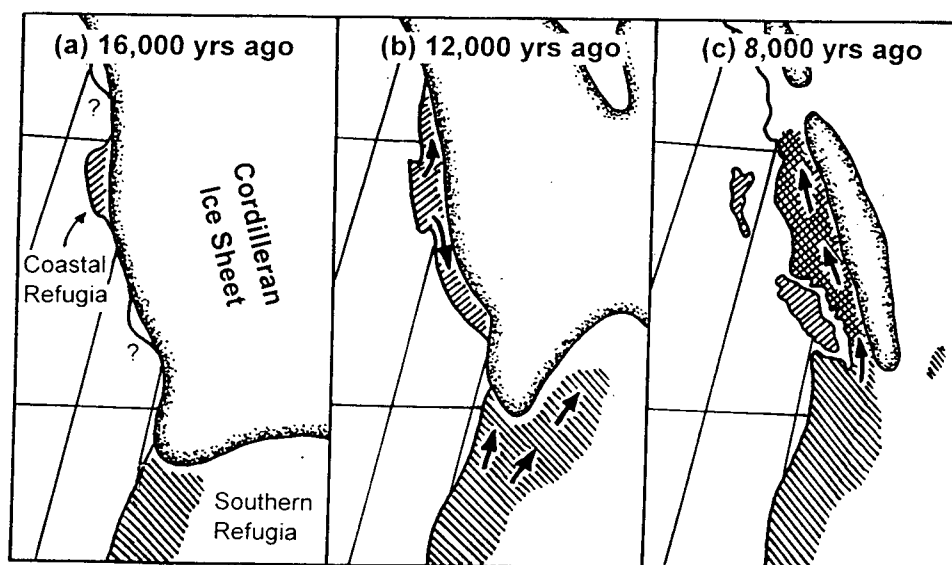


Figure 3. 6. Hypothetical refugia and migration of red alder since the height of the last glaciation adapted from Pielou (1991).

utilize a growing season with late bud break and late leaf abscission, the most common allele of each locus occurs at higher frequencies than for small trees except for the locus ACO.

3. 5. Discussion

3. 5. 1. Differentiation in quantitative traits

Clinal variation was associated with all three investigated geographic variables that presumably represent environmental gradients. When interpreting the results in detail, it is important to keep in mind that the planting site is located at a southeastern, low elevation position relative to the sampled range. Thus, local sources are observed in comparison to provenances transferred from north to south, from the coast to a more inland position, and from high to low elevation.

Along the latitudinal gradient, the length of the growing season in the north is shorter and average temperatures are lower. Provenances can be distinguished by their response in vegetative phenology and growth traits. The northern provenances break bud earlier and drop leaves earlier than local provenances, which is commonly observed in other tree species when transferred south (Morgenstern 1996). Since local sources perform better than those transferred from the north, it can be inferred that adaptation with respect to the synchronization with the seasonal cycle has taken place. Transferred provenances which retain their genetic adaptation to the short growing season do not fully utilize the end of the available growing season at the planting site resulting in generally smaller trees compared to local sources. The early start of the growing period in transferred trees has apparently no advantage due perhaps to the lack of synchronization with the

local climatic conditions, or because the number of days gained early in the growing season is too small to result in a measurable difference in annual growth. The magnitude of latitudinal effects on adaptive traits (Table 3. 4.) corresponds well to results for red alder from Cannell et al. (1987), who observed that frost hardening occurred two days earlier for each degree latitude north.

The second important trend is observed along a gradient from the coast to approximately 300 km inland, which represents a cline from a maritime climate with high precipitation and little amplitude in daily and seasonal temperature extremes to a more continental climate with low precipitation and high temperature amplitudes. Local sources begin their growing period earlier and perform better with respect to growth traits than those transferred from coastal sites further inland. Coastal sources presumably have a higher heat sum requirement because trees are exposed to winter days in coastal British Columbia that are warm enough to encourage bud break (more details in Chapter 6). The reduced performance of coastal sources at an inland site could also be due to lower water use efficiency and stomatal control of coastal sources, leading to water stress during the summer months. However, an investigation of ecophysiological parameters could not clearly demonstrate such a differentiation (Dang et al. 1994).

A third trend, which would have gone unnoticed without utilizing multivariate techniques, is the effect of elevation of the seed source. Trees from high elevations grow smaller in height but larger in diameter than the average and have a reduced above ground biomass. They break bud later and abscise leaves earlier, although the last trend was not statistically significant. These growth patterns are expected for high elevation provenances, but have rarely been demonstrated (Morgenstern 1996).

3. 5. 2. Allozymic differentiation and evolutionary history

This analysis revealed a clinal trend toward greater heterozygosity at higher latitudes, which was observed in all 6 loci, although the correlation with the canonical variate was not significant for ACO and UGP (Table 3. 5. and 3. 6., pair 4). A similar continuous trend was observed in Norway spruce, the northern European populations showing a greater heterozygosity than the central and southern European populations (Lagercrantz and Ryman 1990). In the latter study it was concluded that the southern European populations originated from refugia that experienced restrictions in population size in the Dinaric Alps, while the northern provenances originated from large refugia further east, which later mixed to form a continuous cline. Such an explanation seems inappropriate in the case of red alder since a population "bottleneck" was more likely in the coastal refugia than in the area south of the ice. Also, Yeh and O'Malley (1980) found significant correlations of the most common allele at several loci with latitude, longitude and altitude in Douglas-fir. Similar to this study, the majority of the most frequent alleles had negative correlation coefficients with latitude, two of which were significant (p-values not adjusted for simultaneous inference). Yeh and O'Malley cautiously suggested that these frequencies were due to selection. Using multivariate methods comparable to this study, Yeh et al. (1985) also observed a rich structure of genetic variation associated with geographic variables in *Pinus contorta* ssp. *latifolia*, which was not detected in earlier investigations of this species by Wheeler and Guries (1982) and Dancik and Yeh (1983). The previous studies suggest that geographical factors are weakly associated with allozyme frequencies, and these associations may not be easily detected unless a rather large number of populations over a wide geographic range are investigated. Since the expected heterozygosity is consistently higher in northern provenances in this study, a possible explanation would be different historic effective population sizes as a result of limited pollen or seed dispersal over the observed environmental gradient.

However, a decrease of variation due to genetic drift as a consequence of smaller effective population sizes would be expected in the north rather than the south, where climatic conditions could result in limited pollen or seed dispersal. An alternative explanation may be that effective population sizes in northern populations were larger in the past, considering that red alder is an aggressive colonizer of recently disturbed or impoverished sites. Recently disturbed areas sustaining large populations of red alder may have been more frequent in northern environments (e.g. in the vicinity of retreating glaciers), while red alder populations further south may have been more transient prior to large scale human disturbance in the Pacific Northwest.

Canonical correlations among quantitative traits and allozyme frequencies were not significant, but some significant simple correlations among allozyme loci and quantitative traits (before adjustment for simultaneous inference) were found in this study as well as in others (Yeh and O'Malley 1980; El-Kassaby 1982, 1983). However, a functional relationship among the two data sets is not expected and it appears plausible that the environmental gradients (as measured by geographic variables) have both selective effects on quantitative traits and influence on effective population sizes, either due to effects on seed and pollen dispersal, or by favoring or restricting the overall competitiveness of a species in a specific habitat.

Cluster analysis revealed non-clinal variation in allele frequencies at the locus AAT. In provenances from Vancouver Island and the Queen Charlotte Islands the most common allele is fixed or at very high frequencies while it ranges between 30 and 70% in mainland provenances. The genetic similarity of the geographically distant populations on Vancouver Island and the Queen Charlotte Islands may be explainable by the reinvasion history after the most recent glaciation. British Columbia was entirely covered by the Cordilleran ice sheet, and it is generally assumed that during the coldest period of the Pleistocene the current species survived in refugia

south of the ice front (Critchfield 1984). There is, however, evidence of coastal refugia west of the ice that sustained a woody flora and that persisted throughout the entire glaciation, in sediments found at the east coast of the Queen Charlotte Islands (Josenhans et al. 1997; Warner et al. 1982). The climate in these refugia was thought to be relatively mild, since arctic currents were blocked by the Beringian land bridge. Red alder could have reinvaded the coastal areas of British Columbia from such a refugium as shown in Figure 3. 6. (adapted from Pielou 1991). When the ice started to retreat (Figure 3. 6. b) Vancouver Island and the Queen Charlotte Islands were connected to the coastal mainland due to isostatic rise of the coastal area and a low sea level, forming a continuous coastal strip that was still separated from areas south of the ice by glaciers covering the Olympic mountains. Under this hypothesis red alder reinvaded the coastal mainland subsequently also from southern refugia, when the islands were already separated (Figure 3. 6. c). A further indication for coastal refugia west of the ice shield is the rapid appearance of lodgepole pine woodlands after deglaciation on northern Vancouver Island, which is difficult to explain by migration from the south (Hebda 1983, Wainman and Mathewes 1987). Also phylogeographic studies based on chloroplast DNA with several species of the Pacific Northwest including red alder suggest that there is a major genetic discontinuity among northern and southern genotypes that could be explained by isolated refugia (Soltis et al. 1997).

Allozyme loci are commonly considered selectively neutral or nearly neutral, but occasionally, allozymes are apparently selected for or linked to other loci, as in the case of APH in Norway spruce (Bergmann 1978). The same may be true for the alleles at the locus for AAT, which could have experienced selection pressure leading to the fixation of one allele for this locus on the island populations. Since there is no indication of environmental conditions particular to the islands today, if such selection occurred, it must have been during glaciation in a refugium west of the ice shield. Frequencies of allozymes or chloroplast DNA comparable to those at the AAT locus have not been found in any other species investigated in this area. Considering that

allozyme loci which are influenced by selective forces are rather exceptional, it probably requires a different approach to test our hypothesis. Pollen and fossil records, for example, could be specifically inspected for the timing of reappearance of woody species along the coast.

3. 6. References

- Ager, A. A. and R. F. Stettler. 1994 . Genetics of red alder and its implication for future management. In *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 92-105.
- Bergmann, F. 1978. The allelic distribution at an acid phosphatase locus in Norway spruce (*Picea abies*) along similar climatic gradients. *Theor. Appl. Genet.* 52: 57-64.
- Bousquet, J., Cheliak, W. M., Wang, J. and M. Lalonde. 1990. Genetic divergence and introgressive hybridization between *Alnus sinuata* and *A. crispa* (Betulaceae). *Pl. Syst. Evol.* 170: 107-124.
- Cannell, M. G. R., Murrey, M. B., and Shepard, L. J. 1987. Frost hardiness of red alder (*Alnus rubra*) provenances in Britain. *Forestry* 60: 57-67.
- Cheliak, W. M. and Pitel, J. A. 1984. Techniques for starch gel electrophoresis of enzymes from forest tree species. Petawawa National Forestry Institute, Info. Rep. PI-X-42: 1-49.
- Clayton, J. W. and Tretiak D. N. 1972. Amine-citrate buffers for pH control in starch gel electrophoresis. *J. Fish. Res. Board Can.* 29: 1169-1172.
- Conkle, M. T., Hodgkiss, P. D., Nunnally, L. B., and Hunter, S. C. 1982. Starch gel electrophoresis of conifer seeds: A laboratory manual. USDA For. Serv. Gen. Tech. Rep. PSW-64.
- Cooley, W. W. and Lohnes, P. R. 1971. Multivariate data analysis. John Wiley & Sons, Inc., New York.
- Critchfield, W. B. 1984. Impact of the Pleistocene on the genetic structure of north American conifers. 8th North American Forest Biology Workshop. Pp 70-118.
- Dancik, B. P., and Yeh, F. 1983. Allozyme variability and evolution of lodgepole pine (*Pinus contorta* var. *latifolia*) and jack pine (*Pinus banksiana*) in Alberta. *Can. J. Genetic. Cytol.* 25: 57-64.

Dang, Q. L., Xie, C. Y., Ying, C., and Guy, R. 1994. Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.) Can. J. For. Res. 24: 2150-2156.

DeBell, D. S., and Wilson B. C. 1978. Natural variation in red alder. In Briggs, D. G., DeBell, D. S., and Atkinson W. A. eds. Utilization and Management of Alder. USDA For. Serv. Gen. Tech. Rep. PNW-70, pp. 209-222.

Dillon, W. R. and Goldstein, M. 1984. Multivariate Analysis - Methods and Applications. John Wiley & Sons, New York.

El-Kassaby, Y. A. 1982. Associations between allozyme genotypes and quantitative traits in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Genetics 101: 103-115.

El-Kassaby, Y. A. 1983. Repeated relation between allozyme genotypes and quantitative traits in Douglas-fir. Egypt. J. Genet. Cytol. 12: 329-344.

El-Kassaby, Y. A., Ying, C., Xie, C.-Y. and Barnes, S. A. 1998. Genetic diversity, differentiation, inbreeding, and gene conservation of red alder from British Columbia. (in preparation).

Gittins, R. 1985. Canonical Analysis: a Review with Applications in Ecology. Biomathematics Vol. 12, Springer Verlag, Berlin, New York, Tokyo.

Hebda, R. J. 1983. Late-glacial and postglacial vegetation history at Bear Cove Bog, northeast Vancouver Island, British Columbia. Can. J. Bot. 61: 3172-3192.

Hibbs, D. E., DeBell, D. S., and Tarrant R. F. eds. 1994. The Biology and Management of Red Alder. Oregon State University Press, Corvallis, Oregon

Josenhans, H., Fedje, D., Pienitz, R., and Southon, J. 1997. Early humans and rapidly changing Holocene sea levels in the Queen Charlotte Islands - Hecate Strait, British Columbia, Canada. Science 277: 71-74.

Lagercrantz, U., and Ryman, N. 1990. Genetic structure of Norway spruce (*Picea abies*): Concordance of morphological and allozymic variation. Evolution 44: 38-53.

Morgenstern, E. K. 1996. Geographic Variation in Forest Trees: Genetic Basis and Applications of Knowledge in Silviculture. UBC Press, Vancouver.

Nei, M. 1978. Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics 89: 583-590.

Pielou, E. C. 1991. After the Ice Age. Return of Life to Glaciated North America. University of Chicago Press, Chicago, London.

- Rice, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43: 223-225.
- Ridgeway, G. J., Sherburne, S. W., and Lewis, R. D. 1970. Polymorphism in the esterase of Atlantic herring. *Trans. Am. Fish. Soc.* 99: 147-151.
- SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition, Cary, N. C.
- Sneath, P. H. A., and Sokal, R. R. 1973. *Numerical Taxonomy*. W. H. Freeman and Company, San Francisco.
- Soltis, D. E., Gitzendanner, M. A., Streng, D. D., and Soltis, P. S. 1997. Chloroplast DNA intraspecific phylogeography of plants from the Pacific Northwest of North America. *Pl. Syst. Evol.* 206: 353-373.
- Wainman, N., and Mathewes, R. W. 1987. Forest history of the last 12000 years based on plant macrofossil analysis of sediment from Marion Lake, southwestern British Columbia. *Can. J. Bot.* 65: 2179-2187.
- Warner, B. G., Mathewes, R. W., and Clague, J. J. 1982. Ice free conditions on the Queen Charlotte Islands, British Columbia, at the height of late Wisconsin glaciation. *Science* 218: 675-677.
- Wheeler, N. C., and Gurries, R. P. 1982. Population structure, genetic diversity, and morphological variation in *Pinus contorta* Dougl. *Can J. For. Res.* 12: 595-606.
- Xie, C. Y., and Ying, C. 1994. Genetic variability and performance of red alder. *Proc. Ecol. Manage. of B. C. Hardwoods*. Dec. 1 and 2 1993, Richmond, B.C., Canada.
- Yeh, F. C. 1978. Isozyme variation in *Thuja plicata* (Cupressaceae) in British Columbia. *Biochem Syst. Ecol.* 16: 373-377.
- Yeh, F. C., and El-Kassaby Y. A. 1980. Enzyme variation in natural populations of Sitka spruce (*Picea sitchensis*), 1. Genetic variation patterns among trees from 10 IUFRO provenances. *Can. J. For. Res.* 10: 414-422.
- Yeh, F. C., and O'Malley, D. 1980. Enzyme variation in natural populations of Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, populations from British Columbia. 1. Genetic variation patterns in coastal populations. *Silvae Genet.* 29: 83-92.
- Yeh, F. C., Cheliak, W. M., Dancik, B. P., Illingworth K., Trust, D. C., and Pryhitka, B. A. 1985. Population differentiation in Lodgepole pine, *Pinus contorta* ssp. *latifolia*. *Can. J. Gen. Cytol.* 27: 210-218.

Chapter 4.

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

4. 1. Abstract

Multiple provenance trials of red alder (*Alnus rubra* Bong.) are 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 with 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. I found clinal differentiation of reaction norms along the coast from north to south. 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 I 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 approximately 5 cm in 2-year height. Finally I 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.

4. 2. 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., Campbell 1983, 1991; Rehfeldt 1985, 1991, 1995; Thomas et al. 1990; Grossnickle et al. 1997; 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 different 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 Naamkoong 1990; Raymond and Lindgren 1990; Roberds et al. 1990). For practical application, however, this methodology requires extensive data from multiple provenance tests representing potential planting environments and a testing age reliable for extrapolation to rotation age, which is rarely available (e. g., Ying 1997; Park and Fowler 1988; Wu and Ying 1999; Lindgren and Ying 1999).

In this report I apply geographical information systems (GIS) and apply 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 Niejenhuis 1996), and recently geostatistical software has become available that is compatible with most commercial GIS (Pebesma and Wesseling 1998). I replace regression methods with ordinary kriging, where variation in provenance performance is modeled by a stochastic surface of best linear unbiased predictions. The crucial advantage of this methodology is its ability to model heterogeneous surfaces and that the prediction surface is accompanied by a surface of variance estimates that depend on the density of samples and the residual sampling error (Burrough and MacDonnell 1998). I 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 zonation according to the forester's objectives and willingness to take risks. Finally, I 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 (DeBell and Wilson 1978; Stettler 1978; Agar 1987; Hook et al. 1990; Dang et al. 1994; Xie and Ying 1994; Ager and Stettler 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 I can, however, test the assumption of local optima to some degree and investigate family stability over these planting environments. I 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, I also derive maps aiming at maximum site productivity in multiple traits based on preliminary seedling data from one red alder provenance trial.

4. 3. Material and Methods

4. 3. 1. Study area and data

The British Columbia Ministry of Forests established three long-term provenance tests in the spring of 1994, two on 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 (Figure 4. 1.). The plantations were evaluated for height and survival after two growing seasons. Details about the experimental

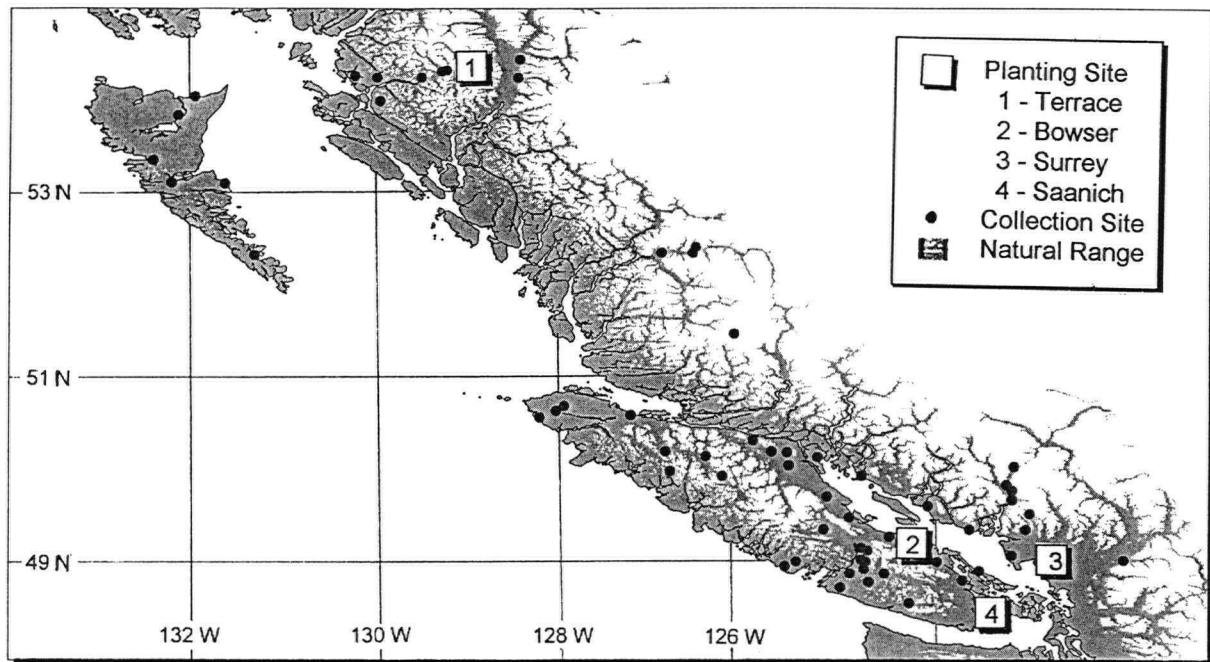


Figure 4. 1. Natural range of red alder in British Columbia, locations where seeds have been collected, and sites where test plantations with these provenances have been established.

design, testing stock, and silvicultural treatments were described in Xie et al. (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 seedlots 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 B. C. weather stations not further than 30 km in distance, and not more than 100 m in elevation from the collection site (Environment Canada 1982). Climatic variables were constructed using mean values for the period from 1951 to 1980. The climatic variables used in this analysis 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 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.

4. 3. 2. Statistical analysis

The experimental design at all sites was a splitplot design with provenances in mainplots, and families in 5-tree row subplots. The Surrey trial had 4 blocks, while the other trials had 3 blocks. Variance components were estimated using the restricted maximum likelihood method (SAS Institute 1997) according to the following model:

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

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

provenance and site with family within provenance; and ϵ_1 , ϵ_2 , and s are mainplot error, subplot error and sampling error, respectively. I assume that provenances are a random sample of the species within a geographic segment of its natural distribution 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 main effects were illustrated by plotting provenance means summarized by geographical regions. Genotype \times environment interactions at the family level were investigated with multivariate techniques. Reaction norms are usually referred to as response functions of a genotype to different environments. Because only four planting sites are evaluated in this study, fitting a response function is not feasible. Instead I 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 of provenances at the planting sites. I 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 in seed zones or breeding zones, if they are geographically clustered.

To guide the decision whether seed transfer rules should be based on climatic or geographic variables I 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).

4. 3. 3. Geostatistical analysis

To predict performance of a seed source at an unsampled location, I used ordinary kriging based on provenance means separately for each trial. The kriging method yields smoothed 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 (Burrough and McDonnell 1998). I 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 (more details in section 5. 3. 3.). The program GSTAT by Pebesma and Wesseling (1998) was used to fit variogram models and to generate maps of predicted values and variances.

The raw maps of predictions and associated variances were then transformed with the GIS software IDRISI as shown in the flowchart in Figure 4. 2. 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 given an accepted range of performance. 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

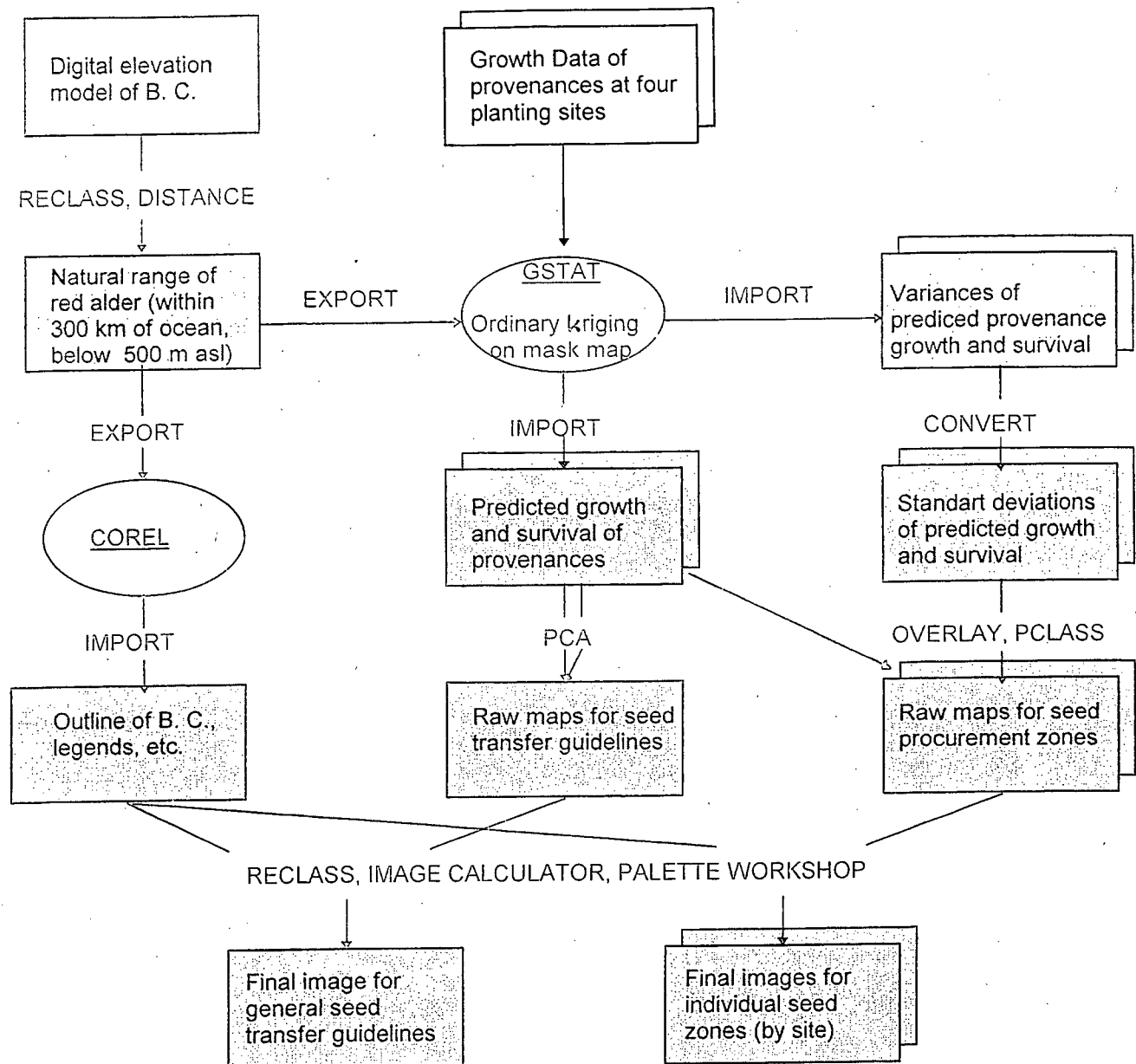


Figure 4. 2. Flowchart of GIS operations for the development of seed transfer guidelines and seed procurement zones from general maps and from data of common garden experiments (shaded boxes are IDRISI-images, capitals denote IDRISI-modules used, and circles represent auxiliary programs used).

locations of the individual prediction maps. To visualize geographic differences in reaction norms, I 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 I 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, this map-based analysis corresponds directly to the sample based evaluation of family reaction norms in the previous section.

4. 4. Results and discussion

4. 4. 1. Genotype \times environment interactions

The analysis of variance shows significant genotype \times environment interactions at all levels of the sampling design (Table 4. 1.). Since site \times provenance and site \times family interactions are significant, main effects cannot be interpreted. However, the large variance component attributable to planting site indicates a major main effect which is illustrated in Figure 4. 3., where performance of provenances at the four planting sites is summarized according to their regional origin. Figure 4. 3. 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 B. C.

Table 4. 1. Analysis of variance and estimated variance components for height.

Source of variation	df	Mean squares	p>F	Variance components (%)	
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 x 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) x 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				

were minimal in survival and only provenances sampled from far south in Oregon and far north in Alaska revealed a substantial decline. This seems to suggest that “ideal” site conditions do not provide an effective screening of provenance adaptability at least for some traits.

Principal component analysis of family means for height at four planting sites yielded two components with Eigenvalues greater than one, which account for 44 and 24% of the total variance. Component loadings in Table 4. 2. reveal similar contrasts for both components among Terrace and the southern planting sites, being orthogonal in a slightly different weighting of the southern sites. In Figure 4. 4. the top 10 families at each site are identified with letters in a plot of

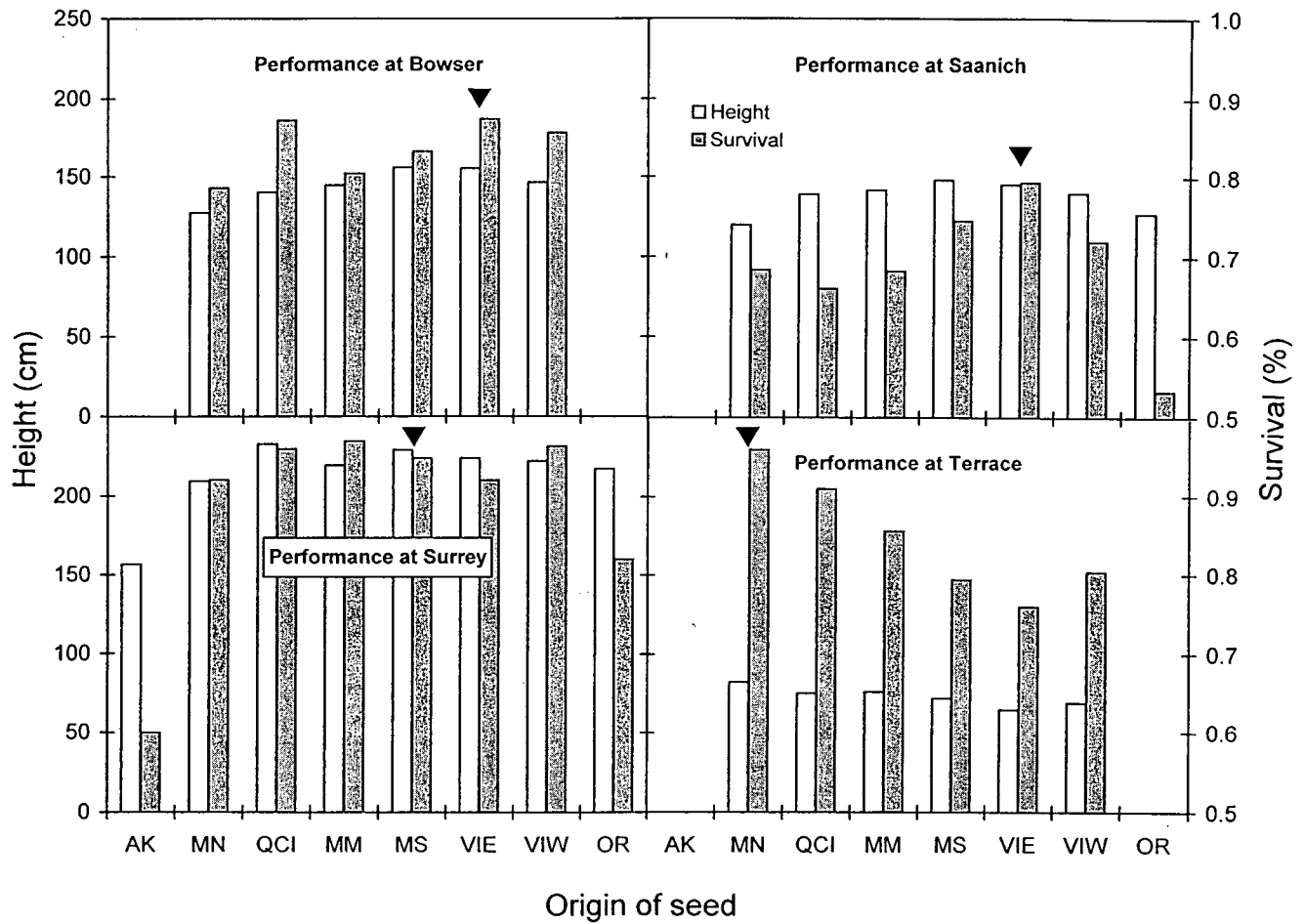


Figure 4. 3. Performance of provenances summarized by regions at the four planting sites. Region of origins are Alaska (AK), British Columbia mainland north 53° to 55°N (MN), mainland middle 51° to 53°N (MM), mainland south 49° to 51°N (MS), Queen Charlotte Islands (QCI), Vancouver Island west coast (VIW), Vancouver Island east coast (VIE), and Oregon (OR).

the first two components. If I 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 Figure 4. 4., delimited approximately by a circle, because opposite correlations of original family values with the principal components would result in a component score near zero. Families that perform well either at just Terrace or at the southern sites would be scattered in the periphery. Figure 4. 4. 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, geographic origin of the top performing families were almost exclusively from the same region where the planting site was located (data not shown).

The presence of significant genotype \times 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 rank order unchanged. Figure 4. 3. 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 4. 2., Figure 4. 4.). 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

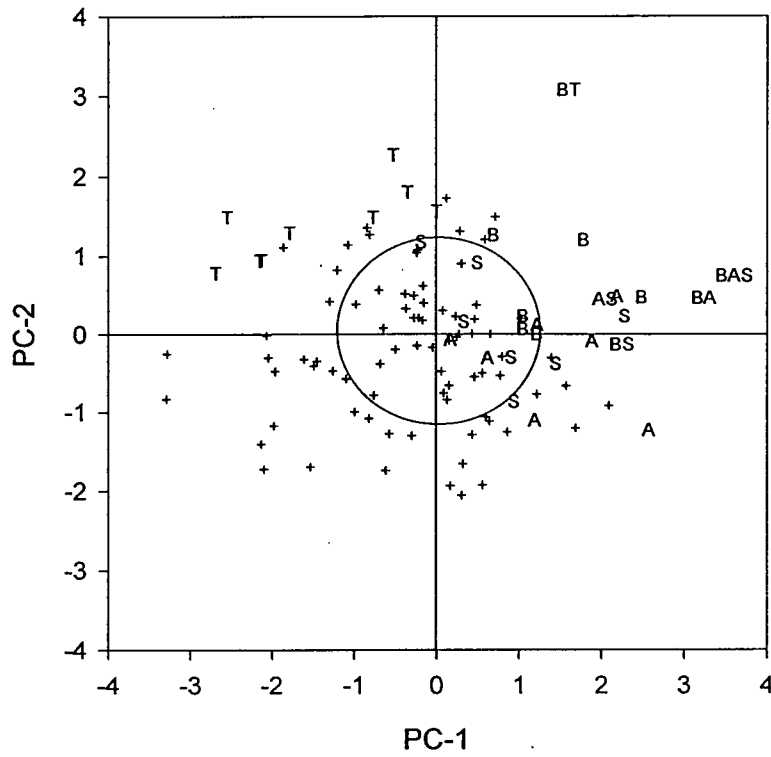


Figure 4. 4. Plot of the first two principal components extracted from height data for four planting sites. Letters refer to the 10 best performing families at Bowser (B), Saanich (A), Surrey (S), and Terrace (T).

Table 4. 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

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.

4. 4. 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 (Table 4. 3. and 4. 4.), although correlations among geographic and climatic variables is relatively low (Table 4. 6.). 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. 3.), and in fact geographic variables account for a large proportion of variance in the climatic data set (Table 4. 5.). It should also be noted that elevation is an important predictor for climatic variables but not for provenance performance (Variate 1 in Table 4. 3. and 4. 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. 4., Variate 1), indicates that gene flow may be an important factor in shaping patterns of adaptation of red alder in British Columbia. This is supported by the observation that elevation is an important factor in explaining variation in climatic variables at the provenance locations (Table 5, Variate 1), but accounts for very little variation in provenance performance (Table 4. 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 may be used to predict provenance performance of red alder with reasonable accuracy.

Results of the redundancy analysis suggests that I 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 advantages 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.

Table 4. 3. Loadings of redundancy variates and variance explained in height by climatic variates.

	HEIGHT1	HEIGHT2	HEIGHT3
Surrey	0.446	0.471	-0.292
Saanich	0.431	-0.416	-0.120
Bowser	0.872	0.211	0.403
Terrace	-0.657	0.243	0.644
	CLIMATE1	CLIMATE2	CLIMATE3
Season Beg.	-0.702	0.172	0.029
Season End	0.500	0.157	-0.354
Temp. Max.	-0.461	-0.181	0.360
Temp. Min.	0.364	0.485	0.371
Temp. July	0.424	0.274	0.547
Temp. Year	0.812	0.411	-0.075
Prec. July	-0.465	-0.043	-0.225
Prec. Year	-0.033	-0.325	-0.533
	Var. explained in HEIGHT by CLIMATE		
Proportion	0.228	0.025	0.020
Cumulative	0.228	0.253	0.273

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

	HEIGHT1	HEIGHT2	HEIGHT3
Surrey	-0.385	0.582	-0.353
Saanich	-0.511	0.134	0.418
Bowser	-0.852	0.495	0.011
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

Table 4. 5. Loadings of redundancy variates and variance explained in climatic variables by geographic variates.

	CLIMATE1	CLIMATE2	CLIMATE3
Season Beg.	-0.317	0.784	0.158
Season End	0.405	-0.726	-0.378
Temp. Max.	-0.193	0.606	0.276
Temp. Min.	0.411	-0.523	-0.411
Temp. July	0.522	-0.294	0.671
Temp. Year	0.194	-0.948	0.068
Prec. July	0.145	0.055	-0.918
Prec. 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

Table 4. 6. Correlations between climatic variables and geographic variables.

	Latitude	Distance	Elevation
Season Beg.	0.29	0.21	0.55
Season End	-0.17	-0.33	-0.61
Temp. Max.	0.22	0.26	0.41
Temp. Min.	-0.03	-0.32	-0.53
Temp. July	-0.08	0.35	-0.38
Temp. Year	-0.51	-0.11	-0.51
Prec. July	0.31	-0.52	-0.18
Prec. Year	-0.11	-0.51	0.02

4. 4. 3. Seed transfer guidelines

Predicted values of seed sources for height at each individual planting site are shown in Figure 4.

5. Height growth of provenances originating near the 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, I 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 greater than one, which accounted for 79% of the variation in height growth. The resulting maps of scores for the first two principal component are shown in Figure 4. 6. 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 4. 7., or directly the predicted

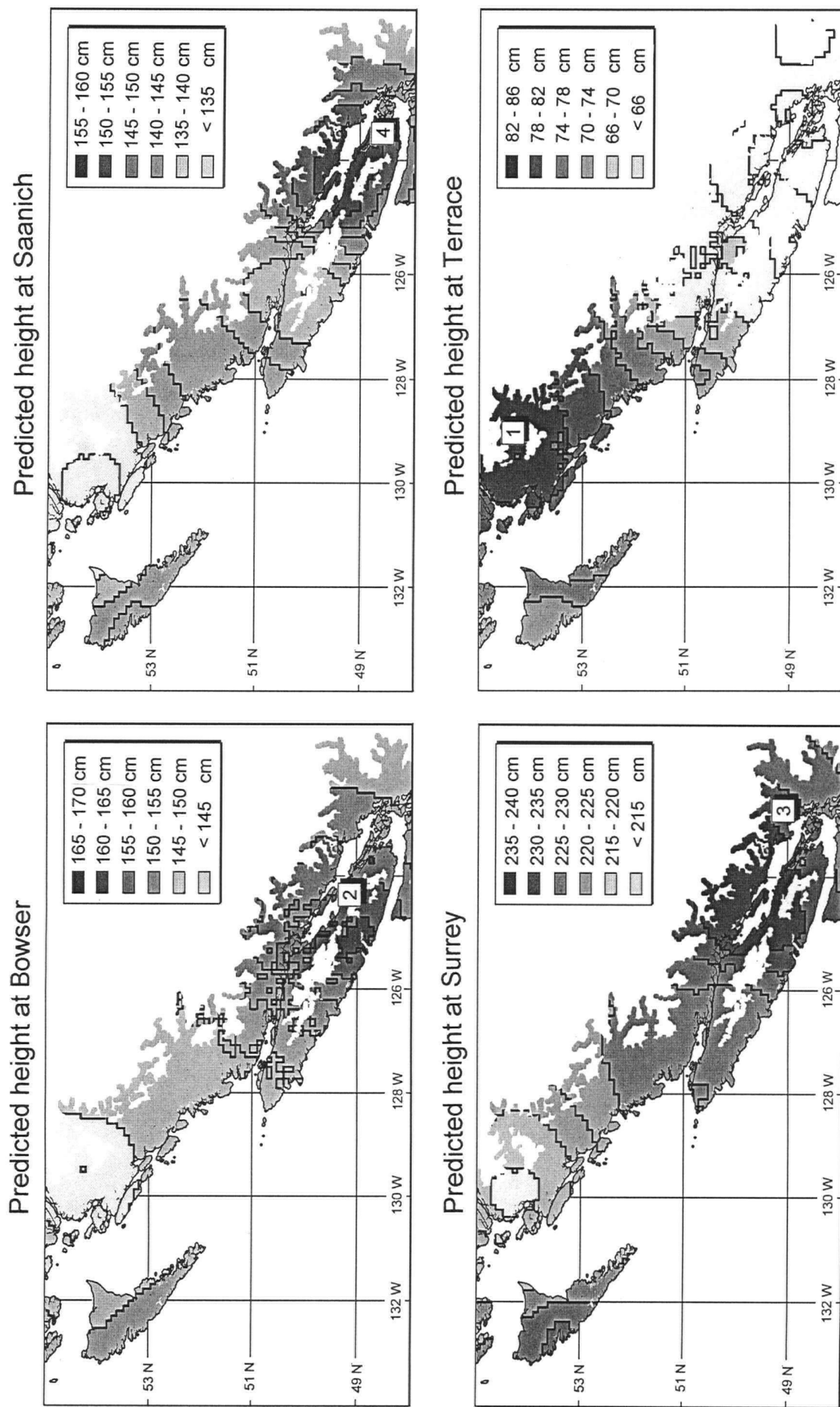


Figure 4. 5. Predicted height of seed sources at four planting sites. One contour interval is equivalent to 0.25 standard deviations at each site.

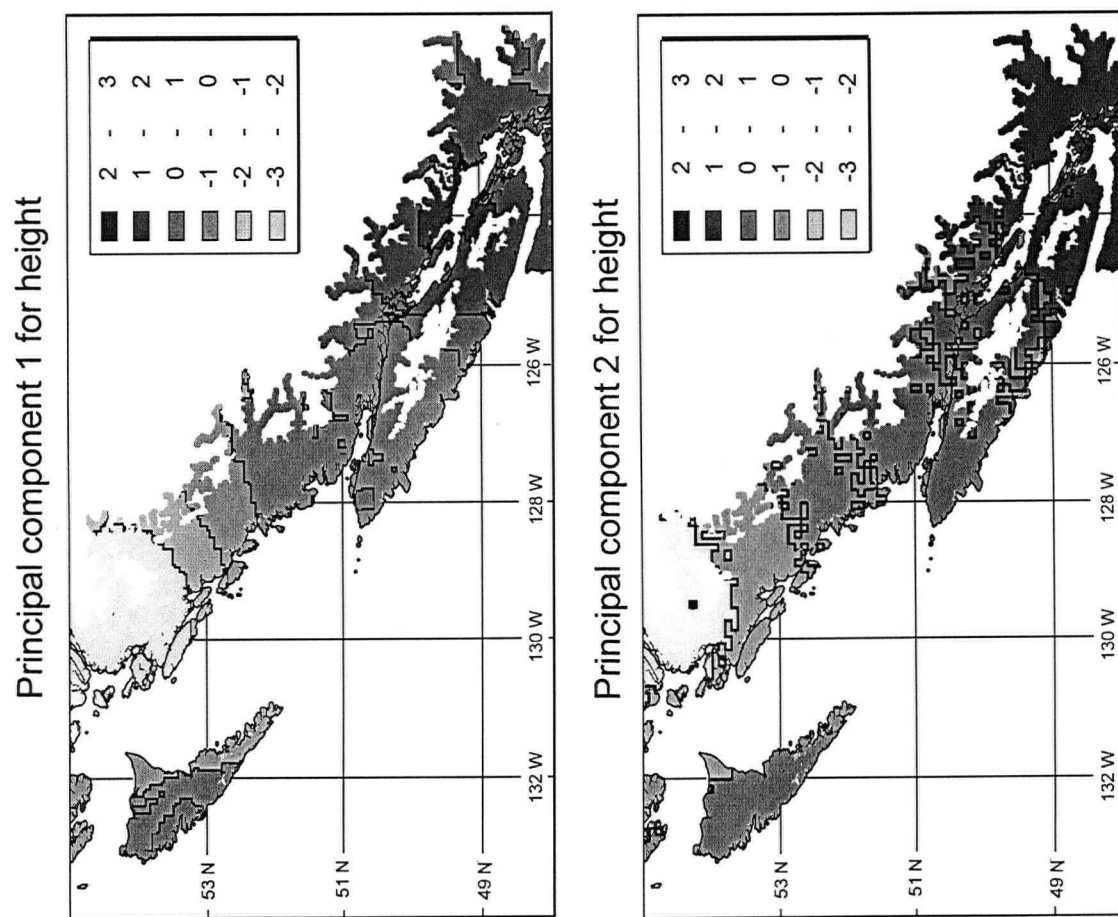


Figure 4. 6. Scores of the first (upper map) and second (lower map) principal component of predicted height at four planting sites.

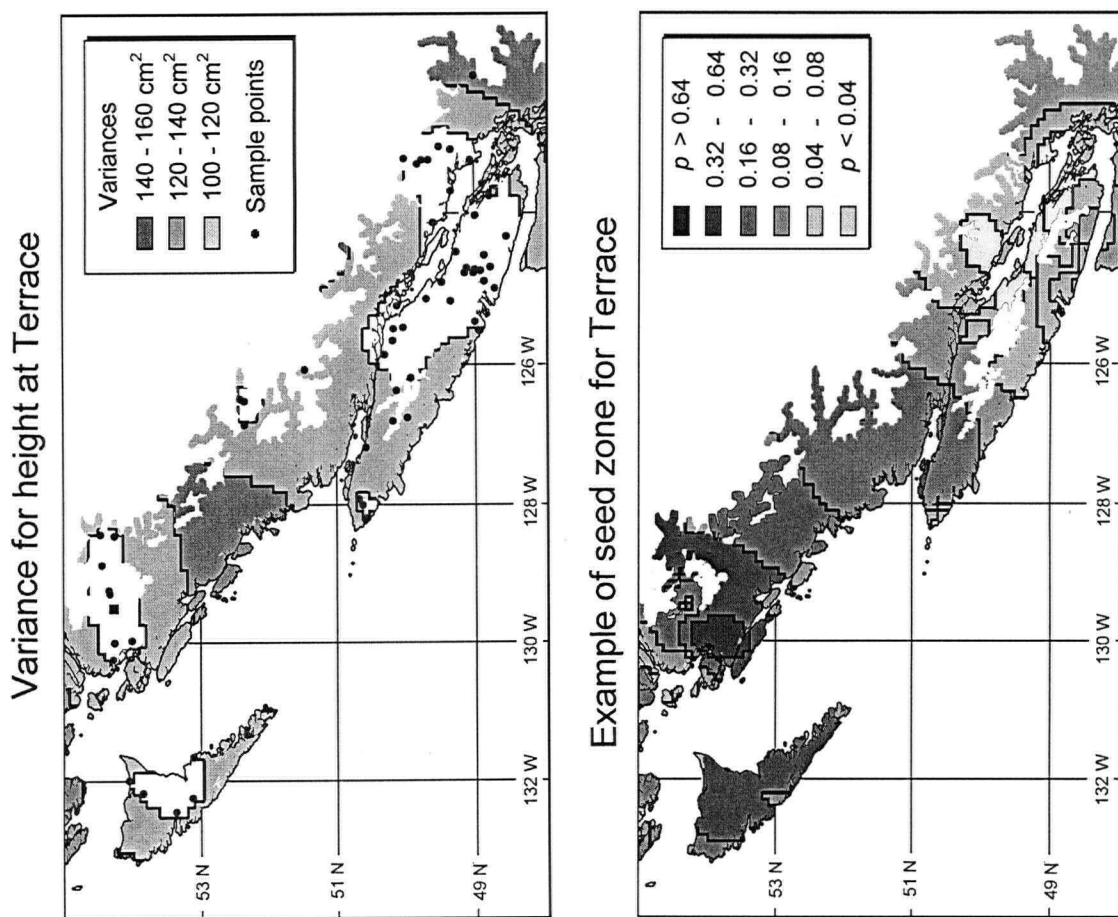


Figure 4. 7. Variance of predicted height growth (upper map) and probability of superior provenance performance in two traits at Terrace (lower map).

Table 4. 7. 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

values in Figure 4. 5. provide insight into the direction and magnitude of changes in growth and survival if provenances are moved perpendicular to the contours in Figure 4. 6. 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 100 km in 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 (Figure 4. 6., 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.

4. 4. 4. Seed procurement zones

Seed zones based on a single trait may be read directly from the prediction maps. Having an estimation 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 (Figure 4. 7.). 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 Figure 4. 7.). 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 the figure. Again, the highest probabilities of a provenance meeting the

requirements can be expected, if the seed source close to this planting site is chosen (lower map in Figure 4. 7.).

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 at a certain date 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.

4. 5. Recommendations

In this report I 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, is in species which are highly differentiated over a complex environments 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 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 complex and GIS based management of a species will likely be necessary to match source and planting environments.

4. 6. References

Ager, A. A. 1987 . Genetic variation in red alder in relation to climate and geography of the Pacific Northwest. Ph. D. Dissertation, University of Washington, Seattle.

Agar, A. A. and Stettler, R. F. 1994 . Genetics of red alder and its implication for future management. In *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 92-105.

Burrough, P. A. and McDonnell, R. A. 1998. *Principles of Geographic Information Systems*. Oxford University Press, Oxford, United Kingdom.

Campbell, R. K. 1979. Genecology of Douglas-fir in a watershed in the Oregon Cascades. *Ecology* 50: 19-33.

Campbell, R. K. 1983. Procedures for determining the biological limits of breeding zones in the Pacific Northwest. In *Proceedings of the Servicewide Genetics Workshop*, Dec. 5-9, Charleston, South Carolina, USFA Forest Service, pp. 24-33.

Campbell, R. K. 1991. Soils, seed-zone maps, and physiography: guidelines for seed transfer of Douglas-fir in southwestern Oregon. *Forest Sci.* 37: 973-986.

- Campbell, R. K. 1986. Mapped genetic variation of Douglas-fir to guide seed transfer in southwest Oregon. *Silvae Genet.* 35: 85-96.
- Dang, Q. L., C. Y. Xie, C. Ying and Guy, R. D. 1994 . Genetic variation of ecophysiological traits in red alder (*Alnus rubra* Bong.). *Can J For Res* 24: 2150-2156
- DeBell, D. S. and Wilson, B. C. 1978 . Natural variation in red alder. In D. G. Briggs, D. S. DeBell and W. A. Atkinson (Editors), *Utilization and Management of Alder*. USDA For. Serv. Gen Tech. Rep. PNW-70. pp. 209-222.
- Environment Canada. 1982. Canadian climate normals, 1951-1980, British Columbia. Atmospheric Environment Service Publication UDC:551.582(711), Downsview, Ontario.
- Grossnickle, S. C. Sutton, B. C. S. Fan ShiHe. King, J. 1997. Characterization of Sitka x interior spruce hybrids: a biotechnological approach to seedlot determination. *Forestry Chronicle*. 73: 357-362.
- Hamann, A., El-Kassaby, Y. A., Koshy, M. P., and Namkoong, G. 1998. Multivariate analysis of allozymic and quantitative trait variation in *Alnus rubra*: geographic patterns and evolutionary implications. *Can. J. For. Res.* 28: 1557-1565.
- Hook, D. D., DeBell, D. S., Ager, A. A., and Johnson, D. 1990 . Dry weight partitioning among 36 open-pollinated red alder families. *Biomass* 21: 11-25.
- Lindgren, D. and Ying, C. C. A model integrating seed source adaptation and seed use. (in preparation).
- Mangold, R. D. and Libby, W. J. 1978. A model for reforestation with optimal and suboptimal tree populations *Silvae Genetica* 27: 66-68.
- Matyas, C. 1990. Adaptation lag: a general feature of natural populations. *Proceedings Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties* Sep. 02-05, 06, 12 and 14. Olympia WA, 9 p.
- Namkoong, G. 1969. Nonoptimality of local races. *Proceedings of the 10th Southern Conference on Forest Tree Improvement*, Texas A&M University, College Station. pp. 149-153.
- Park, Y. S. Fowler, D. P. 1988. Geographic variation of black spruce tested in the Maritimes. *Can. J. For. Res.* 18: 106-114.
- Parker, W. H. 1991. Focal point seed zones: site specific seed zone delineation using geographic information systems. *Can. J. For. Res.* 22: 267-271.
- Parker, W. H. Niejenhuis, A. van. 1996. Seed zone delineation for jack pine in the former northwest region of Ontario using short-term testing and geographic information systems.

NODA/NFP Technical Report No. TR-35. Great Lakes Forestry Centre, Sault Ste. Marie, Ontario, Canada.

Pebesma E. J. and Wesseling C. G. 1998. Gstat, a program for geostatistical modeling, prediction and simulation. *Computers and Geosciences* 24: 17-31.

Raymond C. A. and Lindgren D. 1990. Genetic flexibility - a model for determining the range of suitable environments for a seed source. *Silvae Genet.* 39: 112-120.

Raymond C. A. and Namkoong, G. 1990. Optimizing breeding zones: genetic flexibility or maximum value? *Silvae Genet.* 39: 110-112.

Rehfeldt, G. E. 1995. Genetic variation, climatic models and the ecological genetics for *Larix occidentalis*. *For. Ecol. Managem.* 78: 21-37.

Rehfeldt, G. E. 1991. A model of genetic variation for *Pinus ponderosa* in the Inland Northwest (U.S.A.): applications in gene resource management. *Can. J. For. Res.* 21: 1491-1500.

Rehfeldt, G. E. 1985. Ecological genetics of *Pinus contorta* in the Wasatch and Uinta Mountains of Utah. *Can. J. For. Res.* 15: 524-530.

Rehfeldt, G. E. 1983. Ecological adaptations in Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) populations. III. Central Idaho. *Can. J. For. Res.* 13: 626-632.

Roberds, J. H., Hyun, J. O., Namkoong, G., and Rink, G. 1990. Height response functions for white ash provenances grown at different latitudes. *Silvae Genet.* 39: 121-129.

Russell, J. H. 1998. *Genecology of Chamaecyparis nootkatensis*. Coastally restricted forests. Oxford University Press, New York, USA.

SAS Institute. 1997. SAS/STAT user's guide. Release 6.12, Cary, NC.

Stettler, T. F. 1978. Biological aspects of red alder pertinent to potential breeding programs. In D. G. Briggs, D. S. DeBell and W. A. Atkinson (Editors), *Utilization and Management of Alder*. USDA For. Serv. Gen Tech. Rep. PNW-70. pp. 209-222.

Thomas, B. R. Lester, D. T. Worrall, J. 1990. Guidelines for seed transfer of western white pine in BC based on frost hardiness. FRDA Report No. 125 (Victoria, B.C.). FRDA Research Program, Research Branch, BC Ministry of Forests and Lands, Victoria, Canada.

van den Wollenberg, A. L. 1977. Redundancy analysis: an alternative for canonical correlation analysis. *Psychometrika* 42: 207-219.

Wu, H. X. and Ying, C. C. 1999. Geographic pattern of local optimality in natural populations of lodgepole pine (in preparation)

Xie, C. and Ying, C. C. 1994. Genetic variability and performance of red alder (*Alnus rubra*) in British Columbia. Paper presented at Hardwoods Workshop, Richmond, Dec. 93.

Ying, C. C. 1997. Effects of site, provenance, and provenance and site interaction in Sitka spruce in coastal British Columbia. *Forest Genetics*. 4: 99-112.

Ying, C. C. 1991. Performance of lodgepole pine provenances at sites in southwestern British Columbia. *Silvae Genet.* 40: 215-223.

Chapter 5.

Estimation of genetic parameters in *Alnus rubra*: improving breeding values with kriging

5. 1. Abstract

In order to assess the potential benefits from selection and to evaluate different options for tree improvement, one needs estimates of genetic control for traits of importance. In this section heritabilities and genetic correlations for growth and adaptive traits in red alder (*Alnus rubra* Bong.) were estimated and implications for a tree improvement program were discussed. It was further investigated if within-block variation in field experiments can be removed in order to improve breeding values, gains from selection, and precision of parameter estimates. The kriging method was used to remove spatially autocorrelated error variation in five forestry field trials. Kriging removed block effects and reduced the family \times block interaction in all traits. The variation due to interactions was recovered in simple family or provenance variance components, which increased by to 2 to 40% for various traits. Heritability estimates and expected gains from selection increased accordingly. The improvement was largest in experiments where blocking was clearly inadequate to capture site variation, when block size was large, and for traits that could be influenced by variation in soil properties. Heritabilities estimated from an experiment with incomplete block design with nine trees per block could only be minimally improved. Heritability estimates in bud break and leaf abscission, which are presumed to be relatively independent from variation in soil properties did not increase at all or by a minor amount. The experimental error and standard errors of estimates of genetic parameters did not change or

decreased by only a small amount. It was recommended to routinely test if residuals are spatially autocorrelated. If they are, kriging is proposed as a useful supplement to ANOVA in tree breeding experiments in order to improve estimates of breeding values and precision of genetic parameters.

5. 2. Introduction

Within-block variation due to environmental gradients such as soil fertility, moisture, pests, or previous land use is a common problem in forestry field trials. Careful layout of blocks and intensive site preparation can reduce this residual error in field experiments, but at the time of evaluation inadequate blocking is frequently discovered nonetheless. One of the most effective means to cope with site variation has been the use of small, incomplete blocks. In particular, alpha designs, a class of generalized lattice designs, have been useful for managing environmental heterogeneity in forestry field experiments (Correll and Cellier 1987; Klein 1989; Williams and Matheson 1994; John 1995). Nonetheless, complete block designs are still frequently used, and the old design of many long term forestry experiments poses a serious obstruction to precise estimates of genetic parameters and breeding values. Ericsson (1997) suggested that incomplete blocks should be imposed on a trial at the time of evaluation regardless of how the experiment was originally designed, and that the optimal block size be determined as the one that yields the highest heritability. However, since heritabilities or other genetic parameters are estimated with an error, choosing the block size that yields the highest value for heritability by trial and error almost certainly results in overestimations.

An alternative approach which models site variation as a smooth surface is particularly appealing, since blocks with distinct boundaries are conceptually not ideal to model continuous site variation that is often not directional. Numerous methods have been proposed to model spatial variation, such as trend surface analysis (Thomson and El-Kassaby 1988), least squares smoothing (Green et al. 1985; Clarke et al. 1994; Clarke and Baker 1996), separable ARIMA process (Cullis and Gleeson 1991), nearest neighbor methods (Williams et al. 1983; Stroup and Muhlthaus 1991) or kriging (Bresler et al. 1981; Samra et al. 1989; Lopez and Arrue 1995). Several authors compared these and other methods for use in agricultural field trials (Samra et al. 1990; Brownie et al. 1993; Stroup et al. 1994; Clarke and Baker 1996). Although not often used, kriging proved to be optimal to remove micro-environmental heterogeneity in agricultural experiments, while most other methods have been shown to increase the error of treatment estimates at least occasionally. Moreover, there is a wealth of literature in soil science showing that soil properties such as soil water, nutrient, silt, and clay content are spatially dependent and can be optimally modeled with kriging (e.g., Burgess and Webster 1980a, 1980b; Burroughs 1993). Being a consequence of variation in soil properties, it appears sensible to apply the same methodology to spatial variation in traits of plants grown in field experiments.

The objective of this research was to describe genetic parameters in red alder populations for the purpose of genetic resources management. Genetic testing is necessary to predict gains from future selection and to decide which breeding objectives should be pursued. Further, I investigated the possibility that kriging would be suitable to recover family \times block interactions that are due to environmental within-block variation in forestry field trials, and whether precision of parameter estimates and breeding values could be increased.

5. 3. Materials and Methods

5. 3. 1. Field experiments

Five genetic field trials with different experimental designs, family structure, and seed sources were evaluated in this study. Measurements were obtained after two growing seasons from four trials (Bowser, Saanich, Surrey-I, and Terrace), which were previously described in chapter 3 and 4. They included up to 65 provenances with up to five open-pollinated families per provenance. Field layout and detailed information on provenance locations is provided in Appendices 1 to 5. Additional measurements were taken during a thinning treatment at age 4 for the Surrey-I trial. These included total above ground dry mass, stem dry mass, and wood density. Quality related traits included a subjective score for straightness (0 to 5), pruning ability (number of branches, dead or alive, retained on the lower 2/3 of the tree) , average branch size (branch dry mass / number of branches), and the incidence of multiple leaders. The experiments were all laid out as split plot designs and analyzed according to the following model:

$$Y_{ijkl} = \mu + B_i + P_j + P \times B_{ji} + F(P)_{k(j)} + F(P) \times B_{k(ij)} + \varepsilon_{l(ijk)}$$

where Y is the measurement of seedling l in block i from provenance j and family k ; μ is the overall mean; B , P , and $F(P)$ are the effects of block, provenance, and family within provenance, respectively; $P \times B$ is the interaction effects of block with provenance and also the mainplot error; $F(P) \times B$ is the interaction effects of block with family within provenance; and ε is the experimental error.

The fifth experiment (Surrey-II) was an incomplete block design with four provenances from Alaska and 20 families per provenance. I used a lattice square design with 10 replications, each subdivided into 9 incomplete blocks with 9 trees. Since 9 mutually orthogonal latin squares are known (Graham et al. 1995) a layout could be derived, where each family shared an incomplete block once and only once with every other family. Although this design is for 81 treatments and had a slight imbalance due to one missing treatment in each replication, the statistical efficiency calculated from the incidence matrix according to Williams and Matheson (1994) was 10% better than what could be achieved with computer generated alpha-designs (CISRO/BioSS 1994). Details of the experimental design, field layout and provenance location are given in Appendices 6 and 7. The following linear model was used for analysis:

$$Y_{ijkl} = \mu + B_i + I(B)_{j(i)} + P_k + P \times B_{ik} + P \times I(B)_{jk(i)} + F(P)_{l(k)} + F(P) \times B_{il(k)} \\ + F(P) \times I(B)_{jk(i)} + \varepsilon_{m(ijkl)}$$

where $I(B)$ are incomplete blocks within complete blocks. The other symbols are as above.

Variance components, assuming a random model, were estimated using the restricted maximum likelihood method (SAS Institute 1988).

5. 3. 2. Parameter estimates

From the variance components, σ^2 , individual heritabilities, h^2 , were estimated assuming families are half-sibs as follows:

$$h^2 = 4 \sigma^2_{F(P)} / (\sigma^2_{F(P)} + \sigma^2_{B \times F(P)} + \sigma^2_{I(B) \times F(P)} + \sigma^2_E)$$

This heritability would be used to estimate gains from within provenance selection. Selection in a breeding program for British Columbia would likely be across provenances. I therefore also calculated heritabilities for individual selection across all provenances as an upper bound according to the formula:

$$h_{BC}^2 = 4 \sigma_F^2 / (\sigma_F^2 + \sigma_{B \times F}^2 + \sigma_{I(B) \times F}^2 + \sigma_E^2)$$

A tree breeding program for red alder would likely comprise not one, but two to five breeding populations for different regions of British Columbia. Further, h_{BC}^2 will also be an overestimate since the assumption of random mating and absence of linkage disequilibrium are likely violated across all populations. Heritabilities of traits in actual breeding populations will therefore lie between the two values h^2 and h_{BC}^2 .

The genetic correlations, r_A , were calculated from family within provenance variance components of trait x , σ_x^2 , and trait y , σ_y^2 , according to Stonecypher (1992).

$$r_A = \frac{1}{2} (\sigma_{x+y}^2 - \sigma_x^2 - \sigma_y^2) (\sigma_x^2 \sigma_y^2)^{-1/2}$$

Standard errors of heritabilities, $SE(h^2)$, were estimated according to the delta-method (Lynch and Walsh 1998, Appendix 1) based on the matrix of variances and covariances associated with estimates of variance components generated by the mixed model procedure (SAS Institute 1988). Approximate standard errors of genetic correlations, $SE(r_A)$, were determined according to Falconer (1981):

$$SE(r_A) = \frac{1 - r_A}{h_x^2 h_y^2} SE(h_x^2) SE(h_y^2) (h_x^2 h_y^2)^{-1/2}$$

5. 3. 3. Spatial analysis

Environmental heterogeneity was presumed to be reflected by spatial dependence of residual errors. Maps of residuals from the above models without the block effects were generated, and this variation was partitioned into spatially autocorrelated variation and random error with the kriging method. Kriging is an optimal interpolation method that yields smooth varying surfaces of best linear unbiased predictions (BLUP) of values on a spatial grid. Kriging is a two step process involving the construction of a variogram that provides information for optimal interpolation weights, and the interpolation itself. Variograms are functions that are fitted on a plot of the squared differences among all pairs of sample points against their Euclidean distances. Usually, a so called “spherical model” is fitted 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). The interpolation is then performed with the equation:

$$z(x_0) = \sum(\lambda_i \cdot z(x_i))$$

where $z(x_0)$ is the value to be predicted at location x_0 , $z(x_i)$ is the value of a variable sampled at location x_i , and λ_i is the interpolation weight. This weight depends on the distance between x_i and x_0 and is derived by rather complex calculations based on the variogram function so that the estimate of $z(x_0)$ is unbiased and that the estimation variance for $z(x_0)$ is less than for any other linear combination of the observed values (Burrough and McDonnell 1998). The program GSTAT by Pebesma and Wesseling (1998) was used to fit variogram models and to generate maps of predicted values and variances. Subsequently, I compared results from standard analysis, and the same analysis after original data had been corrected by the values predicted by kriging. The GIS software ARCVIEW was used to generate maps of residuals and predicted values.

5. 4. Results and Discussion

5. 4. 1. Genetic parameters in red alder

Estimated heritabilities for growth traits were moderate with values between 0.30 and 0.50, except at the Bowser and Terrace planting sites, which had highly heterogeneous site conditions (Table 5. 1.). In the 4-year evaluation, the difference between the lower and upper bound for heritability values in growth traits (h^2 and h_{BC}^2) that can be expected in breeding populations for British Columbia was quite narrow, with heritabilities in the order of 0.40 for growth traits. Hook et al. (1990) found similar values for growth traits and biomass partitioning among 36 half-sib families from Washington sources below 300 m elevation. They calculated heritabilities ranging from 0 to 0.39 for growth traits like height, diameter and above ground biomass. Heritabilities for dry weight partitioning were rather high ranging from 0.39 to 0.63. However, when this study was repeated four years later, traits for biomass partitioning were also found to be low (Ager and Stettler 1994). Heritabilities in traits for biomass partitioning, e. g. stem harvest index, were also close to zero in this trial (data not shown).

Branch size and form score showed lower heritability estimates than growth traits (Table 5. 1.), although quality-related traits are usually under stronger genetic control (Cornelius 1994). The form score does not appear to have sufficient genetic variability to allow substantial improvement from selection. It is, however, positively correlated with growth traits (Table 5. 2.) and form will therefore not be adversely influenced by selection for better growth. Breeding for trees with many small rather than a few large branches may not be easily accomplished due to substantial adverse genetic correlations with other growth traits. Pruning ability and the incidence

Table 5. 1. Variance components and individual heritabilities for B. C. provenances evaluated at Surrey (unless planting location specified otherwise).

Trait	Range of P			Range of F			Variance components							
	Mean	Min.	Max.	Min.	Max.		B	P	P*B	F(P)	F(P)*B	E	h ² (Sterr)	h _{BC} ² (Sterr)
<u>Seedling evaluation</u>														
Leaf abscission (day)	329	310	343	312	341		2.5	21.6	2.6	8.1	1.6	50.2	0.54 (0.04)	1.41 (0.04)
Bud break (day)	84	75	93	78	90		0.2	4.5	1.6	3.9	1.4	38.4	0.35 (0.04)	0.68 (0.05)
Diameter (cm)	2.66	2.01	3.11	2.31	2.86		0.2	0.6	0.3	1.6	0.7	17.2	0.33 (0.04)	0.43 (0.04)
Height (m)	2.23	1.64	2.77	1.94	2.55		9.0	15.0	4.0	11.0	16.0	75.0	0.43 (0.04)	0.86 (0.05)
Height (at Terrace)	0.74	0.43	1.03	0.52	0.91		38.2	26.5	64.9	16.9	27.8	363.7	0.17 (0.08)	0.35 (0.08)
Height (at Bowser)	1.54	1.05	1.99	1.28	1.82		5.4	119.6	54.4	28.8	31.1	666.6	0.16 (0.07)	0.66 (0.07)
Height (at Saanich)	1.46	1.01	1.92	1.19	1.74		40.4	50.9	123.8	38.1	49.2	205.7	0.52 (0.09)	0.76 (0.09)
<u>4-year evaluation</u>														
Height (m)	4.89	3.65	5.97	4.11	5.64		67	443	604	448	281	4661	0.33 (0.06)	0.55 (0.06)
DBH (cm)	2.95	1.98	4.35	2.26	3.84		3.35	1.59	0.00	5.42	1.82	56.13	0.34 (0.06)	0.43 (0.06)
Stem dry weight (kg)	1.03	0.62	1.87	0.78	1.38		197	6881	9460	36663	12546	258070	0.48 (0.16)	0.54 (0.15)
Total dry weight (kg)	1.24	0.73	2.34	0.93	1.64		928	8448	9146	56979	18744	425146	0.46 (0.16)	0.50 (0.15)
Form Score	2.98	1.67	3.99	2.19	3.89		0.01	0.03	0.01	0.05	0.00	1.37	0.13 (0.04)	0.22 (0.04)
Branch Size (g)	11.4	4.6	19.9	8.5	13.7		0.17	0.27	0.18	3.28	2.08	33.30	0.34 (0.16)	0.36 (0.14)
Wood density (g/cm ²)	0.36	0.32	0.41	0.34	0.38		0	1E-05	4E-05	8E-06	3E-05	0.0006	0.05 (0.15)	0.10 (0.11)

Note: B, block; P, provenance; F(P), family within provenance; E, experimental error; h², heritability; h_{BC}², heritability for selection across provenances in British Columbia; Sterr, standard error of heritability.

Table 5. 2. Genetic correlations (upper right) and phenotypic correlations (lower left) for traits evaluated at age four.

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Height (1)		0.92	0.75	0.72	0.15	0.62	0.05
Diameter (2)	0.82		0.88	0.85	0.32	0.70	0.01
Stem dry weight (3)	0.80	0.92		0.99	0.35	0.81	0.00
Total dry weight (4)	0.78	0.91	0.99		0.36	0.84	0.08
Form Score (5)	0.37	0.40	0.22	0.23		0.20	0.00
Branch Size (6)	0.57	0.79	0.82	0.84	0.26		0.02
Wood density (7)	0.09	0.07	0.07	0.01	0.01	0.06	

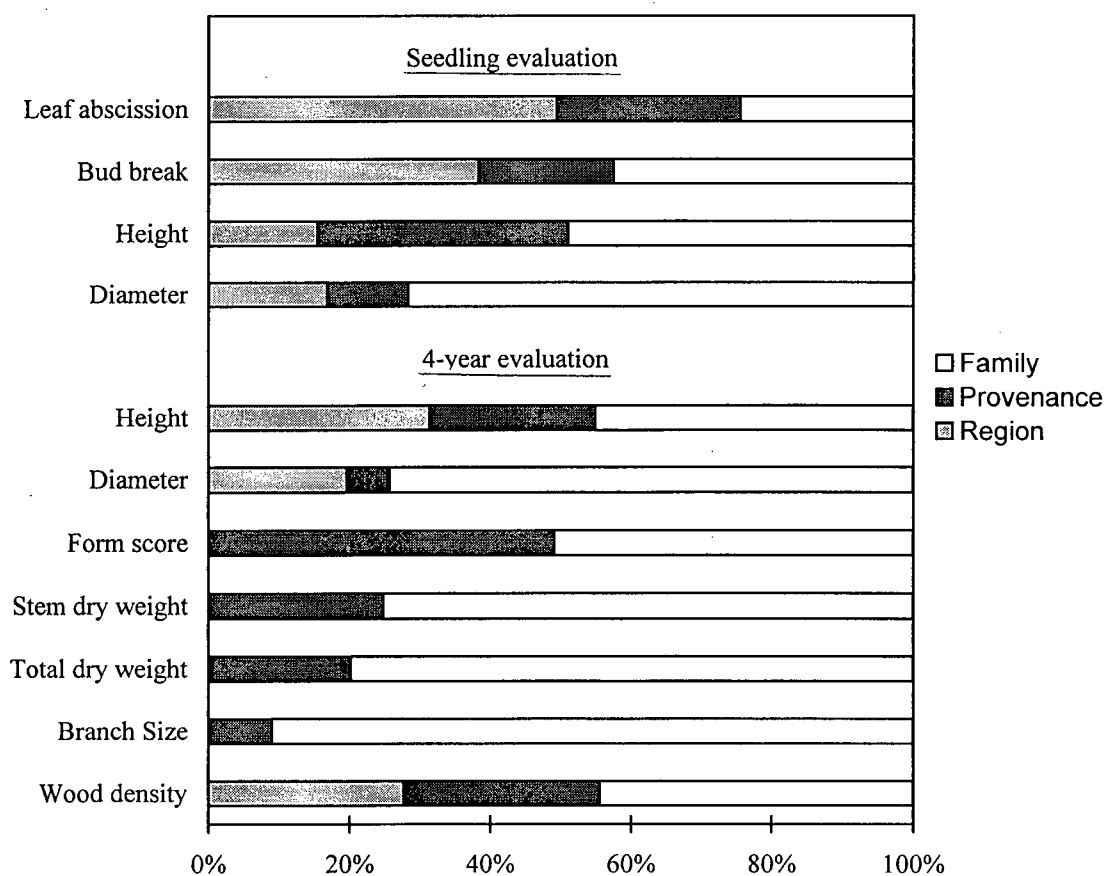


Figure 5. 1. Genetic intraclass correlations for traits in B. C. provenances evaluated at the Surrey-I plantation. Effects due to regions are based on groups of provenances defined in Figure 3. 1.

of multiple leaders could not be subjected to analysis of variance, since the frequency distribution for the measured traits was logarithmic. Most trees had a single leader or retained no lower branches, and few trees had a large number of leaders or retained large numbers of branches on the lower stem. The incidence of more than two leaders and large numbers of branches on the lower bole was clearly restricted to a few families, suggesting that their exclusion from breeding populations would eliminate these characteristics.

Heritability for wood density is close to zero, which is in accordance with results of other studies for this species. Harrington and DeBell (1980) did not find significant differences in wood specific gravity among provenances. Another study conducted in France by Radi and Hibbs (cited in Ager and Stettler 1994) also indicated that differences in wood specific gravity are small and mostly not statistically significant. Further, no significant genetic correlations were found between specific gravity and either growth rate or distance from the pith. There is apparently little potential to improve wood properties in red alder. In general, wood properties are under relatively strong genetic control in most tree species (Zobel and van Buijtenen 1989), and Daniels (1995) warned that ignoring wood specific gravity in red alder would be risky since the studies cited above were rather inconclusive because of limited sample sizes and juvenile material. Since this is also true for this study, the non-genetic literature on red alder wood properties should be reviewed, because it clarifies this problem to some degree.

Lei et al. (1997) investigated wood specific density and other measures as a function of growth rate in red alder plantations. Fiber length and vessel diameter were dependent on growth rates, but they found no correlations in wood properties of economic importance for either timber or pulp production. Lowell and Krahmer (1993) found that tension wood due to lean in red alder has no effect on wood density. Both studies are consistent with results from Gartner et al. (1997), who also found that fiber length and vessel diameter were the only variables that increased from

the center to the periphery (i. e. reflecting growth rate). They also found that reaction wood from lean was not significantly different in a number of measures, and that most wood properties were remarkably uniform throughout stems. These results indicate that growth rates of red alder can be increased through breeding or silvicultural practices with few negative effects on wood and fiber quality.

The results in this study differ from those of Ager and Stettler (1994), who reported large genetic variation between populations but very limited within-population genetic variance. I found substantial within provenance and within family variation in most traits, although adaptive traits in particular had large among population variance components (Table 5. 1., Figure 5. 1.).

5. 4. 3. Improved estimates for selected traits

A plot of the residual error variation revealed non-random patterns that are not necessarily accounted for by blocking at all sites. Spatial patterns of residuals in height are illustrated for the Saanich planting site in Figure 5. 2., where positive residuals for individual observations are in dark shades and negative residuals in light shades. Residuals are spatially dependent up to a distance of approximately 20 m according to the semivariogram in Figure 5. 3a., where the squared difference among any two observations is plotted as a function of their distance. The squared difference does not increase beyond 20 m indicating spatial independence, and it has a value of approximately 800 cm^2 at zero distance, which is the residual variance that cannot be explained by spatial autocorrelations. Predicted residuals based on this semivariogram for the Saanich plantation as well as for two the two trials at Surrey are shown in Figures 5. 4. and 5. 5. The maximum distance of spatial dependence for height growth was around 25 m at the Surrey-I

plantation, and about 40 m at the Surrey-II trial. In contrast to residuals for growth traits, residuals for bud break and leaf abscission measurements were not spatially dependent (Figure 5. 3b.).

After predicted residuals had been subtracted from the original data, the analysis was repeated and the changes in variance components are shown in Table 5. 3. Block effects approach zero as expected, and also interactions of provenance and family effects are eliminated or substantially reduced. Simple effects due to families and provenances increase accordingly, while the residual error variation stays approximately the same. Particularly the variance component due to provenances are substantially increased for height and diameter at the Surrey-I plantation (20% and 40% respectively), which is reflected in increases of heritability for selection across provenances (h_{BC}^2). The explanation for the limited effect on heritability for within provenance selection (h^2) lies in the experimental design. The split plot design with families in subplots ensures a better estimate of family within provenance effects, because they are physically close and therefore less affected by site variation.

The incomplete block design of the Surrey-II plantation accounted for most of the environmental gradient. In fact the complete blocks alone would have been sufficient, since they were positioned from north to south, across the environmental gradient (Figure 5. 6.). Analysis as a complete block design (not shown), as an incomplete block design, and adjustment for spatial dependence (Table 5. 3.) yield approximately the same variance components for provenance and family effects and similar heritabilities.

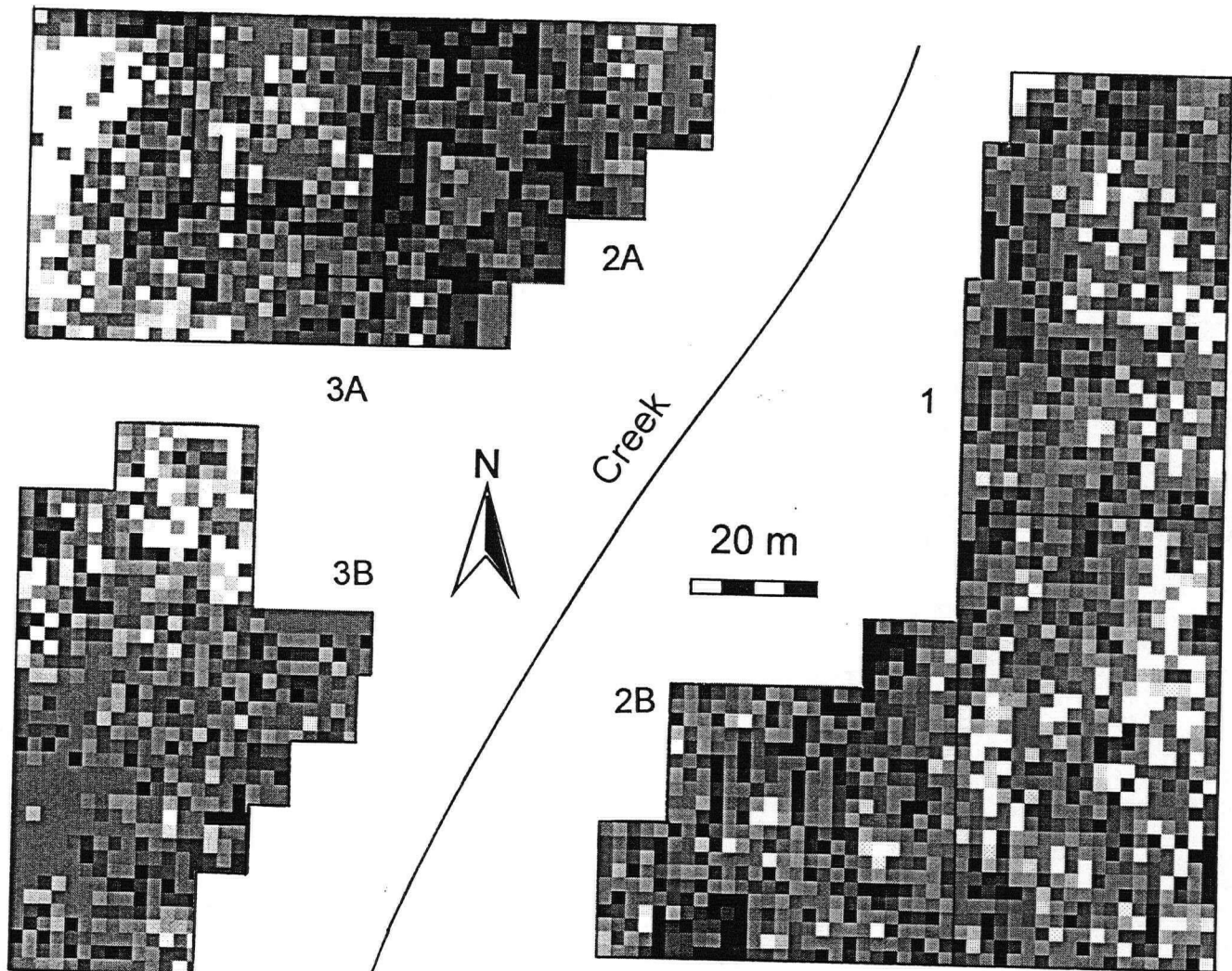


Figure 5. 2. Residual error variation after analysis of variance at the Saanich field trial. Light shades indicate negative residuals, dark shades represent positive residuals (residuals range from -38 to 35 cm)

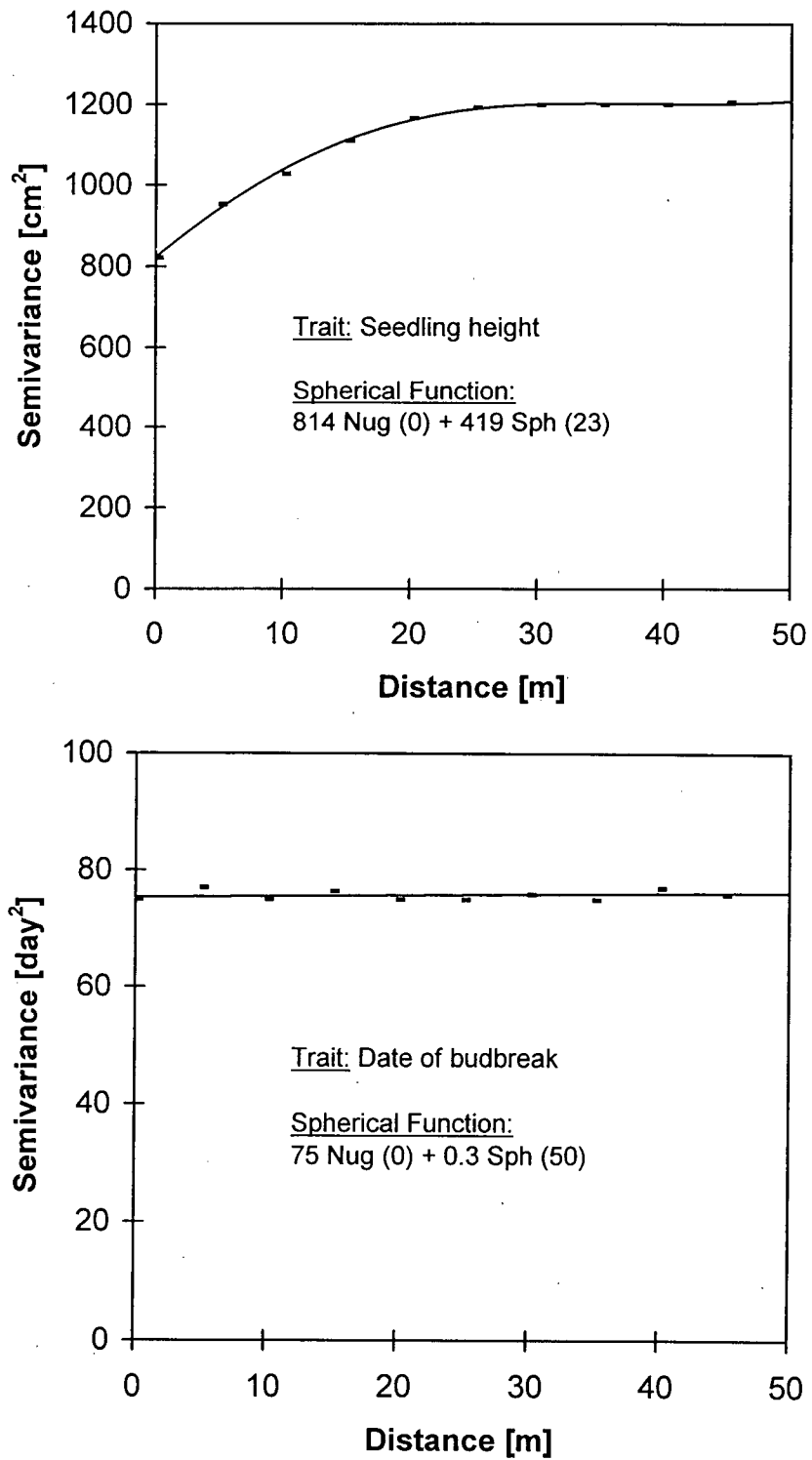


Figure 5. 3. Semivariograms for height at the Saanich trial (above), and bud break at the Surrey-II trial (below).

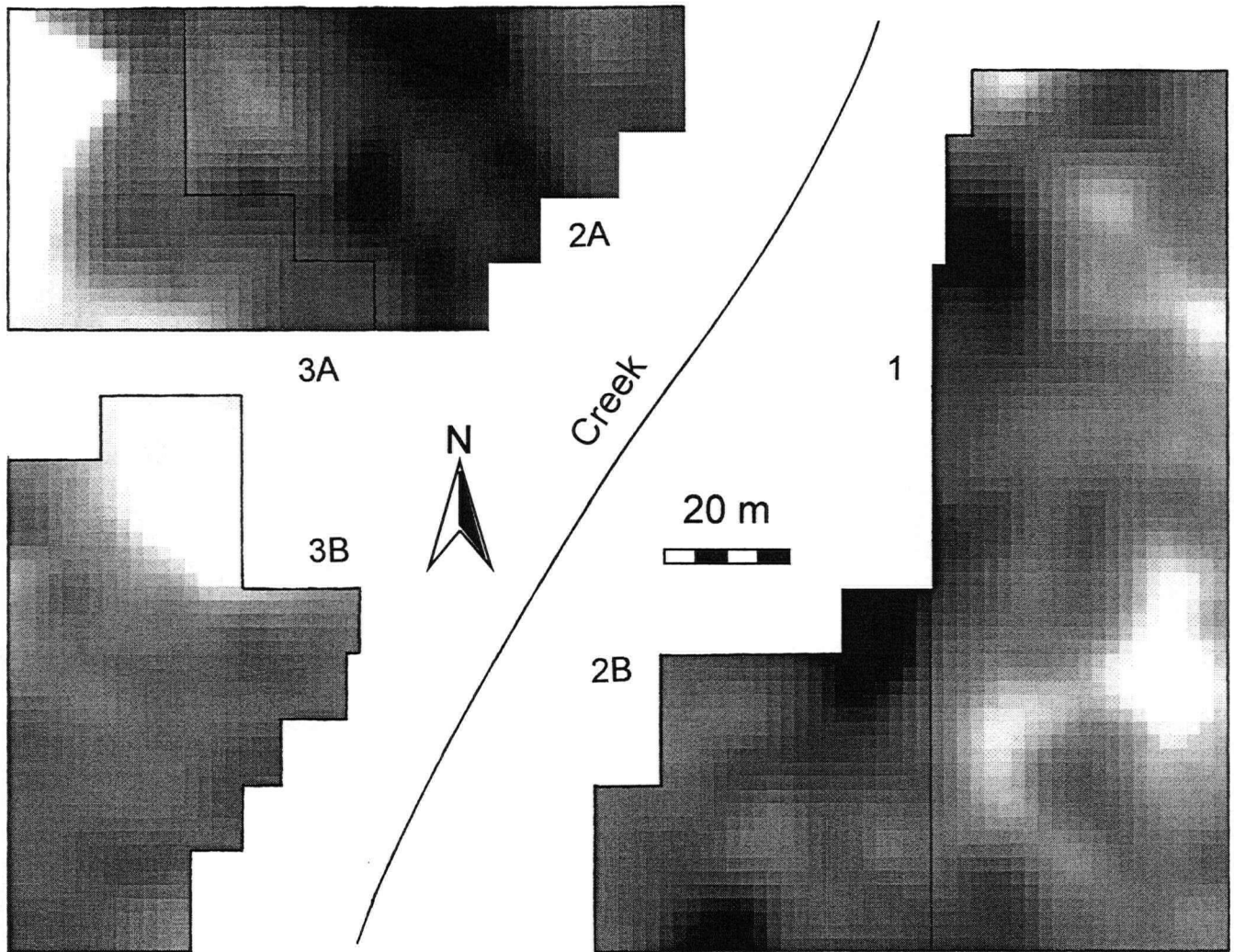


Figure 5. 4. Variation due to autocorrelation in residual values for height, predicted by the kriging method, at the Saanich field trial. Light shades indicate negative residuals, dark shades represent positive residuals (residuals range from -21 to 21 cm)

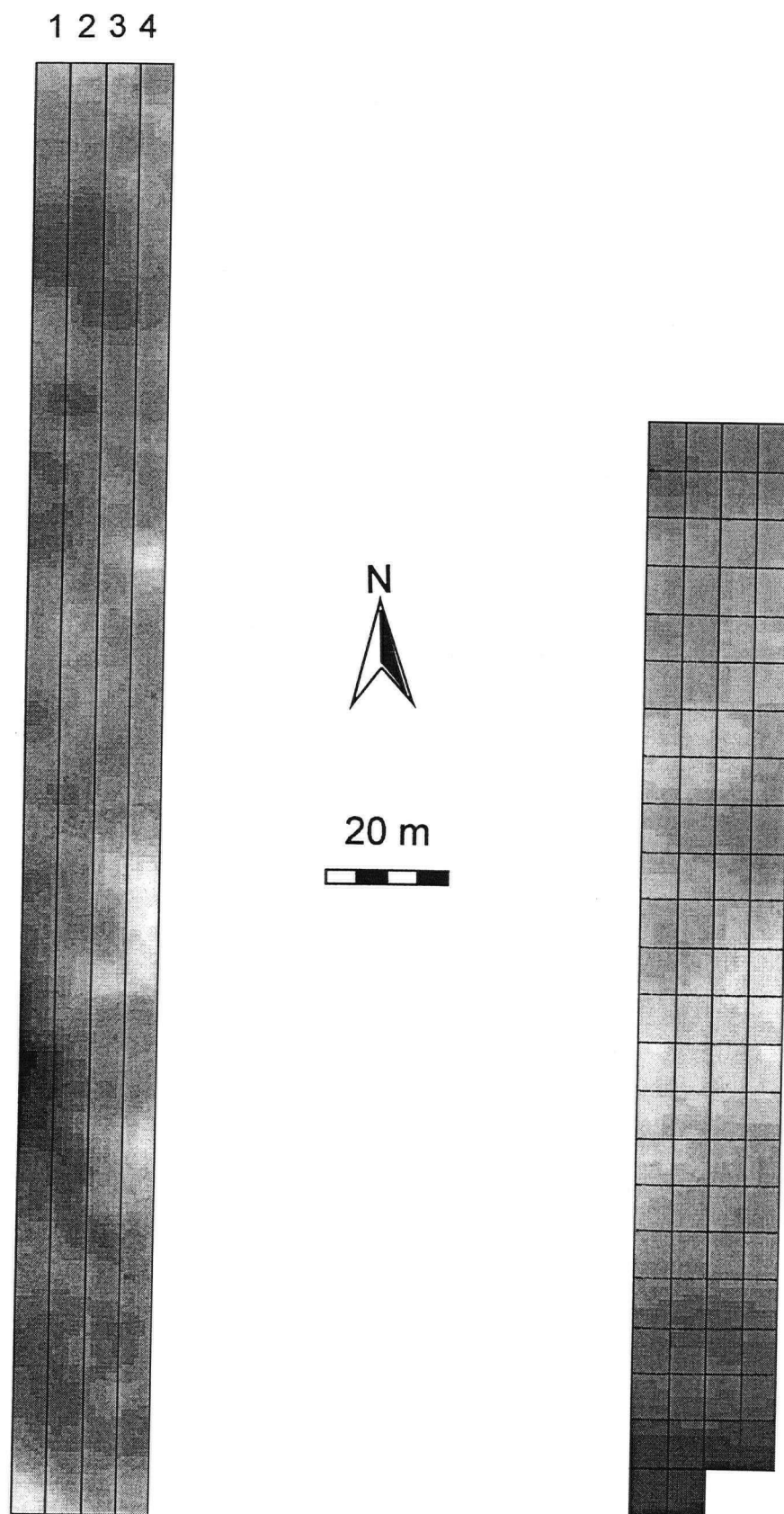


Figure 5.5. Variation due to autocorrelation in residual values for height, predicted by the kriging method, at the Surrey-I (left) and Surrey-II (right) field trials. Light shades indicate negative residuals, dark shades represent positive residuals (residuals range from -48 to 46 cm and from -10 to -12 cm for Surrey-I and II, respectively)

Table 5. 3. Variance components and individual heritabilities using the normal model (N), and after adjustment for spatially autocorrelated variation (A).

Trait	Model	Variance components									h ² (Sterr)	h _{BC} ² (Sterr)
		B	P	P*B	I(B)	P*I	F(P)	F*B	F*I	E		
<u>Surrey I plantation</u>												
Height	N	61	151	280			168	63		1604	0.37 (0.05)	0.56 (0.05)
Height	A	1	191	0			181	27		1563	0.41 (0.05)	0.76 (0.05)
Diameter	N	1.3	0.6	1.0			2.7	0.8		61.2	0.17 (0.04)	0.20 (0.04)
Diameter	A	0.6	1.0	0.0			2.9	0.3		60.9	0.18 (0.04)	0.24 (0.04)
Leaf absc.	N	2.6	21.3	2.7			8.1	1.4		50.4	0.54 (0.06)	1.41 (0.06)
Leaf absc.	A	0.2	21.9	0.0			8.3	0.8		49.7	0.56 (0.06)	1.50 (0.06)
Bud break	N	0.2	4.6	1.6			3.8	1.5		38.4	0.35 (0.05)	0.67 (0.05)
Bud break	A	0.1	4.9	0.0			4.0	0.9		38.4	0.37 (0.05)	0.74 (0.05)
<u>Surrey II plantation</u>												
Height	N	5.4	2.6	1.1	0.2	0.0	7.9	12.1	0.2	35.3	0.57 (0.11)	0.70 (0.11)
Height	A	0.0	2.6	0.5	0.0	0.0	8.1	10.9	0.0	35.2	0.59 (0.11)	0.75 (0.11)

Note: B, block; I(B), incomplete block within block; P, provenance; F(P), family within provenance; E, experimental error; h^2 , heritability; h_{BC}^2 , heritability for selection across provenances in British Columbia; Sterr, standard error.

Table 5. 4. Genetic correlations before (upper right) and after (lower left) adjustment for spatially autocorrelated variation. Standard errors are given in parentheses.

	Trait			
	Height	Diameter	Leaf absc.	Bud break
Height		0.86 (0.04)	0.31 (0.04)	-0.45 (0.04)
Diameter	0.87 (0.04)		0.35 (0.04)	0.56 (0.04)
Leaf abscission	0.32 (0.04)	0.37 (0.04)		0.08 (0.04)
Bud break	-0.46 (0.04)	0.56 (0.04)	0.09 (0.04)	

5. 5. Conclusions

It has been repeatedly stated, that red alder is morphologically remarkably uniform throughout its range. Stem form, branchiness, branch angle, leaf size and leaf shape are all considered homogeneous in populations from California to Alaska including outlying populations in Idaho. Presumably, intense natural selection in dense, even-aged stands has reduced the genetic variability in morphological and other traits (Ager and Stettler 1994). This report suggests that at least for traits of economic importance this is not necessarily true. Daniels (1995) suggested that there is little opportunity for genetic improvement in growth and form traits within populations. Substantial within population variance observed in this study is an important finding and shows that genetic improvement through selection and breeding is possible. Assuming a selection intensity of 1.75 (likely for selection within a subset of provenances in current trials), and given heritabilities in the order of 0.40, genetic gain in growth traits from individual selection would range from 25 to 35%. Small improvements (approximately 5%) would indirectly be achieved in the form score, and exclusion of a few families with extensive incidence of multiple leaders and insufficient self pruning would probably eliminate these undesirable characteristics.

Kriging removed block effects and reduced the family \times block interaction in all traits. The variation due to interactions was recovered in simple family or provenance variance components, which increased by 2 to 40% for various traits. The improvement was largest in experiments where blocking was clearly inadequate to capture site variation, when block size was large, and for traits that could be influenced by variation in soil properties. Changes in provenance and family variance components for phenology traits were relatively minor. Genetic correlations showed only a minimal change. The experimental error and standard errors of estimates of genetic parameters did not change or decreased by only a small amount. The results suggest that

there would be little harm in subtracting values predicted by kriging, even when there are no trends in the experimental material. I recommend that variograms should routinely be constructed to test if residuals are spatially autocorrelated. If they are, kriging is proposed as a useful supplement to ANOVA in tree breeding experiments in order to improve estimates of breeding values and heritabilities.

5. 6. References

- Ager, A. A. and Stettler, R. F. 1994. Genetics of red alder and its implication for future management. In *The Biology and Management of Red Alder*. Oregon State University Press, Corvallis, Oregon, pp. 92-105.
- Bresler, E. S., Dasberg, D. R., and Dagan, G. 1981. Spatial variability of crop yield as a stochastic process. *Soil Sci. Soc. Am. J.* 45: 600-605.
- Brownie, C., Bowman, D. T. and Burton, J. W. 1993. Estimating spatial variation in analysis of data from yield trials: a comparison of methods. *Agron. J.* 85: 1244-1253.
- Burgess, T. M. and Webster, R. 1980a. Optimal interpolation and isarithmic mapping of soil properties: I. The semivariogram and punctual kriging. *J. Soil Sci.* 31: 315-331.
- Burgess, T. M. and Webster, R. 1980b. Optimal interpolation and isarithmic mapping of soil properties: II. Block kriging. *J. Soil Sci.* 31: 333-341.
- Burrough, P. A. 1993. Soil variability: a late 20th century view. *Soils & Fertilizers* 56: 529-562.
- Burrough, P. A. and McDonnell, R. A. 1998. *Principles of Geographic Information Systems*. Oxford University Press, Oxford, United Kingdom.
- CISRO/BioSS Inc. 1994. Alpha+ version 2.3. user's manual. CSIRO Publications, East Melbourne, Australia.
- Clarke, F. R. and Baker, R. J. 1996. Spatial analysis improvement precision of seed lot comparisons. *Crop Sci.* 36: 1180-1184.
- Clarke, F. R., Baker, R. J., and DePauw. 1994. Moving mean and least squares smoothing for analysis of grain yield data. *Crop Sci.* 34: 1479-1483.

- Cornelius, J. 1994. Heritabilities and additive genetic coefficients of variation in forest trees. *Can. J. For. Res.* 24: 2, 372-379.
- Correll, R. L. Cellier, K. M. 1987. Effects of plot size, block size and buffer rows on the precision of forestry trials. *Austr. For. Res.* 17: 11-18.
- Correll, R. L. Anderson, R. B. 1983. Removal of intervarietal competition effects in forestry varietal trials. *Silv. Genet.* 32: 162-165.
- Cullis, B. R. and Gleeson A. C. 1991. Spatial analysis of field experiments - an extension to two dimensions. *Biometrics* 47: 1449-1460.
- Daniels, J. D. 1995. Managing red alder genetic resources: options for cooperative tree improvement. Unpublished manuscript prepared for Oregon Department of Forestry and USDA Forest Service, State and Private Division.
- Ericsson, T. 1997. Enhanced heritabilities and best linear unbiased predictors through appropriate blocking of progeny trials. *Can. J. For. Res.* 27: 2097-2101.
- Gartner, B. L., Lei, H., and Milota, M. R. 1997. Variation in the anatomy and specific gravity of wood within and between trees of red alder (*Alnus rubra* Bong.). *Wood & Fiber Sci.* 29: 10-20.
- Graham, R. L., Grotschel, M., and Lovasz, L. 1995. Handbook of combinatorics. Elsevier, New York.
- Green, P. J., Jennison, C., and Seheult, A. H. 1985. Analysis of field experiments by least squares smoothing. *J. R. Statis. Soc. B.* 47: 299-315.
- Harrington, C. A. and DeBell, D. S. 1980. Variation in specific gravity of red alder (*Alnus rubra* Bong.). *Can. J. For. Res.* 10: 293-299
- Hook, D. D., DeBell, D. S., Ager, A. A., and Johnson, D. 1990. Dry weight partitioning among 36 open-pollinated red alder families. *Biomass* 21: 11-25.
- John, S. E. T. 1995. Using alpha designs to control site heterogeneity in forestry field tests. *ForMat* 7: 3-4.
- Klein, J. I. 1989. Effects of incomplete block design and stand structure on heritability of growth in a jack pine family test in Manitoba. *Can. J. For. Res.* 19: 1044-1050.
- Lei, H., Gartner, B. L., and Milota, M. R. 1997. Effect of growth rate on the anatomy, specific gravity, and bending properties of wood from 7-year-old red alder (*Alnus rubra*). *Can. J. For. Res.* 27: 80-85.

- Lopez, M. V. and Arrue, J. L. 1995. Efficiency of an incomplete block design based on geostatistics for tillage experiments. *Soil Sci. Soc. Am. J.* 59: 1104-1111.
- Lowell, E. C. and Krahmer, R. L. 1993. Effects of lean in red alder trees on wood shrinkage and density. *Wood & Fiber Sci.* 25: 2-7.
- Pebesma E. J. and Wesseling C. G. 1998. Gstat, a program for geostatistical modeling, prediction and simulation. *Computers and Geosciences* 24: 17-31.
- Samra, J. S., Anlauf, R. Weber, W. E. 1990. Spatial dependence of growth attributes and local control in wheat and oat breeding experiments. *Crop Sci.* 30: 1200-1205.
- Samra, J. S., Hill, H. S., Anlauf, R., and Richter J. 1989 Geostatistical evaluation of soil sodicity and growth of *Melia azadarach* L. as simultaneous stochastic process. *Soil Sci.* 148: 361-369.
- SAS Institute Inc. 1988. SAS/STAT user's guide, release 6.03 edition, Cary, N. C.
- Stonecypher, R. W. 1992. Computational methods. In L. Fins, S. T. Friedman, J. V. Brotschol (eds). *Handbook of Quantitative Forest Genetics*, pp 195-228. Kluwer Academic Publishers, Dordrecht, Netherlands.
- Stroup, W. W., Baenzinger, P. S., and Mulitze, D. K. 1994. Removing spatial variation from wheat yield trials: a comparison of methods. *Crop Sci.* 34: 62-66.
- Stroup, W. W. and Mulitze, D. K. 1991. Nearest neighbor adjusted best linear unbiased prediction. *Am. Stat.* 45: 194-200.
- Thomson, A. J. El-Kassaby, Y. A. 1988. Trend surface analysis of a Douglas-fir provenance-progeny transfer test. *Can. J. For. Res.* 18: 515-520.
- Williams, E. R. Matheson, A. C. 1994. *Experimental design and analysis for use in tree improvement*. CSIRO Publications, East Melbourne, Australia.
- Williams, G. N., Eckert, S. A., Hancock, T. W., and Mayo, O. 1983. Nearest neighbor (NN) analysis of field experiments. *J. R. Statis. Soc. B.* 45: 151-200.
- Zobel, B. J. and van Buijtenen, J. P. 1989. *Wood variation, its causes and control*. Springer Verlag, Berlin, 363 pp.

Chapter 6.

A multiple population breeding strategy for uncertain climatic futures: genecological studies and selection experiments with *Alnus rubra*.

6. 1. Abstract

A breeding strategy for red alder in British Columbia was derived as a synthesis of the three preceding chapters, using information on genecology (Chapter 3), risk associated with seed transfer (Chapter 4), and genetic parameters (Chapter 5). Analysis of phenological traits and growth rates throughout the season revealed that synchronization of bud break and growth cessation with the available growing season has important effects on growth. Using breeding populations for existing climatic conditions under the scenario of climatic warming would likely result in a lack of synchronization between phenological and climatic events. Timing of growth cessation, which is largely controlled by day length, would require a uniform shift of deployment targets of breeding populations to the north. Optimal timing of bud break, in contrast, would probably require variable shifts of deployment targets to the south or to the coast, depending on the geographic region. This indicates that coverage of future climatic conditions may not be accomplished by shifting provenances to new locations, but requires the development of populations with novel combinations in adaptive and growth traits. To cope with possible effects of climatic warming, it is suggested to develop populations with alternative combinations in adaptive traits for all regions in British Columbia. A multiple breeding strategy with six breeding populations was proposed, and a breeding experiment using restricted index selection for

multiple traits was carried out to estimate genetic parameters and to investigate if selection targets could be met.

6. 2. Introduction

Timing of phenological events in forest trees such as bud burst, onset of dormancy, and frost hardening are considered essential adaptations in temperate climates. If the phenology is not well synchronized with climatic conditions, trees may suffer frost damage or fail to fully utilize favorable growing conditions at the site. Global climate change could cause such a lack of synchronization. The global temperature is expected to rise in future decades, and warming has been predicted to be especially pronounced during autumn, winter, and spring in regions located at high latitudes, such as British Columbia (Pedersen 1993). The predicted warming could have various impacts on the synchronization of phenological events in forest trees and climatic events at the site. First, the dates marking the beginning and the end of favorable growing conditions may shift; second, environmental cues that control phenological events may disappear or shift to different dates; and third, probabilities of climatic events (e. g. frost) subsequent to an environmental cue may change. In addition to lack of synchronization, there could be a lack of adaptation to conditions such as a higher moisture deficit during summer.

The response of phenotypes to climate change is likely to differ among provenances of wide ranging species. For example, consider that bud flush in trees is usually initiated after chilling during winter gradually releases dormancy, and after a certain heat sum that depends on previous chilling is accumulated in spring (Vegis 1964; Perry 1971). In regions with mild winters, climatic warming could cause a chilling deficit and therefore a delayed bud burst, resulting in failure to

utilize favorable growing conditions in earlier springs (Kramer 1994). In other regions, where chilling requirements are far exceeded by winter temperatures, climatic warming would only advance bud burst and could enhance the risk of frost injuries in spring (Murray et al 1989; Hänninen 1991). Other examples could be theoretically constructed, where the response and potential problems that arise depend on particular site conditions (e. g., snow cover, moisture deficit, temperature amplitude in fall and spring), and physiological characteristics of the genotypes (e. g., base temperature for growth, heat sum requirements, day length). Whether such problems could and should be addressed by a breeding strategy depends on genetic control and variability of adaptive traits, and whether changes entail serious problems for forestry operations. There is some indication that frost damage is a particular problem for interior and northern regions of Canada where species (or genotypes) usually have a shorter period of dormancy than in coastal areas (Braatne 1957; van der Kamp and Worrall 1990).

Since there is a limited understanding of response of genotypes to changes in climate, and potentially a large error in predicted climate change itself, a breeding strategy must incorporate these elements of uncertainty. Multiple population breeding has been suggested for such a situation (Namkoong et al. 1988; Eriksson et al. 1993). A system of multiple populations is also useful to manage and maintain genetic diversity of a large genetic resource (Namkoong 1976, 1984, 1986). According to this system, a large resource is subdivided into several smaller populations, so that some of the genetic variability is captured among populations. In the most elaborate form, these populations are established over a broad array of sites, thus sampling a wide range of environmental conditions. Then selection within populations can aim at improved adaptedness of each population to specific site conditions and increased genetic variability among them. This approach could be extended to include not only breeding populations for existing environmental conditions, but also for probable future requirements. Coverage of future climatic conditions may be accomplished by simply assigning new deployment targets for

multiple populations, or it may require the development of populations with novel combinations in adaptive and growth traits.

Designing a breeding strategy for a species that takes effects of climate change into account requires knowledge of the response in phenological traits to warming for a sample of populations from the region of interest. Such data are not available for red alder in British Columbia, and are generally lacking in any breeding program. However, the mechanisms that control phenological traits in trees, and the relation of these mechanisms to climatic conditions at the source location of provenances is well researched. In this chapter I review these mechanisms with emphasis on studies with species related to, or sympatric with red alder. The objective of this section is to design a multiple breeding strategy that can cope with possible effects of climatic warming, given existing provenance data and incomplete information on phenotypic response to climate change. I derive which trait combinations are most likely required for current and possible future climates in British Columbia, and I use genetic data from a breeding experiment to investigate if selection targets could be met.

6. 3. Material and Methods

6. 3. 1. Selection experiment

This experiment establishes multiple breeding populations of red alder from diverse sources throughout B. C. Within each population a combination of traits is selected for, using a restricted selection index (Kempthorne and Nordskog 1959), that emphasizes advance in one or two traits,

while keeping the others constant (Figure 6. 1.). The computing algorithm for index weights that satisfy this restriction is:

$$\mathbf{b} = [\mathbf{I} - \mathbf{P}^{-1} \mathbf{G} \mathbf{C} (\mathbf{C}' \mathbf{G}' \mathbf{P}^{-1} \mathbf{G} \mathbf{C})^{-1} \mathbf{C}' \mathbf{G}'] \mathbf{P}^{-1} \mathbf{G} \mathbf{a}$$

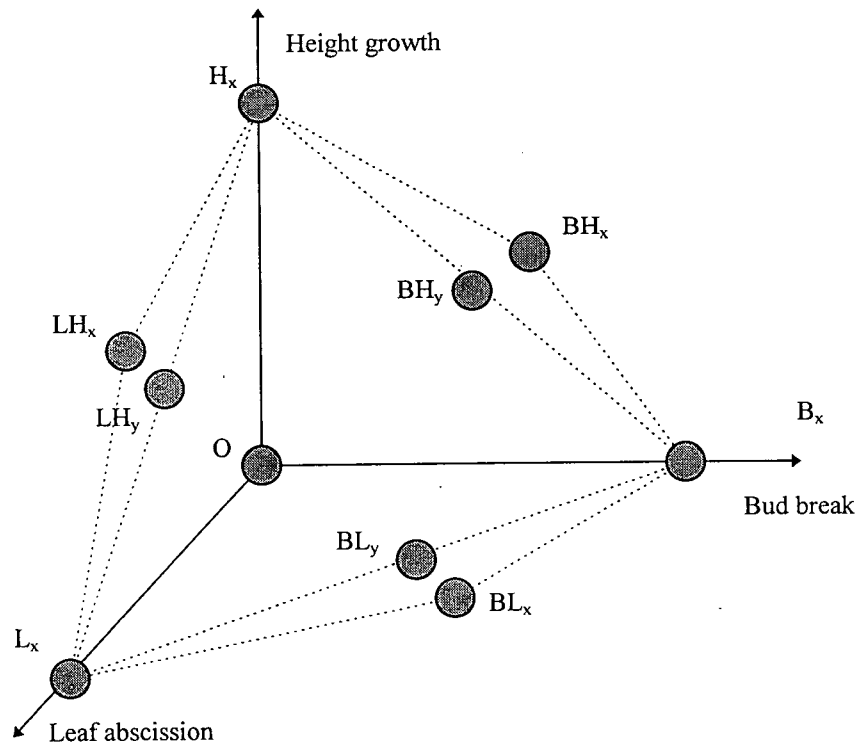


Figure 6. 1. Selection scheme for breeding experiment (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, population based on parents selected for the same trait or trait combination; y, population based on parents selected for different traits).

		female								L								H							
		1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8	1	2	3	4	5	6	7	8
male	9	x	x	x	x													y	y	y	y				
	10	x	x	x	x													y	y	y	y				
	11	x	x	x	x													y	y	y	y				
	12	x	x	x	x													y	y	y	y				
	13					x	x	x	x					y	y	y	y								
	14					x	x	x	x					y	y	y	y								
	15					x	x	x	x					y	y	y	y								
	16					x	x	x	x					y	y	y	y								
B	9	y	y	y	y					x	x	x	x												
	10	y	y	y	y					x	x	x	x												
	11	y	y	y	y					x	x	x	x												
	12	y	y	y	y					x	x	x	x												
	13													x	x	x	x				y	y	y	y	
	14													x	x	x	x				y	y	y	y	
	15													x	x	x	x				y	y	y	y	
	16													x	x	x	x				y	y	y	y	
L	9									y	y	y	y					x	x	x	x				
	10									y	y	y	y					x	x	x	x				
	11									y	y	y	y					x	x	x	x				
	12									y	y	y	y					x	x	x	x				
	13																								
	14																								
	15																								
	16																								
H	9																	x	x	x	x				
	10																	x	x	x	x				
	11																	x	x	x	x				
	12																	x	x	x	x				
	13					y	y	y	y													x	x	x	x
	14					y	y	y	y													x	x	x	x
	15					y	y	y	y													x	x	x	x
	16					y	y	y	y													x	x	x	x

		female							
		1	2	3	4	5	6	7	8
male	9	x	x	x	x				
	10	x	x	x	x				
	11	x	x	x	x				
	12	x	x	x	x				
	13					x	x	x	x
	14					x	x	x	x
	15					x	x	x	x
	16					x	x	x	x
BL	9								
	10								
	11								
	12								
	13								
	14								
	15								
	16								

		female							
		1	2	3	4	5	6	7	8
male	9	x	x	x	x				
	10	x	x	x	x				
	11	x	x	x	x				
	12	x	x	x	x				
	13					x	x	x	x
	14					x	x	x	x
	15					x	x	x	x
	16					x	x	x	x
BH	9								
	10								
	11								
	12								
	13								
	14								
	15								
	16								

		female							
		1	2	3	4	5	6	7	8
male	9	x	x	x	x				
	10	x	x	x	x				
	11	x	x	x	x				
	12	x	x	x	x				
	13					x	x	x	x
	14					x	x	x	x
	15					x	x	x	x
	16					x	x	x	x
LH	9								
	10								
	11								
	12								
	13								
	14								
	15								
	16								

		female							
		1	2	3	4	5	6	7	8
male	9	x	x	x	x				
	10	x	x	x	x				
	11	x	x	x	x				
	12	x	x	x	x				
	13					x	x	x	x
	14					x	x	x	x
	15					x	x	x	x
	16					x	x	x	x
O	9								
	10								
	11								
	12								
	13								
	14								
	15								
	16								

Figure 6. 2. Mating design for breeding experiment (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, cross among parents selected for the same trait or trait combination; y, cross among parent selected for different traits).

where \mathbf{b} is a vector of index weights for a number of traits, \mathbf{I} is the identity matrix, \mathbf{G} is the covariance matrix between observations and breeding values, \mathbf{P} is the phenotypic covariance matrix, and \mathbf{C} is the matrix of restrictions, and \mathbf{a} is a vector of economic weights, which were set to adjust genetic advance in traits to the same magnitude in units of standard deviations (Cunningham et al. 1970).

Since the number of flowers per tree was low, each selected parent could only be used either as male or female. Therefore a partial factorial mating design was used (Figure 6. 2.). Three hundred and twenty different controlled crosses with a total parent population of 112 trees were made and each cross was repeated three times to protect against accidental loss and to generate a sufficient amount of seed. Offspring were germinated in March 1997, transplanted into the field in June 1997 and evaluated at the end of the first growing season for bud break, leaf abscission and height according to the methods described in Chapter 3. 3. 2. Because of variable success in obtaining offspring from controlled crosses (the experiment was designed for a total of 3200 trees and only 420 seedlings could be used), an incomplete unbalanced block design was employed (Appendix 8) and data were evaluated with the mixed model procedure of the SAS statistical software package (SAS Institute 1997). Parameter estimates and standard errors were estimated according to formulas given in Chapter 5. 3. 1. and 5. 3. 2. Individual heritabilities were calculated as the mean of male and female family variance components.

6. 3. 2. Breeding techniques

The proportion of flowering trees at age four was less than 1% and was mostly restricted to border trees. Therefore flower induction treatments were applied during the fifth growing season

to obtain sufficient material for breeding experiments. Little information is available for floral induction in hardwoods, but release and stem girdling have been successfully applied in some cases (Owens and Blake 1985). In two blocks of the Surrey provenance trial branches were girdled, two other blocks received regular stem girdling treatments by cutting two overlapping half circles with a sharp knife through the bark. The fifth block served as a control. Differences among these treatments were minimal, but a thinning treatment applied to all blocks apparently helped to generate sufficient flowering in approximately one quarter of the trees to be included as a male parent (at least four clusters of catkins), and 10% of the trees could be used as female parents (at least 12 clusters of catkins).

Since it is practical to harvest pollen several days before maximum receptivity of female flowers, male flowering was forced 10 days prior normal flowering time by bringing larger branches into a greenhouse. Pollen was collected in paper envelopes fixed at the flowers and was stored in a cooler for later use. Controlled pollination was either carried out with a brush or with syringe when enough pollen was available. Female flowers were pollinated when they changed in orientation from drooping to an upright position and red styles protruding from bracts exuded a pollination drop, indicating receptivity. Pollination bags commonly used for conifers proved to be impractical, since flower buds of red alder are borne terminally on slender new growth and bags could not be tied around sturdier growth of previous years. Therefore mini-bags as described by Wright (1976) were used. Pollination bags were fixed three weeks before flowering and were removed three weeks after pollination work was finished to provide space for shoot and flower development. Seeds were harvested in October and stored in two batches at 4°C and -20°C.

6. 3. 3. Genecological aspects

Monthly height measurements over the period of one year were evaluated to examine differences in growth patterns over the year for provenances from eight regions: Alaska, Queen Charlotte Islands, British Columbia Mainland 49°-51°N, Mainland 51°-53°N, and Mainland 53°-55°N latitude, Vancouver Island Westcoast, Vancouver Island Eastcoast, and Oregon. Further, provenance means for adaptive traits, analyzed in Chapter 3 with regression and multivariate techniques, were investigated with spatial statistical methods described in Chapter 4. 3. 3. to better visualize patterns of geographic variation. (Otherwise, genecology and the effect of climatic warming on phenological traits was discussed drawing mainly on results of the analysis presented in Chapter 3.)

6. 4. Results and discussion

6. 4. 1. Genetic parameters and response to selection

Population means of parent populations selected with restricted selection indices (Table 6. 1.) and the resulting population means of offspring populations are shown in Figure 6. 3. The experiments was originally meant to investigate the effectiveness of different selection methods for simultaneous advance in several traits, and the effects of divergent selection on genetic correlations within breeding populations. There appears to be some response to selection, but because many crosses did not yield offspring, and some populations (BH_x, LH_x, and BL_x) are not represented at all, the original objective, to compare different selection methods

Table 6. 1. Weights for restricted selection indices.

Restriction	Height	Bud break	Leaf abscission
Leaf abscission	-0.0112	0.0312	-0.0112
Bud break	0.0291	0.0130	0.0472
Height	-0.0051	0.0448	0.0458
Leaf ab. & Bud br.	0.0239	0.0164	-0.0116
Leaf ab. & Height	0.0101	0.0349	-0.0065
Bud br. & Height	-0.0148	-0.0135	0.0352

Table 6. 2. Estimated variance components and heritabilities for traits based on fullsib offspring of controlled crosses.

	Height	Bud break	Leaf abscission
B	0.69	0.00	0.14
P	30.52	2.69	4.23
B x P	0.00	0.00	0.00
M(P)	71.35	1.82	6.75
B x M(P)	0.00	0.33	0.00
F(P)	53.44	2.51	3.36
B x F(P)	0.00	0.00	0.00
M(P) x F(P)	0.16	0.29	2.54
Error	381.79	10.94	31.94
Total	537.95	18.58	48.96
V_A (stderr)	249 (27.1)	8.66 (1.01)	20.22 (2.81)
V_D (stderr)	0.64 (1.12)	1.16 (2.34)	10.16 (5.35)
h^2 (stderr)	0.46 (0.21)	0.47 (0.22)	0.41 (0.21)

Note: B, block; P, breeding population; M, male; F, female; V_A , additive variance; V_D , dominance variance; h^2 , individual heritability, Stderr, Standard error.

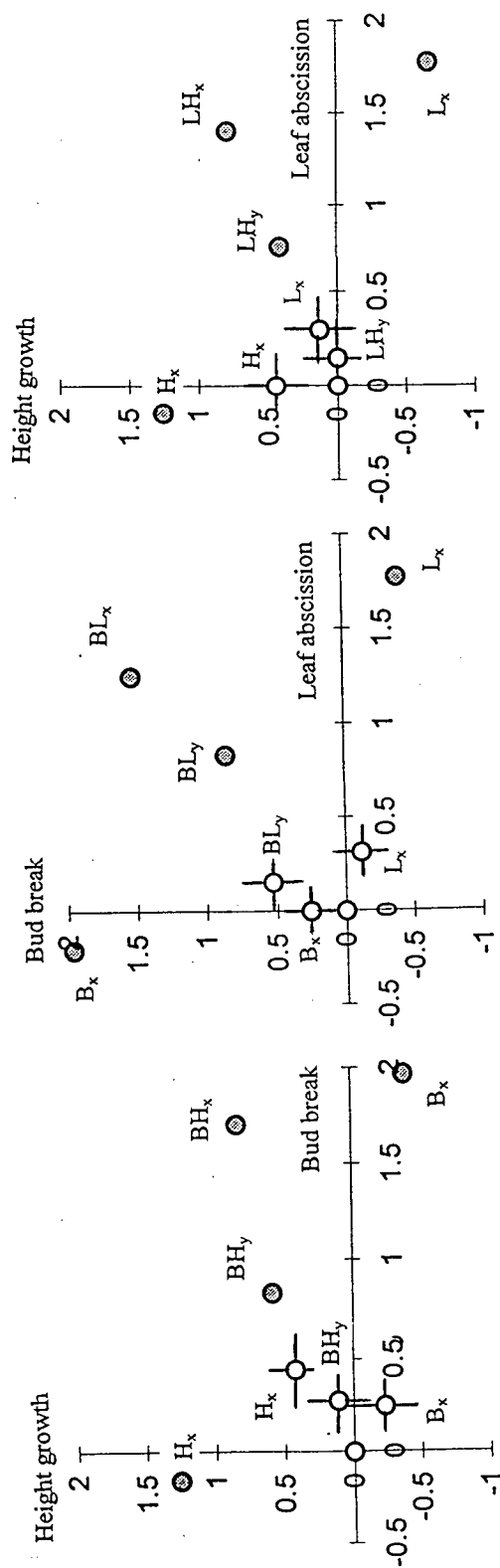


Figure 6.3. Population means for parents (dark) and population means and standard errors for offspring (open). (B, parents selected for late bud break; H, parents selected for height growth; L, parents selected for early leaf abscission; O, no selection (control); x, population based on parents selected for the same trait or trait combination; y, population based on parents selected for different traits).

for multiple trait selection, could not be accomplished. Because of the limited sample size no attempt has been made to estimate genetic correlations. However, partitioning of variance components in this experiment yielded some additional estimates of genetic parameters (Table 6. 2.). Heritabilities are very similar to those obtained in Chapter 5, and the standard error of the estimates is relatively small, considering the limited number of crosses. Further, a large proportion of dominance variation was found for the date of bud break.

6. 4. 2. Possible response to climatic warming

Growth cessation

In determinate species such as oaks and most conifers, which have their leaves preformed in the buds, growth is often completed by the end of June, long before there is danger of fall frost (Perry 1971). Red alder is not determinate in its growth habit, and seedlings grow actively until November (Figure 6. 4.). Although temperatures, nutrient, and moisture availability can prolong or advance the time of growth cessation, the shortening of the photoperiod is the key factor in the initiation of dormancy for temperate tree species in general (Perry 1971). The biology of growth cessation has been very well investigated in birch species, which are closely related to alders (Vaartaja 1954, 1959; Wang and Perry 1958; Clausen and Garrett 1969; Sharik and Barnes 1976; Downs and Bevington 1981; Myking and Heide 1995; Myking 1997), and it can be assumed that photoperiod is the primary cue for growth cessation in alder as well. The date of leaf abscission, used in this study to represent growth cessation, is a reliable indicator, because relatively young leaves that are formed late in the season will not drop readily (note that indeterminate species retain their most peripheral, hence youngest leaves in fall).

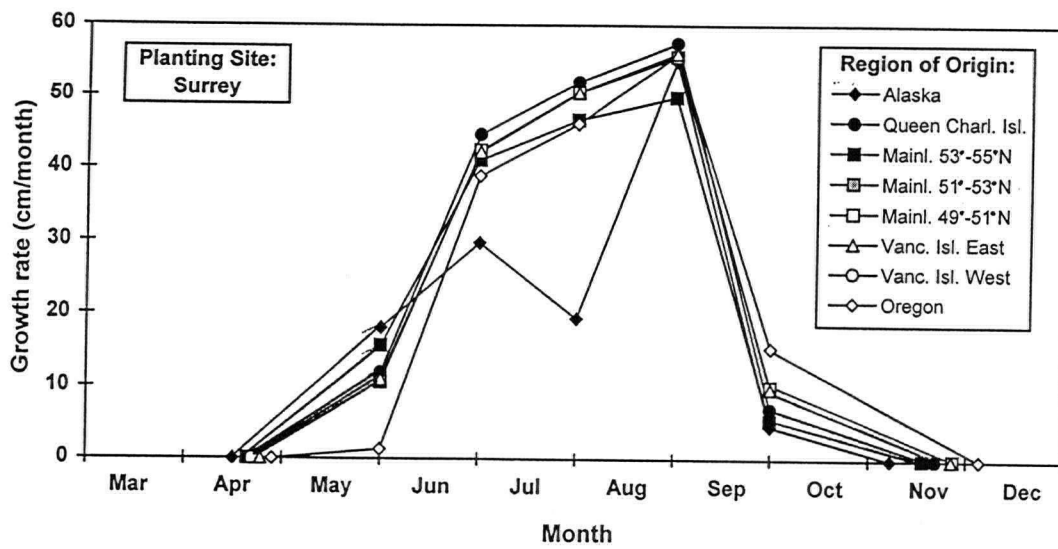


Figure 6. 4. Growth rates during the second growing season for provenances summarized by regions of origin

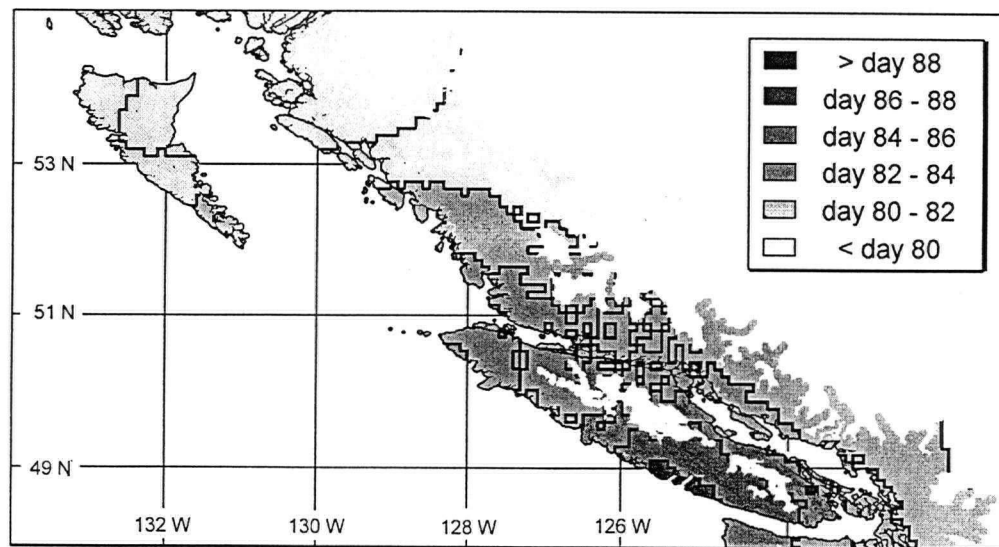


Figure 6. 5. Date of budbreak predicted for provenances when grown at the Surrey planting site. Contours are drawn at intervals of approximately 0.25 standard deviations.

In red alder, northern provenances cease growth earlier, and thus at longer critical photoperiods than southern sources, but there were no significant trends of leaf abscission along elevational clines or with distance from the coast (Figure 6. 4., Table 3. 3., 3. 4. and 3.5). A longer critical photoperiod for growth cessation in northern than in southern provenances has been observed in the related genus of birches (Myking and Heide 1995), as well as in sympatric species such as western hemlock (Kuser and Ching 1980), Sitka spruce (Burley 1966a, 1966b; Douglas et al. 1975), and Douglas-fir (Irgens-Moller 1968). The trend generally holds true for temperate species, since in colder northern environments favorable growing conditions end at longer photoperiods than in southern environments (Morgenstern 1996). Although trends were not significant in this study, high elevation and inland provenances from the same latitude usually cease growth earlier for the same reason (Vaartaja 1954, 1959; Perry 1971; Myking 1997). Campbell and Sorensen (1978) found elevational clines in growth cessation for interior but not for coastal Douglas-fir, the latter being sympatric with red alder, indicating that coastal elevational clines are not steep enough to generate selection pressures that result in genetic differentiation for growth cessation.

When northern provenances are transferred to a southern site with favorable environments in fall, premature growth cessation clearly appears to be a disadvantage compared to local sources. In Table 3. 3. early leaf abscission was associated with reduced height and biomass at the end of the growing season. The adaptive value of timely growth cessation in harsher environments is more questionable. It could be argued that damage by fall frost should not have serious consequences, since it only prevents the recovery of nutrients from leaves, which is not an important process in red alder anyway. However, provenances that cease growth later than local sources (Oregon sources in Figure 6. 4.) exhibit severely retarded growth rate during the first 30 days after bud break. Active growth late in the season may expend resources in the form of carbohydrates that would otherwise be available in spring to sustain high growth rates early in the season. Hence,

premature as well as delayed growth cessation relative to local climates in target areas of breeding populations should be avoided.

The situation for red alder with respect to growth cessation and global warming appears to be quite straight forward, since there is a simple linear cline over latitude and the environmental cue for growth cessation is independent of climate change itself. A multiple population breeding strategy could cope with climatic warming resulting in longer favorable growing conditions in fall simply by shifting deployment to the north.

Bud break

The consequences of climatic warming on growth initiation is more difficult to assess, since warmer springs are not only an environmental change that requires further adaptation, but temperature is also the environmental cue that controls bud burst phenology. First, winter dormancy must be released by exposure to a low temperatures (usually $<5^{\circ}\text{C}$) for a defined period. Then a specified heat sum (e. g., 15°C for 3 weeks or 20°C for 2 weeks) above a threshold temperature (in this case 5°C) will initiate bud flush. Partial chilling usually results in a larger heat sum requirement. Chilling requirement, heat sum requirement, and threshold temperature could be under independent genetic control and can be considered adaptive traits that use temperature as an indicator of the probability of a subsequent frost event. Sometimes short days stabilize dormancy in partially chilled buds (Myking and Heide 1994; Myking 1997), which was interpreted as an additional safeguard for premature bud burst in late fall under mild coastal conditions. Generally, however, photoperiod plays a subordinate role during dormancy release in trees (Vegis 1964, Perry 1971).

In this study, bud break was the only trait that did not follow a general latitudinal cline. The principal component analysis in Chapter 3 revealed that most of the variation in bud break is

orthogonal to variation in other traits (Figure 3. 1., Table 3. 2.). A closer investigation of geographic patterns in bud break shows that coastal provenances in the southern part of British Columbia break bud later than inland sources (Figure 6. 5.). Because this trend is less pronounced further north, and because there were few samples for southern inland sources, the same trend was mainly perceived as a north-south cline by simple regression techniques employed in Chapter 3 (Table 3. 3. to 3. 5.).

Also in other species geographic patterns of genetic variation in bud burst tend to be more complicated than those in growth cessation. They are not consistent among species and trends even vary within wide ranging species for different regions. Dormancy was released earlier in northern than in southern sources in several birch species (Wang and Perry 1958; Clausen and Garrett 1969; Sharik and Barnes 1976; Myking and Heide 1995), lodgepole pine (Hagner 1970), white pine (Mergen 1963), sugar maple (Kriebel and Wang 1962), western hemlock (Kuser and Ching 1980), and Norway spruce (Worrall and Mergen 1967). Opposite trends were described for red maple (Perry and Wang 1960; Kriebel and Wang 1962), Walnut (Bey 1971), sweetgum (Farmer 1968), Douglas-fir (Campbell and Sugarno 1979), and several spruce species (Nienstaedt 1967). More complex patterns in the Pacific Northwest have been described for Sitka spruce (Burley 1966a, 1966b), where in northern regions provenances from higher latitudes flushed first, and inconsistent patterns were found in southern regions. A pattern, where trends in bud flush over latitude are opposite in the northern and southern portion of the species range has been observed for *Populus deltoides* (Nienstaedt 1974). In Douglas-fir Campbell (1974) and Campbell and Sugarno (1979) found that high and low elevation provenances break bud earlier than mid elevation provenances.

These complicated and conflicting geographic trends cannot be understood without the knowledge of the particular climatic conditions over geographic gradients. In southern coastal

British Columbia, winter days warm enough to encourage growth are interspersed with periods of freezing, and trees are exposed to forcing temperatures throughout the winter. Further inland, further north and at higher elevations, temperature fluctuations between growing and freezing conditions are restricted to shorter periods in fall and spring. Therefore, high dormancy stability to prevent premature bud burst is of greater importance in southern, coastal, and low-elevation populations. Campbell and Sugarno (1979) observed that latitudinal trends for Douglas-fir tend to be opposite in continental areas. Continental climates have larger seasonal temperature amplitudes and less rainfall, and populations in southern regions tend to experience a larger moisture deficit, which marks the end of the season rather than fall frost. In the case of a severely limited period of favorable growing conditions, the greater risk associated with early bud burst may be compensated by gains in growth early in the season. Then, bud break should be earlier in the south, reflecting the probability of spring frost followed shortly by drought. The same reasoning could apply for high elevations, where the summer is usually short and spring frost (or melting of snow cover, which is relevant for seedlings to accumulate heat sum) is followed shortly by cold temperatures (Campbell and Sugarno 1979). Red alder, however, conforms to maritime patterns over all investigated gradients. Trends related to latitude, elevation, and the distance from the ocean in British Columbia primarily reflect the selection pressures due to temperature average and amplitude rather than growing seasons restricted by drought or cool temperatures.

The effects of climatic warming on bud burst cannot easily be deduced from provenance experiments, because bud burst of a provenance transferred to a warmer, or more variable climate is observed relative to other sources, and is not compared to the date of bud burst at its origin. There are, however, a number of experiments with seedlings of forestry species under controlled environments simulating different scenarios of climatic warming. These studies suggests that bud burst could be later, because winter chilling requirements that completely release dormancy are

not met, bud break could also be earlier because heat sum requirements for bud burst are met earlier, or the date of bud break remains the same, because both effects cancel. In Hanninen's (1991) study for Finland, forcing due to global warming clearly overrides delays due to insufficient dormancy release, because chilling requirements are far exceeded in northern Scandinavian winters. Given the additional scenario of greater temperature fluctuation associated with climatic warming in his model, he predicts bud burst during mid-winter, and possible subsequent exposure to temperatures of -20°C . A similar model of climate change applied to Scotland (Murray et al. 1989) predicts no change in the date of bud burst, because delayed dormancy release and advanced forcing due to increased temperatures canceled each other more or less precisely out. The 15 species investigated broke bud at higher temperatures and failed to exploit favorable conditions during earlier springs. In regions of Europe further south with even milder winters this effect was exaggerated because the chilling deficit overrides the effect of spring forcing and bud burst shifts to a later calendar date despite warmer springs (Kramer 1994).

In red alder all these cases seem plausible over its geographic range. In populations from Alaska and at high elevations with severe winters, chilling requirements would be met regardless of warming, and the date of bud break will be advanced. Coastal populations somewhere at medium latitudes could suffer chilling deficits, so that the effect of forcing is canceled or even surpassed, resulting in delayed bud burst. An additional scenario seems possible for the most southern portion of red alder's range. Perry and Wang (1960) give an example for a Florida provenance of red maple, that completely lacked chilling requirements, while New York provenances required a month or more of winter chilling before they could resume active growth. This could also be expected for red alder sources from southern California, where chilling temperatures never occur. Then, warming would again advance the date of bud burst without an opposing mechanism.

To make an accurate prediction of the response of red alder sources in British Columbia to climatic warming, the relative importance of biological mechanisms that control bud burst need to be understood as a function of geographic clines. Such data are not available. However, experiments under controlled environments have been conducted with *Alnus incana*, which is sympatric with red alder throughout British Columbia and Alaska, and with *A. glutinosa*, which is closely related to red alder (Heide 1993). Heat sum requirements decreased with increased duration of chilling, but in comparison to other species he found that alders had particularly high chilling requirements resulting in late dormancy release, which was then associated with a rapid decline in heat sum requirements. These results indicate that if there is a lack of chilling due to climatic warming, this effect probably overrides increased heat sum accumulation. As a consequence, a delayed bud flush despite warmer springs may be a problem for southern coastal sources in British Columbia. Prolonged dormancy would result in suboptimal growth if the available season is not fully utilized.

A breeding program could ameliorate this effect of global warming deploying populations south or toward the coast, using sources with less dormancy stability than local sources. Unfortunately, the opposite recommendation has been made previously to cope with the effect of global warming on growth cessation.

6. 4. 3. Required populations

The previous section suggests that it will be necessary to develop novel genotypes to cope with the expected effects of climatic warming. A simple shift of existing provenances to new locations will not be a satisfactory solution. It is impossible with the current data to predict the magnitude

of changes that would be required to achieve optimal synchronization of phenological traits with future climates even if reliable predictions of climatic warming were available. Therefore, I base selection targets of new breeding populations only on the most likely direction of required changes with a new population mean different by some minimum amount that would justify the use of a new breeding population over another. This population would replace the previous one for deployment when the lack of synchronization due to climate change warrants it.

It has been argued that given a fixed number of parent trees in a breeding program, the breeding effort for one large or many small breeding populations will mainly be an additional intellectual effort, and will not require increased practical management (Namkoong et al. 1988). However, the economic feasibility of a tree improvement program depends on its overall size. Thus, the number of breeding populations should not be greater than necessary. The number of breeding populations for red alder in British Columbia depends on acceptable threshold values for different traits. A reduction of about 10% in growth or survival compared to the local source is generally accepted as a consequence of seed transfer in British Columbia which is commonly associated with a 4 day shift in phenology (Chapter 2. 3. 2.). In red alder a 10% change in growth or survival over the main latitudinal gradient is associated with approximately 8 days change in the date of growth cessation and 4 days in the date of bud break. Taking these values as thresholds for the seed transfer, results from Chapter 3 and 4 suggest that two seed- or breeding zones, separated by 51°N latitude would meet this requirement with respect to height, survival, and the date of leaf abscission. The differentiation of provenances from the west coast of Vancouver Island, where populations exhibit exceptional dormancy stability (Figure 6. 5.) further requires that the southern portion is separated into a breeding zone for the Georgia Depression (as delineated in Figures 2. 5 and 2. 6.) and the west coast of Vancouver Island.

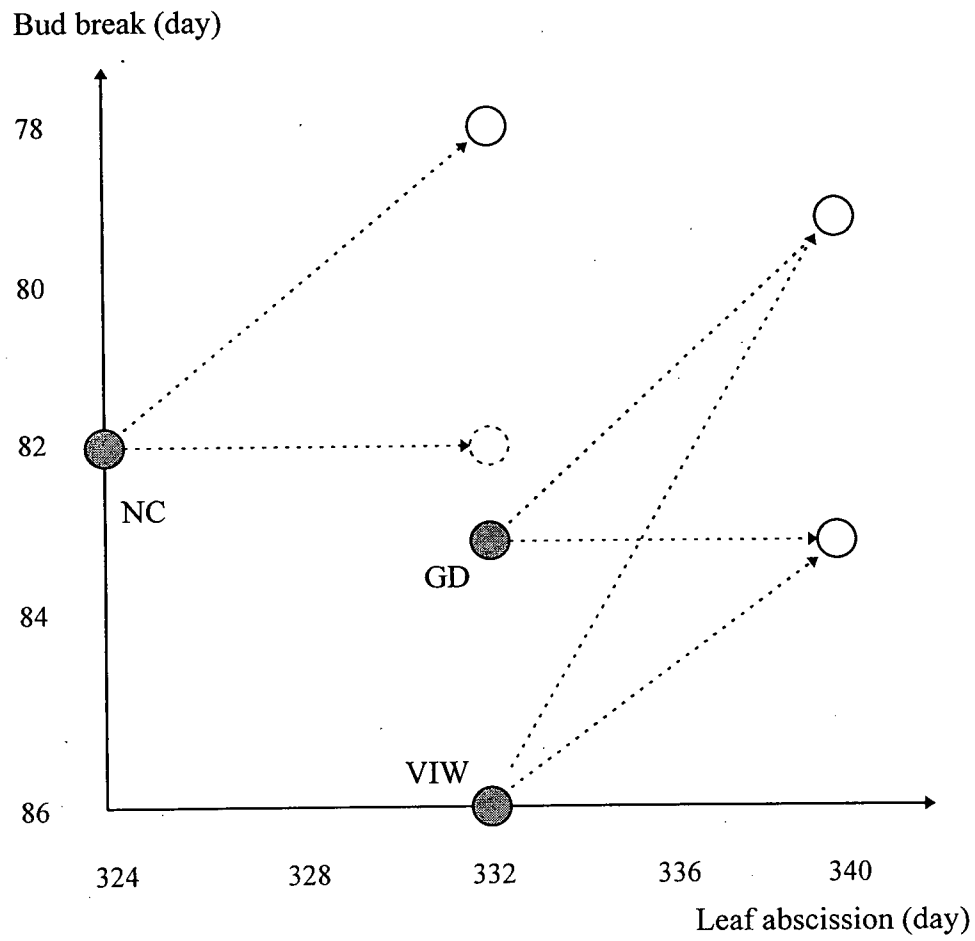


Figure 6. 6. Proposed multiple breeding populations for current (dark circles) and possible future (light circles) climatic conditions (NC, British Columbia north of 51°N latitude; GD, Georgia Depression; VIW, Vancouver Island Westcoast).

Assuming that current regional means for the timing of bud break and leaf abscission reflect optimal synchronization to current climates, breeding populations for northern coastal B. C., the Georgia Depression, and West Vancouver Island should maintain population means in phenological traits given in Figure 6. 6. Since there is greater certainty in the requirements for leaf abscission under the scenario for climate warming, all three breeding populations should have a delayed date of growth cessation with a selection magnitude of approximately 8 days. Response in the date of bud break is more questionable. Bud break in current populations will probably occur too late to fully utilize extended growing conditions in warmer springs. A conservative approach would be to retain one population with current dormancy stability and select another for advanced bud break by 4 days for each of the three breeding zones. Delayed bud break could be a particular problem for Westcoast Vancouver Island. In this region populations have high dormancy stability and will likely suffer a chilling deficit due to climatic warming, which could result in a delayed calendar date of bud break despite warmer springs. In addition to selecting for 4 days, a population selected for 8 days of advanced bud could account for the possibility of extensive problems due to dormancy stability. Provided that the current population for the Georgia Depression could serve as one of the potential future populations for Northern British Columbia, three additional breeding populations would be required to cope with climatic warming (Figure 6. 6.). It should be noted that selection targets refer to observations in current test plantations and that the actual advance of bud burst in production populations would be smaller.

6. 5. Recommendations

Risk of damage due to spring and fall frost due to global warming appears to be an unlikely szenario for red alder in British Columbia. It has been suggested that climatic warming could be

associated with a larger temperature amplitude that entails greater risks of frost damage, but it is debated whether fluctuating temperatures are more effective in breaking dormancy than corresponding constant temperatures (Garber 1983; Hänninen 1991; Heide 1993). A biological response that results in later bud set is not expected, neither is an advanced date of bud break for red alder in British Columbia. Both changes would have an overall neutral or positive effect if they reflect indeed a prolonged growing season. A conservative approach to increased risk of frost damage would be the use of breeding populations for existing climatic conditions under the scenario of global warming. The more aggressive alternative would require novel genotypes with populations selected for advanced bud break and/or delayed growth cessation. Growth traits will be positively influenced by this selection due to genetic correlations (Chapter 5). In this context, observations by van der Kamp and Worrall (1990) of frost damage after a cold spell following four months of unusually warm winter conditions should be noted. Buds were destroyed in interior species and provenances, while trees in coastal and low elevation regions retained their hardiness. These observations should encourage a more aggressive approach for tree breeding in coastal species, while the opposite should probably apply for interior regions of British Columbia.

A cost effective way to implement this breeding strategy would be the conversion of at least one red alder progeny trial into a "breeding seedling orchard", where genetic testing, maintenance of a large number of individuals representing several breeding populations, and quality seed production through progressive roguing of undesirable genotypes could be carried out in one physical unit. Selection in one trial could nevertheless take advantage from information about family performance in multiple tests. This would have the advantage of avoiding the cost of establishing, maintaining and managing seed orchards, which is prudent as long as demand for planting stock is uncertain.

6. 6. References

- Bey, C. F. 1971. Early growth of black walnut trees from twenty seed sources. USDA Forest Service Research Note NC-105, 4 pp.
- Braathe, P. 1957. Is there a connection between birch dieback and the March thaw of 1936?. *For. Chron.* 33: 358-363.
- Burley, J. 1966a. Genetic variation in seedling development of Sitka spruce (*Picea sitchensis* (Bong.) Carr. *Forestry* 39: 69-94.
- Burley, J. 1966b. Provenance variation in growth of seedling apices of Sitka spruce *Forest Science* 12: 170-175.
- Campbell, R. K. 1974. Use of phenology for examining provenance transfer in reforestation of Douglas-fir. *J. Appl. Ecol.* 11: 1069-1080.
- Campbell, A. G. and Sorensen, F. C. 1978. Effect of test environment on expression of clines and on delimitation of seed zones in Douglas-fir. *Theoretical and Applied Genetics* 51: 233-246.
- Campbell, R. K. and Sugano, A. 1979. Genecology of bud burst phenology in Douglas-fir: response to flushing temperature and chilling. *Bot. Gaz.* 140: 223-231.
- Cannell, M. G. R. 1984. Spring frost damage to young *Picea sitchensis* 1. occurrence of damaging frosts in Scotland compared with western North America. *Forestry* 57: 160-175.
- Cannell, M. G. R. 1985. Autumn frost damage on young *Picea sitchensis* 1. occurrence of damaging frosts in Scotland compared with western North America. *Forestry* 58: 131-143.
- Cannell, M. G. R. and Smith, R. I. 1986. Climatic warming, spring bud burst and frost damage on trees. *Journal of Applied Ecology* 23: 177-191.
- Clausen, K. and Garrett, P. W. 1969. Progress in birch genetics and tree improvement. *Birch Symposium Proceedings*, Upper Darby PA, USDA Forest Service, Northeastern Forest Experiment Station.
- Cunningham, E. P., Moen, R. A., and Gjedrem, T. 1970. Restriction of selection indices. *Biometrics* 26: 67-74.
- Downs R. J. and Bevington, J. M. 1981. Effect of temperature and photoperiod on growth and dormancy of *Betula papyrifera*. *Am. J. Bot.* 68: 795-800.
- Eriksson, G., Namkoong, G., and Roberts, J. H. 1993. Dynamic gene conservation for uncertain climatic futures. *Forest Ecology and Management* 62: 15-37.

Pollard, D. F. W., Teich, A. H., and Logan, K. T. Seedling shoot and bud development in provenances of Sitka Spruce, *Picea sitchensis* (Bong.) Carr. Can J. For Res. 5: 18-25.

Farmer, R. E. 1968. Sweetgum dormancy release: effects of chilling, photoperiod and genotype. *Physiol. Plant.* 21: 1241-1248.

Flint, H. L. Phenology and genecology of woody plants. In Lieth, H. (Editor), *Phenology and Seasonal Modeling. Ecological Studies 8*, Springer Verlag, New York, pp. 83-97.

Fuchigami, L. H., Weiser, C. J., Kobayashi, K., Timmins, R., and Gusta, L. V. 1982. A degree growth stage (GS) model and cold acclimation in temperate woody plants. In Li, P. H. and Sakai, A. (Editors) *Plant Cold Hardiness and Freezing Stress. Vol. 2*. Academic Press, New York, pp 93-116.

Hänninen, H. 1991. Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell and Environment* 14: 449-454.

Irgens-Moller, H. 1968. Geographical variation in growth patterns of Douglas-fir. *Silvae Genet.* 17: 106-110.

Kempthorne, O and A. W. Nordskog. 1959. Restricted selection index. *Biometrics* 15: 10-19.

Kramer K. 1994. A modeling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in the Netherlands and Germany. *Plant, Cell and Environment* 17: 367-377.

Kriebel, H. B. and Wang, C. W. 1962. The interaction between provenance and degree of chilling in bud break of sugar maple. *Silvae Genet.* 11: 125-130.

Kuser J. E. and Cing, K. K. 1980. Provenance variation in phenology and cold hardiness of western hemlock seedlings. *Forest Sci.* 26: 463-470.

Mergen, F. 1963. Ecotypic variation in *Pinus strobus* L. *Ecology* 44: 716-727.

Morgenstern, E. K. 1996. *Geographic Variation in Forest Trees: Genetic Basis and Applications of Knowledge in Silviculture*. UBC Press, Vancouver.

Murrey, M. B., Cannell, M. G. R., and Smith, R. I. 1989. Date of bud burst of fifteen tree species in Britain following climatic warming. *J. Appl. Ecol.* 26: 693-700.

Namkoong, G. 1976. A multiple index selection strategy. *Silvae Genetica* 25:199-201.

Namkoong, G. 1984. A control concept of gene conservation. *Silvae Genetica* 33:160-163.

Namkoong, G. 1986. Genetics and the forests of the future. *Unasylva* 152:2-18.

Namkoong, G., Kang, H. C., and Brouard, J. S. 1988. Tree Breeding: Principles and Strategies. Springer Verlag, New York, 177 pp.

Nienstaedt, H. 1974. Genetic variation in some phenological characteristics of forest trees. In H. Lieth (ed), Phenology and seasonal modeling. Pp 389-400. Ecological studies 8, Springer Verlag, New York.

Nienstaedt, H. 1967. Chilling requirements in seven *Picea* species. *Silvae Genet.* 16: 65-68.

Owens, J. N. and M. D. Blake. 1985 . Forest tree seed production. Forestry Canada Information report PI-X-53.

Perry, T. O. 1971. Dormancy of trees in winter. *Science* 171: 29-36.

Perry, T. O. and Wang, C. W. 1960. Genetic variation in winter chilling requirement for date of dormancy break for *Acer rubrum*. *Ecology* 41: 785

SAS Institute. 1997. SAS/STAT user's guide. Release 6.12, Cary, NC.

Sharik, T. L. and Barnes, B. V. 1976. Phenology of shoot growth among divers populations of yellow birch (*Betula alleghaniensis*) and sweet birch (*B. lenta*). *Canadian Journal of Botany* 54: 2122-2129.

Tremblay, M. F. and Lalonde, M. 1987. Effect of photoperiod and temperature on the development of cold hardiness in three *Alnus* species *Physiologia Plantarum* 70: 327-331.

van der Kamp B. J. and Worrall, J. 1990. An unususual case of winter bud damage in British Columbia interior conifers. *Can. J. For. Res.* 20: 1640-1647.

Vaartaja, O. 1954. Photoperiodic ecotypes of trees. *Canadian Journal of Botany* 32: 392-399.

Vartaja, O. 1959. Evidence of photoperiodic ecotypes in trees. *Ecological Monographs* 29: 91-111.

Vegis, A. 1964. Dormancy in higher plants. *Annu. Rev. Plant Physiol.* 15: 185-224.

Wang, C. W. and Perry, T. O. 1958. The ecotypic variation of dormancy, chilling requirement, and photoperiodic response in *Betula* species. Volume 2. Proceedings of the 10th International Congress of Genetics. McGill University, Montreal.

Chapter 7. Summary and recommendations

During the last two decades, incentives have increased to develop an intensive forestry management system for red alder. Its abundance and low cost on markets in Washington and Oregon has made it the only hardwood in the Pacific Northwest with major economic importance. Strong and consistent markets have developed, particularly for high quality red alder lumber in North America and overseas, and the previous harvest of most good quality stands in the United States has already lead to shortages and projected declines in the supply of red alder. In the same period, changes in forest management practices have taken place with emphasis on ecologically sound and sustainable use of forest ecosystems.

Red alder has always been a neglected resource in British Columbia, and although it has firmly established itself on international markets, the species is not used extensively in British Columbia. The reason is the low quality of the majority of stands, and good stands are often located in riparian habitats that are off-limits to harvesting. If red alder is to become a significant forestry species in British Columbia, there is an obvious need to develop a forestry system aiming at high quality red alder saw log production. Biomass or fiber production with red alder is unlikely to be economically viable, because of strong competition on international markets and the low value of alder wood chips. An intensive management program for red alder would diversify the currently softwood oriented-plantation forestry, and add an ecologically important component of coastal ecosystems to forestry in British Columbia.

Growth and yield of red alder implies that a product, equal or greater in value to any softwood currently managed in British Columbia can be produced in considerably shorter time. One major goal of a tree improvement program would be to shorten the rotation length even further. In order

to exploit the full early growth potential of red alder, it must be grown on fair to good sites (site index 27_{50} or better). Contradicting the notion that alder should be grown on sites too poor for conifers, site index curves indicate that red alder loses its wide margin in profitability compared to softwoods on poor sites. Breeding populations should therefore consist of genotypes selected for above average-site conditions.

There had been concern that in red alder, being an aggressive colonizer, intensive natural selection for height growth may have reduced variability in growth traits, leaving little opportunity for tree improvement. The substantial within-population variation observed in this study is an important finding and shows that genetic improvement through selection and breeding is possible. Genetic gains in growth traits from individual selection would range from 25 to 35% for selection in current provenance trials. Small improvements (approximately 5%) would indirectly be achieved in form, and exclusion of a few families with extensive incidence of multiple leaders and insufficient self-pruning would reduce or eliminate these undesirable characteristics.

This study has further described a complex structure of genetic differentiation over geographical and environmental clines in growth and adaptive traits. Geographic and climatic variates accounted for approximately equal amounts of the variation, indicating that both, gene flow and selection by environmental factors likely shaped geographic patterns of genetic differentiation in red alder. Principal component analysis showed that variation in quantitative traits can be reduced to two underlying dimensions, one representing general vigor including the termination of the growing period, the other being the start of the growing period. Canonical correlation analysis among quantitative traits and geographic variables revealed complex associations of genotypes with the latitude, distance to the coast, and elevation of the seed source. It is difficult

to account for such ordered patterns, except as a complex response of populations to natural selection.

An evaluation of multiple provenance trials showed that populations are adapted to local environments, and provenances perform optimally in growth and survival when planted close to the source location. The presence of significant genotype \times site interaction at the provenance and family level, and rank order changes of families from one environment to the next implies that unrestricted seed transfer or using a single breeding or seed zone for red alder in British Columbia is not biologically practicable. Conforming to generally accepted reduction in growth or survival as a consequence of seed transfer in British Columbia, provenances should not be relocated more than 400 km in either direction along the coast of British Columbia. Seed transfer between the Georgia depression and the west coast of Vancouver Island should also be avoided.

Assuming that regional means for bud break and leaf abscission reflect optimal synchronization of phenological traits to current climates, I recommend three breeding populations British Columbia: North Coast (north of 51°N latitude), Georgia Depression, and western Vancouver Island. Given that a tree breeding effort is a long-term investment, and that considerable climatic warming has been predicted for northern latitudes over the next few decades, I recommend that this element of uncertainty should be incorporated in a breeding strategy for red alder.

Considering the biological response of phenological traits to climatic warming, a simple shift of existing provenances to new locations will not be a satisfactory solution. Using breeding populations for existing climatic conditions under the scenario of global warming could result in suboptimal performance because favorable growing conditions in spring and fall are not utilized. An effective countermeasure would be the development of multiple populations selected for novel combinations in bud break and growth cessation, that could be deployed under different scenarios of climatic warming and biological response in phenological traits.

A cost effective way to implement this breeding strategy would be the conversion of at least one red alder progeny trial into a "breeding seedling orchard", where genetic testing, maintenance of a large number of individuals representing several breeding populations, and quality seed production through progressive roguing of undesirable genotypes could be carried out in one physical unit. Selection in one trial could nevertheless take advantage from information about family performance in multiple tests. This would have the advantage of avoiding the cost of establishing, maintaining and managing seed orchards, which is prudent as long as demand for planting stock is uncertain. The test plantation that should be converted as outlined would preferably be at Surrey, because of its favorable logistics at a Ministry of Forests nursery facility.

To account for synchronization of phenological traits to current climates, and possible future environments, I recommend that a breeding strategy based on 6 populations outlined in the previous chapter should be followed in a commercial tree improvement effort. Simultaneous advance in growth traits will not be adversely affected by the suggested restrictions and directional selection in phenological traits due to the nature of genetic correlations. Given the market demand for high-grade alder logs, tree breeding should further include quality related traits such as stem form, sweep and lean, branch number and size. Cultural measures such as control of spacing at plantation establishment and thinning will further enhance growth rates and quality of trees, compared to natural stands in British Columbia. In combination with moderate genetic gains in growth and form from selection, short rotation silviculture with red alder for high quality saw timber production appears to be a reasonably profitable option for forestry in British Columbia.

Appendix 1. Layout of B. C. provenance trial at Surrey

Fam	Block 1					Fam	Block 2					Fam	Block 3					Fam	Block 4					row
12 1	o	X	x	X	o	55 5	X	x	X	o	X	57 4	x	X	o	X	x	69 0	X	x	X	o	X	1
12 3	X	o	X	x	X	55 4	x	X	o	X	x	57 3	X	x	X	o	X	69 0	o	X	x	X	x	2
12 4	x	X	x	X	o	55 2	X	o	X	x	X	57 5	x	X	o	X	x	69 0	X	x	X	x	X	3
12 2	X	o	X	x	X	55 1	x	X	x	X	o	57 2	X	x	X	o	X	18 1	o	X	x	X	x	4
12 5	x	X	x	X	o	55 3	X	o	X	x	X	57 1	x	X	o	X	x	18 5	X	x	X	o	X	5
58 2	X	o	X	x	X	2 0	x	X	x	X	o	18 1	X	x	X	o	X	18 2	o	X	x	X	x	6
58 1	x	X	x	X	o	2 0	X	o	X	x	X	18 2	x	X	o	X	x	18 4	X	x	X	o	X	7
58 5	X	o	X	x	X	2 0	x	X	x	X	o	18 4	X	x	X	o	X	18 3	o	X	x	X	x	8
58 4	x	X	x	X	o	16 5	X	o	X	x	X	18 3	X	X	o	X	x	40 3	X	X	X	o	X	9
48 3	X	o	X	x	X	16 2	x	X	x	X	o	18 5	X	x	X	o	X	40 4	X	X	x	X	x	10
48 2	x	X	x	X	o	16 4	X	o	X	x	X	39 4	o	X	X	X	x	40 1	X	x	X	o	X	11
48 1	X	x	X	o	X	16 1	X	r	x	X	o	39 1	X	x	X	o	X	40 5	o	X	x	X	x	12
48 5	x	X	x	X	o	16 3	X	o	X	X	X	39 3	x	X	o	X	x	40 2	X	o	X	x	X	13
48 4	X	o	X	X	X	38 0	x	X	o	X	x	39 5	X	x	X	o	X	50 2	o	X	x	X	x	14
62 7	x	x	X	X	o	38 0	X	o	X	x	X	39 2	x	X	o	X	x	50 5	X	o	X	x	X	15
62 5	X	o	X	x	X	38 0	x	X	x	X	o	64 4	X	x	X	o	X	50 3	o	X	x	X	x	16
62 3	x	X	x	X	o	40 5	X	o	X	x	X	64 5	X	X	o	X	x	50 4	X	x	X	o	X	17
62 4	X	o	X	x	X	40 2	x	X	x	X	o	64 2	X	x	X	o	X	50 1	o	X	x	X	x	18
62 2	x	X	o	X	x	40 4	X	o	X	x	X	64 3	x	X	x	X	o	21 1	X	x	X	o	X	19
38 0	X	o	X	x	X	40 3	x	X	x	X	o	64 1	X	x	X	x	X	21 5	o	X	x	X	x	20
38 0	x	X	x	X	r	40 1	X	x	X	o	X	53 3	x	X	o	X	x	21 3	X	x	X	o	X	21
38 0	X	o	X	x	X	53 2	x	X	o	X	x	53 1	X	x	X	o	X	21 4	o	X	x	X	x	22
43 2	x	X	x	X	o	53 3	X	X	X	o	X	53 5	x	X	o	X		21 2	X	x	X	o	X	23
43 5	X	o	X	x	X	53 1	X	X	x	X	o	53 4	X	x	X	o	X	33 4	x	X	o	X	x	24
43 4	x	X	x	X	o	53 5	X	x	X	o	X	53 2	x	X	o	X	x	33 1	X	x	X	o	X	25
43 3	X	o	X	x	X	53 4	x	X	x	X	o	71 1	X	X	X	r	X	33 2	o	X	x	X	x	26
43 1	x	X	x	X	o	51 3	X	o	X	x	X	71 4	r	X	X	X	X	33 3	X	x	X	o	X	27
42 2	X	o	X	x	X	51 5	x	X	x	X	o	71 5	X	X	X	r	X	33 5	X	X	o	X	x	28
42 4	x	X	o	X	x	51 4	X	o	X	x	X	71 3	X	X	r	X	X	36 3	X	x	X	o	X	29
42 5	X	o	X	x	X	51 1	x	X	x	X	o	71 2	X	r	X	X	X	36 4	o	X	x	X	x	30
42 1	x	X	x	X	o	51 2	X	X	X	o	X	62 5	x	X	o	X	x	36 2	X	x	X	o	X	31
42 3	X	o	X	x	X	19 4	x	X	x	X	o	62 4	X	x	X	o	X	36 5	o	X	x	X	x	32
11 2	x	X	o	X	x	19 2	X	o	X	x	X	62 7	x	X	o	X	x	36 1	X	o	X	X	X	33
11 5	X	o	X	x	X	19 5	x	X	x	X	o	62 2	X	o	X	x	X	27 5	r	X	X	X	X	34
11 3	x	X	x	X	o	19 1	X	o	X	x	X	62 3	x	X	o	X	x	27 1	X	X	X	r	X	35
11 4	X	o	X	x	X	19 3	x	X	x	X	o	8 2	X	x	X	o	X	27 4	r	X	X	X	X	36
11 1	x	X	x	X	o	50 3	X	o	X	x	X	8 3	x	X	o	X	X	27 3	X	X	X	r	X	37
52 5	X	o	X	x	X	50 5	x	X	o	X	x	8 1	X	x	X	o	X	27 2	X	X	r	X	X	38
52 1	x	X	o	X	x	50 2	X	o	X	x	X	8 4	o	X	X	X	x	49 7	X	x	X	x	X	39
52 2	X	o	X	x	X	50 4	x	X	o	X	x	8 5	X	x	X	o	X	49 3	o	X	x	X	x	40
52 4	x	X	x	X	o	50 1	X	o	X	x	X	49 5	X	X	o	X	x	49 5	X	x	X	o	X	41
52 3	X	o	X	x	X	18 2	x	X	x	X	o	49 2	X	o	X	x	X	49 2	x	X	o	X	x	42
51 2	x	X	X	X	o	18 4	X	o	X	x	X	49 7	x	X	o	X	x	49 6	X	o	X	x	X	43
51 4	X	o	X	x	X	18 3	x	X	x	X	o	49 6	X	x	X	o	X	51 3	o	X	x	X	x	44
51 3	x	X	x	X	r	18 1	X	x	X	o	X	49 3	x	X	o	X	x	51 4	X	x	X	o	X	45
51 1	X	o	X	x	X	18 5	x	X	o	X	x	43 4	X	x	X	o	X	51 2	o	X	x	X	x	46
51 5	x	x	X	X	o	68 4	X	o	X	x	X	43 2	x	X	o	X	X	51 1	X	x	X	o	X	47
36 2	x	X	r	X	X	68 2	o	X	X	X	o	43 1	X	x	X	o	X	51 5	X	X	o	X	x	48

36 5	X	o	x	X	x	68 1	X	x	X	o	X	43 3	X	X	x	X	o	6 5	X	x	X	o	X	49
36 4	x	X	X	o	X	68 3	x	X	x	X	o	43 5	X	X	X	o	X	6 2	o	X	x	X	x	50
36 3	X	o	x	X	o	68 5	X	o	X	x	X	42 3	x	X	o	X	x	6 4	X	o	X	X	X	51
36 1	x	X	X	o	X	36 5	X	X	x	X	o	42 4	X	x	X	x	X	6 1	x	X	o	X	x	52
49 2	X	o	x	X	x	36 2	X	o	X	x	X	42 5	x	X	o	X	x	6 3	X	x	X	o	X	53
49 3	x	X	X	o	X	36 3	x	X	o	X	X	42 2	X	x	X	o	X	23 3	o	X	x	X	x	54
49 6	X	x	o	X	x	36 4	r	X	X	o	X	42 1	x	X	o	X	x	23 4	X	x	X	o	X	55
49 7	x	X	X	o	X	36 1	x	X	o	X	x	32 2	X	x	X	o	X	23 1	o	X	x	X	x	56
49 5	X	o	X	X	x	12 4	X	x	X	o	X	32 1	x	X	o	X	x	23 5	X	x	X	o	X	57
21 3	x	X	X	o	X	12 5	x	X	o	X	x	32 3	X	o	X	x	X	23 2	o	X	x	X	x	58
21 5	X	x	o	X	x	12 3	X	x	X	o	X	32 4	x	X	o	X	x	29 0	X	x	X	o	X	59
21 4	X	o	X	x	X	12 1	x	X	o	X	x	32 5	X	x	X	o	X	29 0	x	X	o	X	x	60
21 2	x	X	x	r	x	12 2	X	o	X	x	X	27 2	X	X	r	X	X	29 0	X	x	X	o	X	61
21 1	X	o	X	x	X	63 3	x	X	x	X	o	27 5	X	X	X	r	X	66 0	o	X	x	X	x	62
35 4	x	X	o	X	x	63 4	X	o	X	x	X	27 3	X	X	r	X	X	66 0	X	x	X	o	X	63
35 3	X	o	X	x	X	63 2	x	X	x	X	o	27 4	X	r	X	X	X	66 0	x	X	o	X	x	64
35 2	x	X	o	X	x	63 1	X	o	X	x	X	27 1	X	X	r	X	X	26 4	X	x	X	o	X	65
35 5	X	o	X	x	X	63 5	x	X	x	X	o	9 2	X	x	X	o	X	26 5	o	X	x	X	x	66
35 1	o	X	X	X	o	4 4	X	o	X	x	X	9 1	x	X	o	X	x	26 2	X	X	X	r	X	67
56 4	X	o	X	x	X	4 1	x	X	x	X	o	9 4	X	x	X	o	X	26 1	x	X	o	X	x	68
56 2	x	X	o	X	x	4 5	X	o	X	x	X	9 3	x	X	o	X	x	26 3	X	X	X	r	X	69
56 3	X	o	X	x	X	4 2	x	X	x	X	o	9 5	X	x	X	o	X	1 0	o	X	x	X	x	70
56 1	x	X	o	X	x	4 3	X	o	X	x	X	67 0	x	X	o	X	x	1 0	X	x	X	o	X	71
56 5	X	o	X	x	X	57 3	x	X	x	X	o	67 0	X	x	X	o	X	1 0	X	X	X	X	X	72
61 5	x	X	x	X	o	57 1	X	o	X	x	X	67 0	x	X	x	X	o	10 0	X	x	X	o	X	73
61 3	X	o	X	x	X	57 5	x	X	x	X	o	28 3	X	x	X	o	X	10 0	o	X	x	X	x	74
61 2	x	X	x	X	o	57 4	X	o	X	x	X	28 2	x	X	x	X	o	10 0	X	x	X	o	X	75
61 4	X	o	X	x	X	57 2	x	X	x	X	o	28 4	X	x	X	o	X	39 5	o	X	x	X	x	76
61 1	x	X	o	X	x	73 0	X	r	X	X	X	28 1	x	X	o	X	x	39 3	X	x	X	o	X	77
68 2	X	o	X	x	X	73 0	X	X	X	X	X	28 5	X	x	X	o	X	39 1	x	X	o	X	x	78
68 3	x	X	x	X	o	73 0	X	X	X	r	X	37 1	o	X	o	X	x	39 2	X	x	X	o	X	79
68 5	X	o	X	x	X	23 1	x	X	x	X	o	37 4	X	x	X	o	X	39 4	o	X	x	X	x	80
68 1	x	X	x	X	o	23 3	X	o	X	x	X	37 3	x	X	o	X	x	41 3	X	x	X	o	X	81
68 4	X	o	X	x	X	23 5	x	X	x	X	o	37 2	X	x	X	o	X	41 1	X	X	x	X	o	82
37 5	x	X	o	X	x	23 4	X	o	X	x	X	37 5	x	X	o	X	x	41 4	X	o	X	x	X	83
37 4	X	o	X	x	X	23 2	x	X	x	X	o	10 0	X	o	X	x	X	41 2	x	X	o	X	x	84
37 1	x	X	x	X	o	65 2	X	o	X	x	X	10 0	x	X	x	X	o	41 5	r	x	X	x	X	85
37 2	X	o	X	x	X	65 4	o	X	x	X	x	10 0	X	x	X	o	X	67 0	o	X	x	X	x	86
37 3	x	X	x	X	o	65 1	X	o	X	x	X	58 5	x	X	o	X	x	67 0	X	x	X	x	r	87
16 3	X	o	X	x	X	65 3	X	X	x	X	o	58 1	X	x	X	o	X	67 0	o	X	x	X	x	88
16 2	x	X	x	X	o	65 5	X	o	X	x	X	58 2	x	X	x	X	o	11 4	X	X	X	o	X	89
16 1	x	x	X	o	X	24 4	x	X	X	X	o	58 4	X	x	X	o	X	11 5	o	X	x	X	x	90
16 4	X	o	x	X	x	24 5	X	o	X	x	X	33 1	x	X	o	X	x	11 3	X	x	X	o	X	91
16 5	x	X	X	o	X	24 1	x	X	x	X	o	33 5	X	x	X	o	X	11 2	o	X	X	X	x	92
27 5	X	x	x	X	o	24 2	X	x	X	o	X	33 4	x	X	x	X	o	11 1	X	x	X	o	X	93
27 3	o	X	X	x	X	24 3	o	X	o	X	x	33 3	X	x	X	x	X	16 1	x	X	o	X	x	94
27 4	X	o	x	X	x	21 2	X	x	X	o	X	33 2	x	X	x	X	o	16 2	X	x	X	o	X	95
27 1	o	X	X	o	X	21 5	x	X	x	X	o	11 2	X	x	X	o	X	16 4	X	X	o	X	x	96
27 2	X	X	x	X	o	21 3	X	o	X	x	X	11 3	x	X	o	X	x	16 3	X	x	X	o	X	97
73 0	X	X	X	X	X	21 4	x	X	o	X	x	11 4	X	x	X	o	X	16 5	o	X	x	X	x	98
73 0	X	X	X	X	X	21 1	X	o	X	x	X	11 5	x	X	o	X	x	52 5	X	x	X	o	X	99
73 0	X	X	X	X	X	61 4	x	X	o	X	x	11 1	X	x	X	o	X	52 1	o	X	x	X	x	100

15 2	X	o	x	X	x	61 5	X	o	X	x	X	36 2	x	X	o	X	X	52 2	X	x	X	o	X	101
15 4	x	X	X	o	X	61 3	x	X	o	X	x	36 4	X	x	X	o	X	52 3	x	X	o	X	x	102
15 1	X	o	x	X	x	61 2	X	o	X	x	X	36 3	x	X	o	X	x	52 4	X	x	X	o	X	103
15 3	x	X	X	o	X	61 1	x	X	x	X	o	36 1	X	x	X	o	X	2 0	r	X	X	X	X	104
15 5	X	o	x	X	x	52 2	X	o	X	x	X	36 5	x	X	o	X	x	2 0	X	X	X	r	X	105
2 0	o	X	X	X	X	52 1	x	X	x	X	o	16 1	X	x	X	o	X	2 0	X	X	r	X	X	106
2 0	X	x	o	X	x	52 4	X	o	X	x	X	16 3	x	X	o	X	x	15 4	X	x	X	o	X	107
2 0	x	X	X	o	X	52 5	x	X	x	X	o	16 4	X	x	X	o	X	15 1	x	X	x	X	o	108
60 0	X	x	o	X	x	52 3	X	o	X	x	X	16 5	X	X	o	X	x	15 3	X	x	X	o	X	109
60 0	o	X	X	x	X	43 5	x	X	X	X	o	16 2	X	x	X	o	X	15 5	o	X	x	X	x	110
60 0	X	x	x	X	o	43 2	X	X	X	o	X	21 1	x	X	o	X	x	15 2	X	x	X	o	X	111
8 2	x	X	X	o	X	43 1	x	X	x	X	o	21 4	X	x	X	o	X	60 0	r	X	X	X	X	112
8 3	X	x	o	X	x	43 4	X	o	X	x	X	21 5	x	X	o	X	x	60 0	X	X	X	r	X	113
8 5	x	X	X	o	X	43 3	x	X	X	X	o	21 2	X	x	X	o	X	60 0	r	X	X	X	X	114
8 4	X	o	x	X	x	30 5	X	o	X	x	X	21 3	x	X	o	X	x	24 5	X	x	X	r	X	115
8 1	x	X	X	o	X	30 2	x	X		X	o	38 0	X	x	X	o	X	24 2	o	X	x	X	x	116
64 1	o	x	X	X	x	30 3	X	o	X	x	X	38 0	x	X	x	X	o	24 1	X	x	X	o	X	117
64 4	X	o	X	X	X	30 1	x	X	o	X	x	38 0	X	x	X	o	X	24 3	x	X	x	X	o	118
64 2	x	X	x	r	x	30 4	X	o	X	x	X	50 4	x	X	o	X	x	24 4	X	x	X	o	X	119
64 3	X	x	X	X	X	41 2	o	X	x	X	x	50 2	X	x	X	o	X	63 3	o	X	x	X	x	120
64 5	o	X	x	X	x	41 4	X	o	X	x	X	50 5	x	X	o	X	x	63 5	X	X	X	x	X	121
34 4	X	x	X	o	X	41 5	x	X	x	X	o	50 1	X	x	X	o	X	63 1	o	X	x	X	x	122
34 1	x	X	x	X	o	41 1	X	o	X	x	X	50 3	x	X	o	X	x	63 2	X	x	X	o	X	123
34 5	X	o	X	x	X	41 3	x	X	o	X	x	30 2	X	x	X	o	X	63 4	x	X	x	X	o	124
34 2	o	X	X	X	x	17 1	X	x	X	x	X	30 4	x	X	o	X	x	55 2	X	o	X	x	X	125
34 3	r	r	r	r	r	17 2	x	X	x	X	o	30 5	X	x	X	o	X	55 3	o	X	x	X	x	126
1 0	x	r	x	X	x	17 4	X	o	X	x	X	30 1	x	X	o	X	x	55 5	X	x	X	o	X	127
1 0	X	x	X	x	r	17 3	x	X	x	X	o	30 3	X	x	X	o	X	55 1	o	X	x	X	x	128
1 0	x	r	x	X	x	17 5	X	o	X	x	X	52 3	x	X	o	X	x	55 4	X	x	X	o	X	129
65 5	X	x	X	x	r	44 5	x	X	x	X	o	52 5	X	x	X	o	X	34 3	x	X	o	X	x	130
65 3	x	r	x	X	x	44 4	X	X	X	o	X	52 4	x	X	o	X	x	34 4	X	x	X	o	X	131
65 1	X	x	X	x	r	44 3	x	X	x	X	o	52 2	X	x	X	o	X	34 2	o	X	x	X	x	132
65 2	x	r	x	X	x	44 2	X	o	X	x	X	52 1	X	X	o	X	x	34 1	X	x	X	o	X	133
65 4	X	x	X	x	r	44 1	x	X	x	X	o	20 1	X	x	X	o	X	34 5	o	X	x	X	x	134
23 3	x	r	x	X	x	27 3	X	r	X	X	X	20 3	x	X	o	X	x	12 4	X	x	X	o	X	135
23 5	X	x	r	x	X	27 1	X	X	X	X	r	20 2	X	x	X	o	X	12 5	x	X	o	X	x	136
23 4	x	X	x	o	x	27 4	X	r	X	X	X	20 4	x	X	x	X	o	12 1	X	x	X	o	X	137
23 2	X	x	r	x	X	27 5	X	X	X	X	r	20 5	X	x	X	o	X	12 2	o	X	x	X	x	138
23 1	x	r	x	X	x	27 2	X	r	X	X	X	29 0	x	X	o	X	x	12 3	X	x	X	o	X	139
25 1	X	x	X	x	r	34 2	X	X	x	X	o	29 0	X	x	X	o	X	58 2	x	X	o	X	x	140
25 4	x	r	x	X	x	34 4	X	x	X	o	X	29 0	x	X	x	X	o	58 1	X	x	X	o	X	141
25 2	X	x	X	x	r	34 5	x	X	x	X	o	25 4	X	X	X	r	X	58 5	o	X	X	X	X	142
25 6	x	r	X	X	X	34 3	X	o	X	x	X	25 2	X	X	r	X	X	58 4	X	o	X	x	X	143
25 3	X	o	X	x	X	34 1	x	X	x	X	o	25 1	X	X	X	o	X	48 1	o	X	x	X	x	144
18 1	x	o	x	X	x	56 3	X	o	X	x	X	25 3	X	X	o	X	x	48 4	X	x	X	o	X	145
18 5	x	X	X	o	X	56 2	r	X	x	X	o	25 6	X	x	X	o	X	48 5	o	X	x	X	x	146
18 2	X	o	x	X	x	56 4	X	x	X	o	X	65 5	x	X	o	X	x	48 3	X	x	X	o	X	147
18 4	x	X	X	o	X	56 5	x	X	x	X	o	65 2	X	o	X	x	X	48 2	o	X	x	X	x	148
18 3	X	o	X	X	x	56 1	X	x	X	o	X	65 3	x	X	x	X	o	38 0	X	x	X	o	X	149
39 4	x	X	X	o	X	9 1	x	X	x	X	r	65 4	X	x	X	o	X	38 0	x	X	x	X	x	150
39 3	x	x	X	X	o	9 2	X	x	X	x	X	65 1	x	X	o	X	x	38 0	X	o	X	x	X	151
39 2	X	o	X	X	X	9 3	o	X	o	X	x	22 3	X	x	X	o	X	30 3	o	X	x	X	x	152

39 1	X	x	o	X	x	9 4	X	X	X	o	X	22 4	x	X	o	X	x	30 2	X	o	X	x	X	153
39 5	x	X	X	o	X	9 5	x	X	x	X	o	22 2	X	x	X	x	X	30 1	o	X	x	X	x	154
53 4	X	o	X	X	x	26 5	X	o	X	x	X	22 5	x	X	X	X	o	30 5	X	x	X	o	X	155
53 1	x	X	X	o	X	26 2	X	X	X	X	o	22 1	X	x	X	o	X	30 4	o	X	x	X	x	156
53 5	X	o	X	X	x	26 1	r	x	X	x	X	66 0	x	X	o	X	x	14 4	X	x	X	o	X	157
53 3	x	X	r	x	X	26 4	x	r	x	X	x	66 0	X	x	X	o	X	14 3	o	X	x	X	x	158
53 2	X	x	x	X	o	26 3	X	X	X	o	X	66 0	x	X	o	X	x	14 5	X	x	X	o	X	159
6 2	x	X	X	X	X	69 0	x	X	o	X	x	4 1	X	o	X	x	X	14 2	x	X	o	X	x	160
6 3	X	o	x	X	x	69 0	X	X	X	o	X	4 4	o	X	x	X	o	14 1	X	x	X	o	X	161
6 5	x	X	X	o	X	69 0	x	X	x	X	o	4 3	X	o	X	x	X	35 3	o	X	x	X	x	162
6 1	X	o	x	X	x	14 5	X	o	X	x	X	4 2	x	X	x	X	o	35 5	X	x	X	o	X	163
6 4	x	X	X	o	X	14 3	x	X	o	X	x	4 5	X	o	X	x	X	35 4	X	X	o	X	x	164
50 5	X	o	x	X	x	14 2	X	o	X	o	X	56 5	x	X	o	X	x	35 2	X	x	X	o	X	165
50 1	x	X	X	o	X	14 4	x	X	x	X	r	56 3	X	x	X	o	X	35 1	o	X	x	X	x	166
50 2	X	o	x	X	x	14 1	X	x	X	o	X	56 4	x	X	o	X	x	64 5	X	x	X	o	X	167
50 3	x	X	X	o	X	8 4	x	X	x	X	o	56 1	X	x	X	o	X	64 4	o	X	x	X	x	168
50 4	X	o	x	X	x	8 3	X	o	X	x	X	56 2	x	X	o	X	x	64 1	X	x	X	o	X	169
31 4	o	X	X	x	X	8 2	x	X	o	X	x	6 5	X	x	X	o	X	64 2	x	X	o	X	x	170
31 2	X	x	x	X	o	8 5	X	x	X	o	X	6 4	x	X	o	X	x	64 3	X	x	X	o	X	171
31 5	x	X	X	o	X	8 1	x	X	x	X	o	6 3	X	x	X	o	X	28 5	o	X	x	X	X	172
31 3	X	o	X	X	x	22 4	X	x	X	o	X	6 2	x	X	o	X	x	28 2	X	x	X	o	X	173
31 1	x	X	X	o	X	22 2	x	X	x	X	o	6 1	X	x	X	o	X	28 3	o	X	x	X	x	174
26 2	X	o	x	X	x	22 1	X	o	X	x	X	51 2	x	X	o	X	x	28 1	X	x	X	o	X	175
26 3	o	X	X	x	X	22 5	x	X	x	X	r	51 5	X	x	X	o	X	28 4	o	X	x	X	x	176
26 5	X	x	x	X	o	22 3	X	o	X	x	X	51 4	x	X	x	X	o	32 4	X	o	X	x	X	177
26 4	x	X	X	o	X	31 2	o	X	x	X	o	51 3	X	x	X	o	X	32 5	o	X	x	X	x	178
26 1	X	o	X	X	X	31 1	X	o	X	x	X	51 1	x	X	o	X	x	32 1	X	o	X	x	X	179
44 2	x	X	X	o	X	31 5	x	X	x	X	o	1 0	X	x	X	o	X	32 2	o	X	x	X	x	180
44 1	X	o	x	X	x	31 3	X	o	X	X	X	1 0	x	X	x	X	o	32 3	X	x	X	o	X	181
44 4	x	X	X	o	X	31 4	x	X	x	X	o	1 0	X	x	X	o	X	19 5	o	X	x	X	x	182
44 3	X	o	x	X	x	37 5	X	o	X	x	X	59 3	x	X	o	X	x	19 4	X	x	X	o	X	183
44 5	x	X	X	o	X	37 2	x	X	x	X	o	59 4	X	x	X	o	X	19 3	o	X	x	X	x	184
4 4	X	o	x	X	x	37 1	X	o	X	x	X	59 5	x	X	o	X	x	19 1	X	x	X	o	X	185
4 1	x	X	X	o	X	37 3	x	X	o	X	x	59 1	X	x	X	o	X	19 2	o	X	x	X	x	186
4 3	X	o	x	X	X	37 4	X	o	X	x	X	59 2	x	X	o	X	x	46 2	X	x	X	o	X	187
4 5	x	X	X	o	X	58 5	x	X	x	X	o	55 3	X	o	X	x	X	46 5	x	X	o	X	x	188
4 2	X	o	x	X	x	58 2	X	o	X	x	X	55 4	x	X	o	X	x	46 1	X	x	X	o	X	189
57 5	x	X	X	o	X	58 4	x	X	x	X	o	55 1	X	x	X	o	X	46 3	o	X	x	X	x	190
57 1	X	x	o	X	x	58 1	X	o	X	x	X	55 5	x	X	o	X	x	46 4	X	x	X	o	X	191
57 3	o	X	X	x	X	20 3	x	X	x	X	o	55 2	X	x	X	o	X	17 5	X	X	x	X	o	192
57 4	X	x	o	X	x	20 5	X	o	X	x	X	47 4	x	X	o	X	x	17 1	X	o	X	x	X	193
57 2	o	X	X	x	X	20 2	x	X	x	X	o	47 5	X	x	X	o	X	17 4	o	X	x	X	x	194
29 0	X	x	x	X	o	20 4	X	o	X	x	X	47 2	x	X	o	X	x	17 3	X	x	X	o	X	195
29 0	o	X	X	x	X	20 1	x	X	x	X	o	47 1	X	x	X	o	X	17 2	o	X	x	X	x	196
29 0	X	o	x	X	x	25 2	X	x	X	o	X	47 3	x	X	o	X	x	45 4	X	x	X	o	X	197
59 1	x	X	X	o	X	25 3	x	X	X	X	o	13 3	X	x	X	o	X	45 2	X	X	r	X	X	198
59 2	X	o	x	X	x	25 1	X	o	X	o	X	13 1	o	X	x	X	X	45 1	X	o	X	x	X	199
59 4	x	X	X	o	X	25 6	X	X	x	X	o	13 2	X	x	X	o	X	45 3	o	X	x	X	x	200
59 5	X	x	o	X	x	25 4	X	o	X	x	X	13 5	x	X	o	X	x	45 5	X	x	X	o	X	201
59 3	o	X	X	x	X	29 0	x	X	x	X	o	13 4	X	x	X	o	X	44 4	x	X	X	X	x	202
66 0	X	o	x	X	X	29 0	X	o	X	x	X	31 4	x	X	o	X	x	44 2	X	x	X	o	X	203
66 0	x	X	X	o	X	29 0	x	X	o	X	x	31 2	X	o	X	x	X	44 3	x	X	X	X	o	204

66 0	X	o	x	X	x	42 4	X	o	X	x	X	31 3	x	X	o	X	X	44 1	X	x	X	o	X	205
33 4	x	X	X	o	X	42 2	o	X	x	X	o	31 1	X	x	X	o	X	44 5	o	X	X	X	x	206
33 1	X	o	x	X	x	42 5	X	o	X	x	X	31 5	x	X	o	X	x	9 3	X	X	X	o	X	207
33 5	x	X	X	o	X	42 3	x	X	x	X	o	26 2	X	x	X	o	X	9 1	o	X	x	X	x	208
33 3	X	o	x	X	x	42 1	X	x	X	o	X	26 4	x	X	o	X	x	9 4	X	x	X	o	X	209
33 2	o	X	X	x	X	67 0	x	X	x	X	o	26 5	X	x	X	o	X	9 2	o	X	x	X	x	210
45 1	X	o	x	X	x	67 0	X	x	X	o	X	26 3	x	X	o	X	x	9 5	X	o	X	X	X	211
45 5	x	X	X	o	X	67 0	x	X	x	X	o	26 1	X	o	X	x	X	68 5	x	X	o	X	x	212
45 2	X	o	x	X	x	32 2	X	o	X	x	X	48 1	x	X	o	X	x	68 2	X	x	X	o	X	213
45 4	x	X	X	o	X	32 1	x	X	x	X	o	48 4	X	x	X	o	X	68 4	o	X	x	X	x	214
45 3	x	X	x	X	o	32 4	X	X	X	o	X	48 5	x	X	o	X	x	68 3	X	X	X	x	X	215
28 4	X	o	X	x	X	32 5	x	X	x	X	o	48 3	X	x	X	o	X	68 1	o	X	x	X	x	216
28 2	o	X	X	X	x	32 3	X	o	X	x	X	48 2	x	X	x	X	o	59 4	X	x	X	o	X	217
28 5	x	x	X	o	X	33 4	x	X	x	X	o	23 4	X	x	X	o	X	59 1	x	X	o	X	x	218
28 3	X	x	o	X	x	33 1	X	o	X	x	X	23 5	x	X	o	X	x	59 2	X	x	X	x	X	219
28 1	x	o	X	x	X	33 5	x	X	o	X	x	23 3	X	x	X	o	X	59 5	o	X	X	X	x	220
41 4	x	X	x	X	o	33 2	X	o	X	x	X	23 2	x	X	x	X	o	59 3	X	x	X	o	X	221
41 5	x	X	X	o	X	33 3	x	X	o	X	x	23 1	X	o	X	x	X	53 3	o	X	x	X	x	222
41 1	X	o	x	X	x	46 1	X	x	X	o	X	40 3	x	X	o	X	x	53 2	X	x	X	o	X	223
41 3	o	X	X	x	X	46 2	x	X	x	X	o	40 5	X	x	X	o	X	53 1	o	X	x	X	x	224
41 2	X	x	x	X	o	46 4	X	o	X	x	X	40 1	x	X	o	X	X	53 5	X	o	X	X	X	225
46 3	x	X	X	x	X	46 5	x	X	x	X	o	40 2	X	o	X	X	X	53 4	x	X	o	X	x	226
46 5	X	o	x	X	x	46 3	X	o	X	x	X	40 4	x	X	x	X	o	73 0	X	X	X	r	X	227
46 2	x	X	X	o	X	49 5	x	X	x	X	o	46 4	X	x	X	o	X	73 0	X	X	X	X	X	228
46 1	x	o	X	X	x	49 2	X	o	X	x	X	46 5	X	X	o	X	x	73 0	X	X	X	X	X	229
46 4	X	x	X	X	X	49 3	x	X	x	X	o	46 1	X	x	X	o	X	54 5	o	X	x	X	X	230
32 1	o	x	x	X	o	49 7	X	x	X	o	X	46 3	x	X	o	X	x	54 4	X	X	X	o	X	231
32 4	X	o	X	x	X	49 6	x	X	x	X	o	46 2	X	x	X	o	X	54 1	o	X	x	X	x	232
32 5	X	X	x	X	o	45 2	X	o	X	x	X	15 2	x	X	o	X	x	54 3	X	x	X	o	X	233
32 3	X	x	X	o	X	45 5	x	X	o	X	x	15 3	X	x	X	o	X	54 2	o	X	x	X	x	234
32 2	o	X	x	X	o	45 1	X	o	X	x	X	15 4	x	X	o	X	x	22 4	X	x	X	o	X	235
67 0	X	o	X	x	X	45 4	x	X	o	X	x	15 5	X	o	X	x	X	22 3	o	X	x	X	x	236
67 0	x	X	X	X	o	45 3	X	x	X	o	X	15 1	x	X	o	X	x	22 1	X	x	X	o	X	237
67 0	X	o	X	x	X	13 4	x	X	x	X	o	73 0	r	X	r	X	X	22 5	o	X	x	X	x	238
13 3	x	X	x	X	o	13 5	X	x	X	o	X	73 0	X	X	r	X	X	22 2	X	x	X	o	X	239
13 4	X	o	X	x	X	13 2	x	X	x	X	o	73 0	X	r	X	X	X	42 4	o	X	x	X	x	240
13 5	x	X	x	X	o	13 1	X	o	X	x	X	68 5	x	X	x	X	o	42 3	X	x	X	o	X	241
13 1	X	o	X	x	X	13 3	x	X	x	X	o	68 4	X	x	X	o	X	42 5	o	X	x	X	x	242
13 2	o	X	x	X	x	15 4	X	o	X	x	X	68 1	x	X	o	X	x	42 2	X	x	X	o	X	243
20 4	X	x	X	o	X	15 1	x	X	x	X	o	68 3	X	x	X	o	X	42 1	o	X	x	X	x	244
20 5	x	X	x	X	o	15 3	X	o	X	x	X	68 2	o	X	X	X	x	57 3	X	x	X	o	X	245
20 1	X	o	X	x	X	15 5	x	X	x	X	o	69 0	X	x	X	o	X	57 2	o	X	x	X	x	246
20 2	x	X	x	X	o	15 2	X	o	X	x	X	69 0	x	X	o	X	X	57 1	X	x	X	o	X	247
20 3	X	x	X	o	X	35 5	x	X	x	X	o	69 0	X	x	X	o	X	57 4	o	X	x	X	x	248
17 1	o	X	x	X	x	35 4	X	o	X	x	X	45 2	o	X	x	X	x	57 5	X	x	X	o	X	249
17 4	X	x	X	o	X	35 2	x	X	o	X	o	45 4	X	x	X	o	X	71 2	r	X	X	X	X	250
17 3	x	X	x	X	o	35 1	X	o	X	x	X	45 5	x	X	x	X	o	71 3	X	X	X	r	X	251
17 2	X	x	X	o	X	35 3	x	X	x	X	o	45 3	X	x	X	o	X	71 5	r	X	X	X	X	252
17 5	x	X	o	X	x	71 2	X	X	X	r	X	45 1	o	X	x	X	x	71 4	X	r	X	X	X	253
14 4	X	o	X	x	X	71 1	X	X	X	X	r	17 4	X	x	X	o	X	71 1	r	X	X	X	X	254
14 1	x	X	x	X	o	71 5	X	x	X	X	X	17 2	x	X	o	X	x	4 2	X	x	X	o	X	255
14 2	X	o	X	x	X	71 4	X	X	X	X	r	17 3	X	x	X	o	X	4 3	o	X	x	X	x	256

14 3	x	X	o	X	x	71 3	X	X	X	r	X	17 1	x	X	o	X	x	4 5	X	x	X	o	X	257
14 5	X	X	X	o	X	39 4	x	X	x	X	o	17 5	X	x	X	o	X	4 1	o	X	x	X	x	258
71 5	x	X	x	X	o	39 3	X	o	X	x	X	34 1	x	X	o	X	x	4 4	X	x	X	o	X	259
71 1	X	x	X	o	X	39 2	o	X	x	X	x	34 5	X	x	X	o	X	61 4	o	X	x	X	x	260
71 4	x	X	o	X	x	39 1	X	o	X	x	X	34 3	x	X	o	X	x	61 2	X	x	X	o	X	261
71 3	X	x	X	o	X	39 5	o	X	x	X	x	34 4	X	o	X	x	X	61 1	o	X	x	X	x	262
71 2	x	o	X	X	x	11 5	X	o	X	x	X	34 2	x	X	o	X	x	61 5	X	x	X	o	X	263
24 1	X	X	r	X	X	11 3	x	X	x	X	o	19 3	X	x	X	o	X	61 3	o	X	x	X	x	264
24 2	o	x	X	X	x	11 4	X	x	X	o	X	19 5	x	X	o	X	x	47 1	X	x	X	o	X	265
24 4	X	o	X	X	X	11 2	x	X	o	X	x	19 2	X	x	X	o	X	47 2	o	X	x	X	x	266
24 5	x	X	x	X	o	11 1	X	x	X	o	X	19 4	x	X	o	X	x	47 3	X	o	X	x	X	267
24 3	X	o	X	x	X	60 0	X	X	X	X	r	19 1	X	x	X	o	X	47 4	o	X	x	X	x	268
22 4	x	X	x	X	o	60 0	X	r	X	X	X	2 0	x	X	o	X	x	47 5	X	x	X	o	X	269
22 5	X	x	X	x	X	60 0	X	X	X	X	r	2 0	X	X	X	o	X	56 1	o	X	x	X	X	270
22 3	x	X	x	X	o	59 4	X	o	X	x	X	2 0	x	X	o	X	x	56 2	X	x	X	o	X	271
22 1	X	x	X	o	X	59 3	x	X	X	X	o	54 2	X	x	X	o	X	56 3	x	X	o	X	x	272
22 2	x	X	o	X	x	59 2	X	o	X	x	X	54 4	x	X	o	X	x	56 4	X	o	X	x	X	273
19 4	X	o	X	o	X	59 5	x	X	x	X	o	54 1	X	x	X	o	X	56 5	x	X	x	X	x	274
19 3	x	X	o	X	x	59 1	X	x	X	o	X	54 5	x	X	o	X	x	31 2	X	x	X	o	X	275
19 1	X	o	X	x	X	47 3	x	X	x	X	o	54 3	X	x	X	o	X	31 3	x	X	o	X	x	276
19 5	x	X	x	X	o	47 5	X	x	X	o	X	41 5	x	X	X	X	x	31 4	X	x	X	o	X	277
19 2	X	x	X	x	X	47 4	x	X	o	X	x	41 3	X	x	X	o	X	31 1	o	X	x	X	x	278
40 3	x	X	o	X	x	47 1	X	o	X	x	X	41 1	x	X	o	X	x	31 5	X	o	X	x	X	279
40 4	X	x	X	o	X	47 2	x	X	o	X	x	41 2	X	x	X	o	X	8 3	x	X	o	X	x	280
40 2	x	X	x	X	x	54 4	X	o	X	x	X	41 4	x	X	o	X	x	8 2	X	x	X	o	X	281
40 1	X	x	X	o	X	54 2	o	X	x	X	x	60 0	X	X	X	r	X	8 4	o	X	X	X	x	282
40 5	x	X	x	X	o	54 5	X	o	X	x	X	60 0	X	X	X	X	r	8 5	X	x	X	o	X	283
54 4	X	x	X	o	X	54 1	x	X	o	X	x	60 0	X	X	X	r	X	8 1	o	X	x	X	x	284
54 3	x	X	x	X	o	54 3	X	o	X	x	X	14 1	x	X	x	X	o	25 1	X	X	X	X	X	285
54 1	X	o	X	x	X	1 0	x	X	x	X	o	14 5	X	x	X	o	X	25 2	r	X	X	X	X	286
54 5	x	x	o	X	x	1 0	X	o	X	x	X	14 4	x	X	o	X	x	25 4	X	x	X	o	X	287
54 2	X	o	X	x	X	1 0	x	X	o	X	x	14 3	X	x	X	o	X	25 6	r	X	X	X	X	288
30 3	x	X	x	X	o	64 5	X	o	X	x	X	14 2	x	X	o	X	x	25 3	X	o	X	x	X	289
30 1	X	o	X	x	X	64 2	x	X	x	X	o	44 3	X	x	X	x	X	13 1	x	X	o	X	x	290
30 2	x	X	x	X	o	64 1	X	x	X	o	X	44 5	x	X	o	X	x	13 2	X	o	X	x	X	291
30 5	X	o	X	x	X	64 3	o	X	x	X	o	44 2	X	o	X	x	X	13 4	x	X	o	X	x	292
30 4	x	X	x	X	o	64 4	X	o	X	x	X	44 1	x	X	o	X	x	13 3	X	x	X	o	X	293
69 0	X	o	X	x	X	62 4	x	X	x	X	o	44 4	X	x	X	o	X	13 5	o	X	x	X	x	294
69 0	x	X	x	X	o	62 3	X	o	X	x	X	12 5	x	X	o	X	x	20 4	X	x	X	o	X	295
69 0	X	o	X	x	X	62 7	x	X	X	X	o	12 1	X	x	X	o	X	20 1	o	X	x	X	x	296
63 1	x	X	x	X	o	62 5	X	o	X	x	X	12 4	x	X	o	X	x	20 2	X	x	X	o	X	297
63 5	X	o	X	x	X	62 2	x	X	x	X	X	12 3	X	x	X	o	X	20 3	o	X	x	X	x	298
63 2	x	X	x	X	o	6 3	X	o	X	x	X	12 2	x	X	o	X	x	20 5	X	x	X	x	X	299
63 3	X	o	X	x	X	6 1	x	X	x	X	o	63 3	X	x	X	o	X	43 3	o	X	x	X	x	300
63 4	x	X	o	X	x	6 4	X	o	X	x	X	63 1	x	X	o	X	x	43 4	X	x	X	o	X	301
55 2	X	X	X	X	X	6 5	x	X	x	X	o	63 5	X	X	X	o	X	43 2	o	X	x	X	x	302
55 5	x	o	X	X	x	6 2	X	o	X	x	X	63 4	x	X	o	X	x	43 5	X	x	X	o	X	303
55 4	X	x	X	o	X	48 3	x	X	x	X	o	63 2	X	x	X	o	X	43 1	o	X	x	X	x	304
55 3	o	X	x	X	x	48 2	X	o	X	x	X	24 3	x	X	o	X	x	65 5	X	x	X	x	X	305
55 1	X	o	X	x	X	48 1	x	X	x	X	o	24 2	X	x	X	o	X	65 3	o	X	x	X	x	306
9 5	x	X	x	X	o	48 5	X	o	X	x	X	24 5	x	X	o	X	x	65 2	X	x	X	o	X	307
9 2	X	o	X	x	X	48 4	x	X	x	X	X	24 1	X	x	X	o	X	65 1	o	X	x	X	x	308

9 1	x	X	x	X	o	10 0	X	o	X	x	X	24 4	x	X	o	X	x	65 4	X	X	X	x	X	309
9 4	X	x	X	X	X	10 0	x	X	o	X	x	35 2	X	x	X	o	X	62 7	X	X	r	X	X	310
9 3	x	o	X	X	X	10 0	X	o	X	x	X	35 5	x	X	o	X	x	62 5	X	x	X	o	X	311
10 0	X	x	X	o	X	28 4	x	X	x	X	o	35 4	X	x	X	o	X	62 2	o	X	x	X	x	312
10 0	x	X	x	X	o	28 5	X	o	X	x	X	35 3	x	X	o	X	x	62 3	X	x	X	o	X	313
10 0	X	o	X	x	X	28 1	x	X	o	X	x	35 1	X	x	X	o	X	62 4	o	X	X	X	x	314
47 1	x	X	x	X	o	28 2	X	o	X	x	X	61 3	x	X	o	X	x	37 4	X	x	X	X	X	315
47 3	X	o	X	x	X	28 3	x	X	x	X	o	61 4	X	x	X	o	X	37 2	o	X	x	X	x	316
47 4	o	X	x	X	o	66 0	X	o	X	x	X	61 5	x	X	o	X	x	37 5	X	x	X	o	X	317
47 2	X	o	X	x	X	66 0	x	X	X	X	o	61 1	X	x	X	o	X	37 3	o	X	x	X	x	318
47 5	x	X	X	X	o	66 0	X	o	X	x	X	61 2	x	X	x	X	o	37 1	X	x	X	o	X	319

Note: o, standing tree; r, tree replaced by different family;

X, tree removed 1996; x, tree removed 1998.

Appendix 2. Layout of B. C. provenance trial at Saanich

Block 1A					Block 1B						
24-3	45-4	50-1	48-3	18-4	44-4	14-4	47-5	32-3	53-1	17-3	63-1
24-4	45-3	50-2	48-1	18-1	44-2	14-3	47-2	32-1	59-2	17-1	63-4
24-1	45-1	50-5	48-4	18-5	44-1	14-5	47-1	32-2	59-5	17-2	63-5
24-2	45-2	50-3	48-2	18-2	44-3	14-2	47-3	32-5	59-4	17-5	63-3
24-5	45-5	50-4	48-2	18-3	44-5	14-1	47-4	32-4	59-3	17-4	66-B
31-5	23-1	56-1	4-4	68-4	8-3	37-2	40-2	21-5	52-1	42-3	15-7
31-3	23-3	56-3	4-3	68-1	8-5	37-1	40-4	21-3	52-4	42-4	15-2
31-4	23-4	56-4	4-5	68-3	8-4	37-5	40-1	21-1	52-2	42-2	15-5
31-1	23-5	56-2	4-1	68-2	8-1	37-3	40-5	21-4	51-2	42-1	15-4
31-2	23-2	56-5	4-2	68-5	8-2	37-4	40-3	21-2	52-5	62-5	69-B
57-4	61-5	30-3	36-4	53-2	71-5	55-1	65-4	54-4	51-2	62-6	75-4
57-3	61-1	30-2	36-3	53-3	71-3	55-3	65-2	54-5	51-3	62-3	75-1
57-1	31-4	30-5	36-5	53-4	71-2	55-2	65-3	54-1	51-1	62-4	75-2
57-2	61-3	30-1	36-2	53-5	71-1	55-5	65-5	54-2	51-4	60-B	75-5
57-5	61-2	30-4	36-1	53-1	71-4	55-4	65-1	54-3	51-5	5-B	3-B
1-B	2-B	58-2	25-6	11-1	13-2	12-2	6-3	41-1	35-5	33-2	9-4
	38-B	58-4	25-4	11-5	13-3	12-3	6-2	41-4	35-3	33-5	9-5
	67-B	58-5	25-3	11-2	13-1	12-1	6-5	41-2	35-2	33-3	9-3
			10-B	29-B	13-4	12-4	6-4	41-3	35-1	33-1	9-2
								Block 2B			
								11-2	39-3	37-4	50-5
								11-1	39-1	37-3	50-1
								11-5	39-4	37-1	50-3
								6-4	39-2	37-2	50-4
								6-5	39-5	37-3	30-2
								6-3	31-1	18-1	36-4
								6-2	31-4	18-5	36-5
								31-5	18-3	36-1	59-2
								31-2	18-2	36-3	59-5
								31-3	18-4	36-2	59-1
								23-2	55-5	4-3	24-4
								23-4	55-4	4-5	24-3
								23-3	55-2	4-2	24-5
								23-5	55-1	4-1	24-2
								23-1	55-3	4-4	24-1
								61-5	17-1	8-5	54-1
								61-4	17-3	8-2	54-5
								61-4	17-5	8-3	54-2
								61-3	17-4	8-4	54-4
								31-1	17-2	8-1	54-3
								6-B	5-B	43-2	32-1
										43-4	32-4
										43-3	32-3
										43-5	32-2
										43-1	32-5
										10-B	38-B

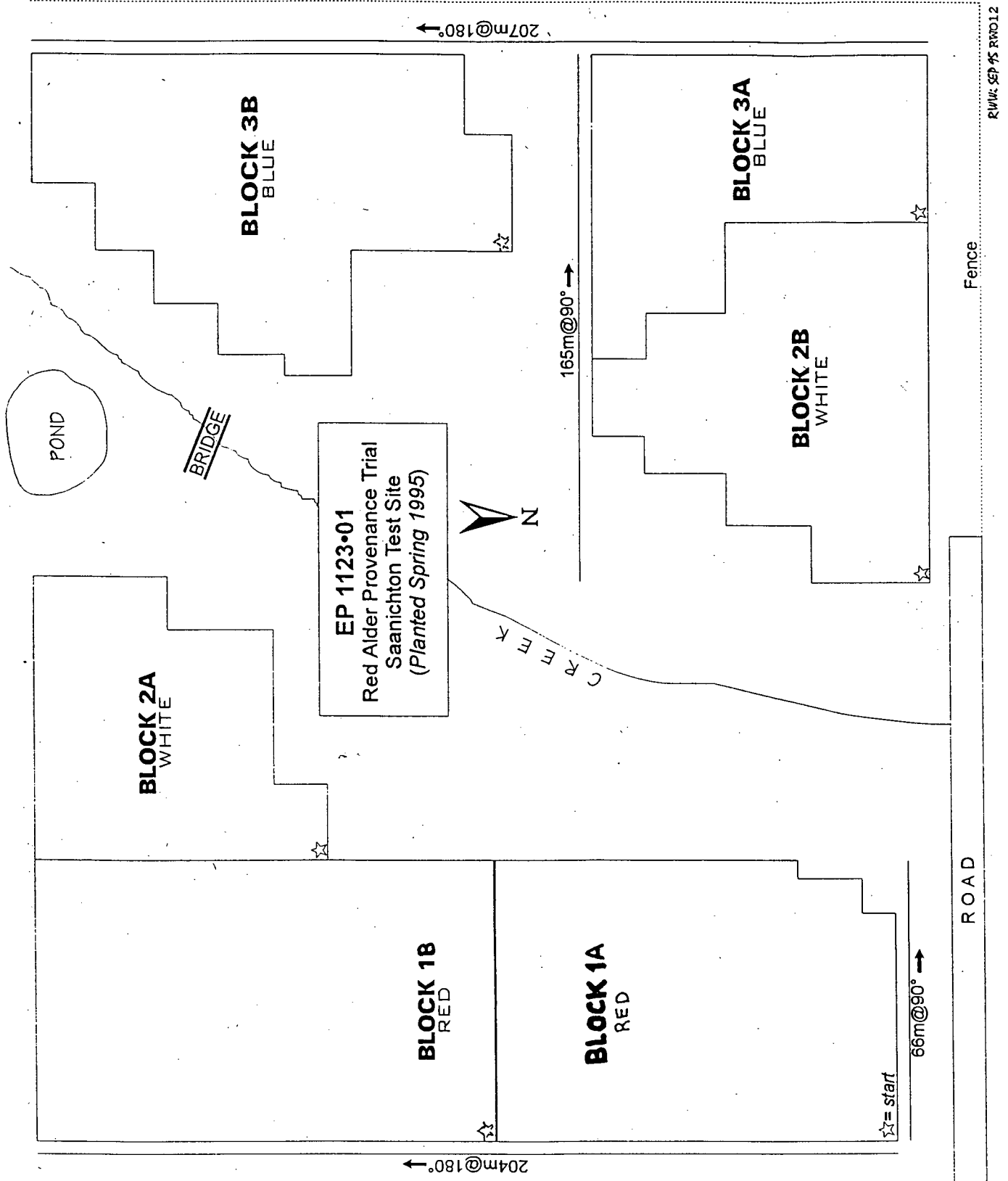
Note: Rectangle represents a 5 tree row plot of a half sib family.

Block 2A

3-B	69-B			
13-4	12-3			
13-1	12-1			
13-2	12-2			
13-3	12-4			
65-4	71-5	45-3		
65-3	71-3	45-5		
65-2	71-4	45-4		
65-5	71-1	45-2		
65-1	71-2	45-1		
52-3	57-2	21-1		
52-1	57-1	21-2	35-5	
52-5	57-3	21-5	35-2	
52-2	57-5	21-3	35-1	
52-4	57-4	21-4	35-3	
48-3	56-2	9-3	75-5	63-1
48-2	56-1	9-4	75-2	63-3
48-4	56-3	9-2	75-4	63-4
48-1	56-4	9-5	75-1	63-5
48-5	56-5	64-4	14-5	25-3
41-1	42-1	64-5	14-2	25-6
41-4	42-4	64-1	14-3	25-4
41-2	42-3	64-3	14-1	62-5
41-3	42-2	33-3	14-4	62-4
40-3	15-4	33-5	47-1	62-6
40-2	15-2	33-1	47-2	62-3
40-5	15-7	33-2	47-3	
40-1	15-5	30-1	47-4	62-4
40-4	51-5	30-4	47-5	62-3
49-1	51-3	30-3		62-6
49-2	51-4	30-5	53-4	62-5
49-3	51-2	30-2	53-5	63-5
49-5	51-1	58-4	53-1	63-4
49-6	68-3	58-2	53-3	63-1
53-4	68-4	58-5	53-2	63-3
53-3	68-1	60-B	68-2	12-1
53-1	68-2	1-B	68-5	12-2
53-2	68-5	29-B	68-4	12-3
53-5	2-B	67-B	68-1	12-4
Block 3A			68-3	44-1
32-2	14-4	43-2	61-5	44-4
32-1	14-3	43-4	61-2	44-2
32-3	14-1	43-1	61-3	44-3
32-5	14-5	43-3	61-4	71-3
32-4	1-5	43-5	61-1	71-5
54-4	31-5	15-4	35-3	71-1
54-2	31-2	15-5	35-5	71-4
54-3	31-4	15-2	35-1	71-2
54-1	31-3	15-7	35-2	57-5
54-5	31-1	33-5	6-2	57-4
25-4	58-2	33-1	6-5	57-2
25-6	58-5	33-3	6-3	57-1
25-3	58-4	33-2	6-4	57-3

Block 3B

69-B	13-4	42-4	23-2	39-1	65-5	1-B	
17-2	13-1	42-3	23-3	39-3	65-3	29-B	
17-3	13-2	42-2	23-5	39-2	65-4	10-B	
17-1	13-3	42-1	30-3	40-5	56-4	49-1	75-5
17-5	9-3	41-4	30-1	40-4	56-3	49-3	75-4
17-4	9-4	41-2	30-5	40-3	56-2	49-5	75-1
21-1	9-5	41-3	30-4	40-2	56-5	49-2	75-2
21-2	9-2	41-1	30-2	40-1	56-1	49-6	51-2
21-4	48-5	11-2	55-5	37-3	52-4	47-3	51-1
21-2	48-1	11-1	55-3	37-4	52-5	47-1	51-3
21-3	48-4	11-5	55-4	37-5	52-3	47-4	51-5
	48-2	2-B	55-1	37-2	52-1	47-5	51-4
	48-3	5-B	55-2	37-1	52-2	47-2	50-4
	4-4	36-4	8-1	18-5	45-5	24-4	50-5
	4-1	36-2	8-5	18-3	45-1	24-5	50-2
	-5	36-5	8-4	18-4	45-4	24-2	50-1
	4-2	36-1	8-3	18-2	45-3	24-3	50-3
	4-3	36-3	8-2	18-1	45-2	24-1	

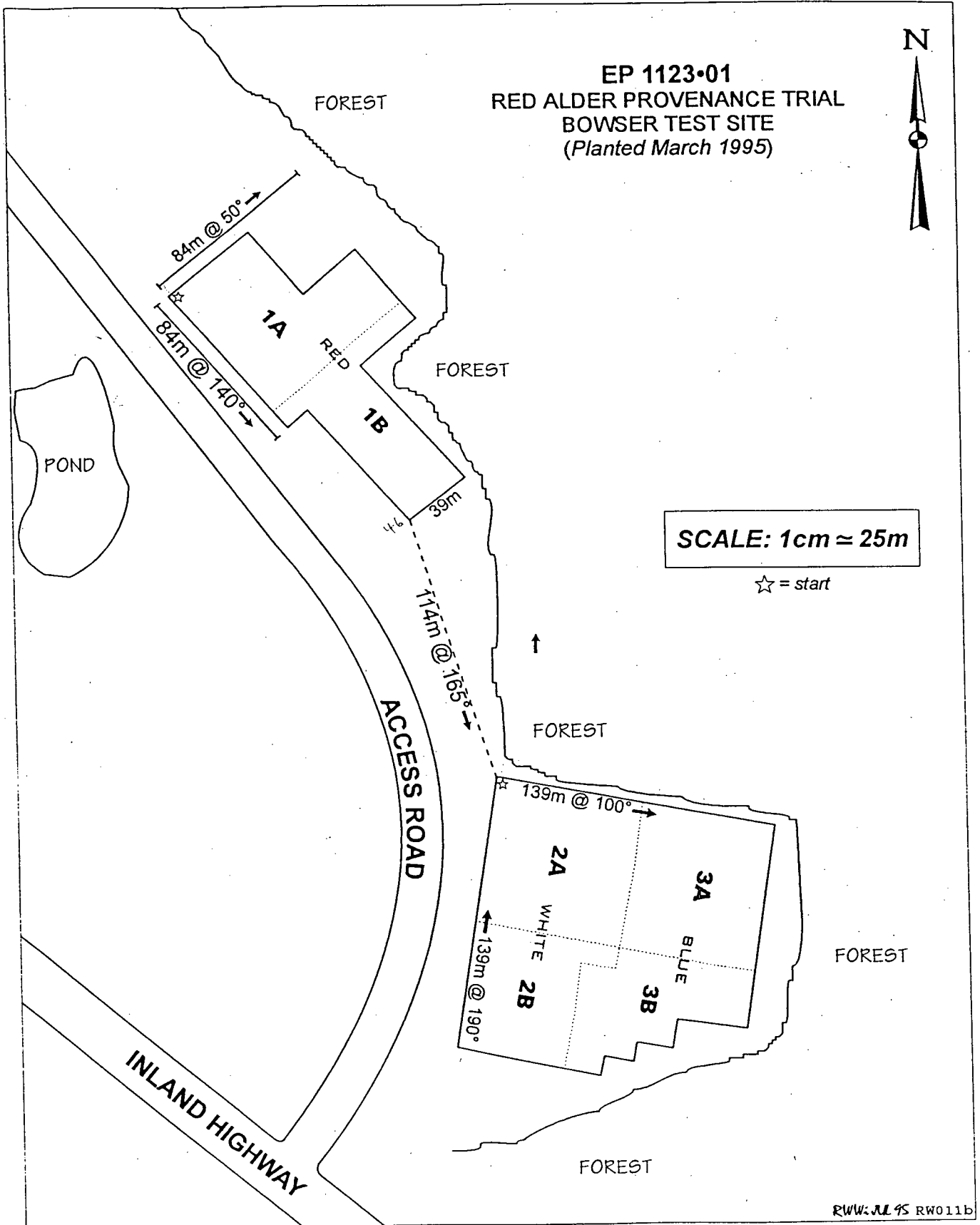


Appendix 3. Layout of B. C. provenance trial at Bowser

Block 1				
62-5	23-5	29-B		
62-4	23-3	29-B		
15-5	14-1	29-B		
15-2	14-2	12-4		
15-8	24-1	12-1		
59-4	24-3	12-2		
59-1	42-5	12-3		
59-3	60-B	50-1		
59-6	52-3	50-3		
59-2	52-1	50-4		
32-2	37-1	50-2	4-5	53-1
32-5	37-2	9-2	4-4	53-2
32-3	37-5	9-3	10-B	53-5
32-1	37-3	9-5	30-3	53-3
61-4	63-2	48-4	30-1	53-4
61-3	63-4	48-5	30-2	51-1
61-3	63-5	48-2	30-4	51-5
61-5	39-5	56-4	30-5	51-2
8-5	39-1	56-5	55-2	51-3
8-4	39-4	56-1	55-5	51-4
8-3	35-2	56-2	55-3	10-B
8-1	35-1	54-1	55-4	6-4
11-3	31-2	54-5	57-3	6-1
11-2	31-4	54-4	57-4	10-B
11-4	31-3	54-3	57-2	
	60-B	69-B		
	1-3	58-2		
	21-1	58-4		
	21-5	58-5		
	21-4	47-3		
	13-5	47-1		
	13-1	40-5		
	13-3	40-1		
	65-5	64-4		
	65-4	64-1		
	68-4	Unk		
	68-1	71-4		
	68-2	71-3		
	67-B	71-5		
	67-B	45-3		
	67-B	45-2		
	43-5	45-1		
	43-4	41-2		
	43-1	41-3		
	43-2	44-1		
	60-B	44-4		

Note: Rectangle represents a 5 tree
row plot of a half sib family.

Block 2				Block 3			
55-3	50-3	68-2	21-5	10-B	56-2	21-3	12-2
55-2	50-4	68-1	21-1	10-B	56-4	21-1	12-1
55-5	50-2	68-4	21-3	10-B	56-1	21-5	12-3
55-4	50-1	58-2	21-4	15-2	56-5	21-4	12-4
15-2	4-4	58-5	9-5	15-8	53-1	59-4	11-2
15-5	4-5	58-4	9-2	15-5	53-4	59-2	11-3
15-8	54-3	45-3	9-3	55-5	53-2	59-1	11-4
52-1	54-3	45-2	24-3	55-4	53-5	59-6	54-3
52-3	54-4	45-1	24-1	55-3	53-3	59-3	54-1
31-2	54-1	32-3	24-5	55-2	51-1	30-5	54-4
31-4	29-B	32-5	35-1	68-2	51-5	30-4	54-5
31-3	29-B	32-1	35-2	68-4	51-2	30-2	40-5
63-4	29-B	32-2	65-4	68-1	51-3	30-3	40-1
63-2	10-B	40-1	65-5	41-2	51-4	30-1	67-B
63-5	10-B	40-5	48-4	41-3	61-5	65-5	67-B
44-1	10-B	8-5	48-2	13-5	61-4	65-4	67-B
44-4	39-4	8-4	48-5	13-3	61-2	39-4	9-3
56-2	39-1	8-3	43-5	13-1	61-3	69-5	9-2
56-1	39-5	8-1	43-4	58-5	31-4	39-1	9-5
56-4	53-2	62-5	43-2	58-4	31-3	48-2	23-5
56-5	53-4	62-4	43-1	58-2	31-2	48-5	23-3
64-1	53-1	23-5	71-5	62-4	60-B	48-4	57-3
64-4	53-5	23-3	71-3	62-5	60-B	43-4	57-2
11-2	53-3	67-B	71-4	6-4	60-B	43-5	57-4
11-4	13-5	67-B	60-B	6-1	45-2	43-2	8-4
11-3	13-3	67-B	69-B	35-1	45-1	43-1	8-3
57-2	13-1	14-2	37-5	35-2	45-3	44-4	8-1
57-4	59-4	14-1	37-2	24-1	50-4	44-1	8-5
57-3	59-6	37-5	37-1	24-5	50-3	14-2	64-4
12-1	59-1	37-3	37-3	24-3	50-1	14-1	64-1
12-3	59-3	37-2	52-1	69-B	50-2		
12-4	59-2	37-1	52-3	69-B	32-3		
12-2	69-B	6-4	63-2	69-B	32-2		
41-3	69-B	6-1	63-5	4-4	32-1		
41-2	69-B	47-1	63-4	4-5	32-5		
51-2	30-4	47-3	71-3	29-B			
51-1	30-5	61-2	71-4	29-B			
51-5	30-2	61-4	71-5	29-B			
51-4	30-3	61-3	47-1				
51-3	30-1	61-5	47-3				



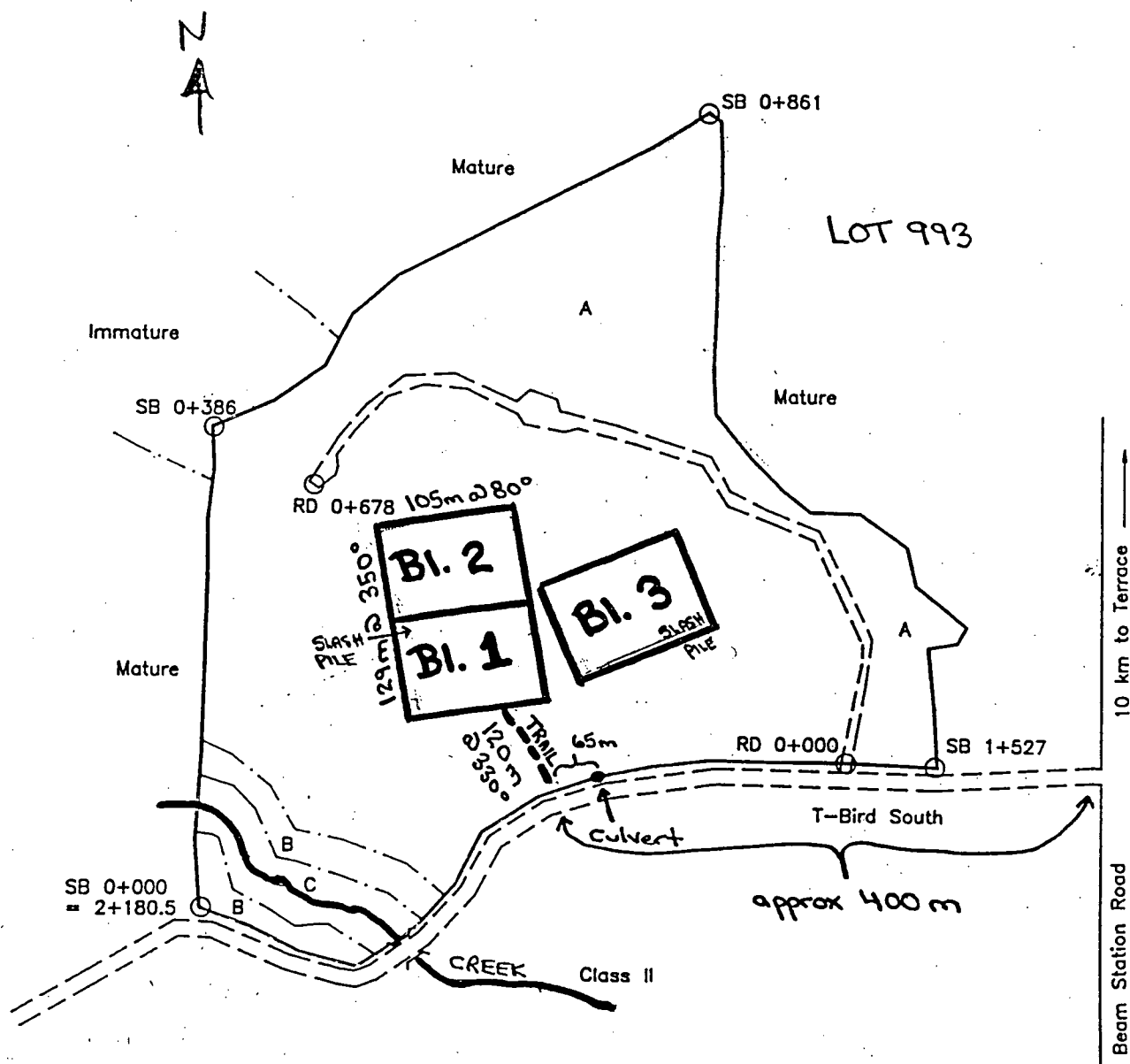
Appendix 4. Layout of B. C. provenance trial at Terrace

Block 1				Block 2			
61-4	11-2	59-1	68-1	52-3	43-1	68-4	41-3
61-5	11-3	59-3	68-2	52-1	43-2	68-1	65-4
61-2	11-4	59-2	68-4	4-5	43-5	68-2	44-1
61-3	29-B	10-B	9-3	4-4	43-4	11-4	9-3
30-1	29-B	10-B	9-2	23-3	8-3	11-3	9-2
30-5	29-B	10-B	9-5	23-5	8-4	11-2	9-5
30-4	53-4	48-2	50-2	58-5	8-1	57-4	50-1
30-3	53-5	48-5	50-1	58-4	8-5	57-2	50-4
12-1	53-2	45-4	50-4	35-1	30-4	57-3	50-2
12-4	53-1	31-4	71-4	35-2	30-5	24-5	48-5
12-3	53-3	31-2	71-5	40-1	30-1	24-1	48-2
12-2	51-1	31-3	71-3	40-5	30-3	24-3	48-4
56-2	51-5	45-2	24-5	6-1	61-2	45-2	37-5
56-1	51-2	45-1	24-1	6-4	61-3	45-1	37-1
56-5	51-3	45-3	24-3	14-1	61-5	45-3	37-3
56-4	51-4	21-3	37-5	14-2	61-4	60-B	21-5
4-5	65-4	21-5	37-3	64-1	55-3	60-B	21-3
4-4	54-3	21-4	37-1	64-3	55-5	60-B	21-4
14-2	54-5	8-1	32-5	13-5	55-2	47-1	31-3
14-1	54-4	8-5	32-2	13-3	55-4	47-3	31-2
6-4	15-8	8-4	32-1	32-1	10-B	62-4	31-4
6-1	15-2	8-3	67-B	32-2	10-B	62-5	12-1
52-1	15-5	55-4	67-B	32-5	10-B	53-1	12-4
52-3	63-4	55-5	67-B	59-3	29-B	53-3	56-5
23-5	63-5	55-2	58-4	59-1	29-B	53-5	56-4
23-3	63-2	55-3	58-5	59-2	29-B	53-4	56-2
13-3	60-B	43-2	62-4	15-2	54-5	53-2	56-1
13-5	60-B	43-4	62-5	15-5	54-4	51-5	12-3
47-1	60-B	43-5	64-3	15-8	54-3	51-3	12-2
47-3	57-3	43-1	64-1	71-4	63-4	51-2	67-B
40-1	57-2	44-1	35-2	71-5	63-5	51-1	67-B
40-5	57-4	41-3	35-1	71-3	63-2	51-4	67-B

Note: Rectangle represents a 5 tree row plot of a half sib family.

Block 3			
12-4	41-3	62-5	29-B
12-3	65-4	62-4	29-B
12-2	44-1	48-2	29-B
12-1	47-3	48-5	54-4
10-B	47-1	48-4	54-5
10-B	6-1	45-3	54-3
10-B	6-4	45-2	57-3
71-4	13-5	45-1	57-2
71-5	13-3	59-2	57-4
71-3	58-5	59-1	67-B
9-5	58-4	59-3	67-B
9-2	40-1	63-2	67-B
9-3	40-5	63-5	37-3
15-8	4-5	63-4	37-1
15-2	4-4	21-3	37-5
15-5	14-1	21-5	68-4
32-2	14-2	21-4	68-1
32-1	52-3	60-B	68-2
32-5	52-1	60-B	30-3
11-2	24-5	60-B	30-1
11-3	24-3	56-1	30-4
11-4	24-1	56-4	30-5
43-4	53-2	56-5	8-5
43-5	53-1	56-2	8-1
43-1	53-4	55-4	8-4
43-2	53-3	55-5	8-3
35-2	53-5	55-3	31-3
35-1	51-5	55-2	31-2
23-5	51-1	61-4	31-4
23-3	51-2	61-5	50-4
64-1	51-3	61-2	50-1
64-3	51-4	61-3	50-2

Ref. Map 103I 048
Scale: 1:5,000



LOCATION OF E.P. 1123.01 THUNDERBIRD
- Red Alder Provenance Test Site

Appendix 5. B. C. provenance information

<u>Provenance # -</u>	<u>Lat.</u>	<u>Long.</u>	<u>Elev.</u>	<u>BEC</u>
<u>Provenance Name</u>	<u>° ' "</u>	<u>° ' "</u>	<u>m.</u>	<u>Zone</u>
01-B				
02-B				
03-B				
04-Port Renfrew	48 36'	124 14'	20	-
05-B				
06-Klanawa #2	48 46'	124 58'	40	CWHvm
08-Nitinat Flats	48 50'	124 40'	30	CWHvm
09-Cowichan M. F.	48 51'	123 39'	150	CWHvm
10-B-Cowichan Lake	48 55'	124 30'	160	CWHvm
11-Sarita Lake	48 55'	124 52'	40	CWHvm
12-Galiano Island	48 57'	123 28'	50	-
13-Between the Lakes	48 58'	124 43'	200	CWHvm
14-Ucluelet	49 00'	125 34'	40	-
15-Cassidy	49 03'	123 56'	107	-
17-Corrigan Creek #2	49 03'	124 42'	500	CWHxm
18-Maggie Lake	49 03'	125 27'	50	CWHvm
21-Britannia Creek	49 07'	123 07'	660	CWHb2
23-China Creek #2	49 10'	124 41'	400	CWHxm
24-Bainbridge Lake	49 12'	124 45'	100	CWHxm
25-Coombs	49 19'	124 27'	50	CWHxm
29-B-Union Bay	49 32'	124 53'	100	CWHxm1
30-Indian River	49 34'	122 56'	190	CWHb1
31-Pender Harbour	49 39'	124 02'	150	CWHdm
32-Mamquam River	49 43'	123 07'	100	CWHa2
33-Headquarters #2	49 45'	125 07'	250	CWHxm
35-Culliton Cr.	49 53'	123 11'	250	CWHc
36-Lund	49 58'	124 45'	150	CWHdm
37-Woss #2	49 58'	126 15'	1000	CWHvm
38-B-Zeballos #2	50 01'	126 49'	200	CWHvm
39-Cheakamus River	50 04'	123 06'	540	CWHb5
40-Snowdon #1	50 05'	125 23'	100	CWHxm
41-Quadra	50 10'	125 13'	50	CWHxm
42-Woss #1	50 11'	126 26'	250	CWHvm
43-Roberts Lake	50 13'	125 33'	700	CWHxm
44-Bigtree #1	50 14'	125 43'	250	CWHxm
45-Bigtree #2	50 14'	125 43'	300	CWHxm
47-Prenticeville	50 21'	125 55'	80	CWHxm
48-Ronning Main	-	-	30	CWHvh
49-Port Hardy	50 37'	127 15'	37	-

<u>Provenance -</u>	<u>Lat.</u>	<u>Long.</u>	<u>Elev.</u>	<u>BEC</u>
<u>Family Number</u>	<u>° ' "</u>	<u>° ' "</u>	<u>m.</u>	<u>Zone</u>
50-San Josef Main	-	-	20	CWHvh
51-NE 62	-	-	170	CWHvh
52-Kingcome Inlet	51 30'	126 08'	30	CWHvm1(CWHb1)
53-Poole Inlet	52 21'	131 21'	1	CWHwh1
54-Hagensborg	52 22'	126 35'	40	CWHds(CWHc2)
55-Bachelor Bay	52 22'	126 55'	30	CWHmm(CWHb6)
56-Salloomt River	52 26'	126 33'	150	CWHmm(CWHb6)
57-Copper Bay	53 07'	131 40'	10	CWHwh1
58-Channel	53 08'	132 15'	20	CWHvh/wh1
59-Rennell Sound	53 22'	132 27'	100	CWHvh
60-B-Port Clement	53 41'	132 11'	15	CWHwh1
61-Masset	54 03'	132 00'	10	CWHwh1
62-Kitimat	54 15'	128 30'	60	-
63-Snow Creek	54 15'	129 33'	10	CWHvn1
64-Rainbow Summit	54 15'	130 02'	160	CWHvh
65-Prince Rupert	54 16'	130 16'	46	-
66-B-Skeena River	54 19'	129 20'	20	-
67-B-Exchamsiks R.	54 20'	129 17'	10	CWHvm1
68-Shames River	54 26'	128 55'	100	CWHws1
69-B-Williams Creek	54 27'	128 29'	100	CWHws1
71-Oliver Lake	-	-	-	-
75-Squamish	49 43'	123 05'	400	CWHdm

Appendix 6. Layout of Alaska provenance trial at Surrey

Rep 1, Block 1			Rep 1, Block 2			Rep 1, Block 3			Rep 1, Block 4		
34	7	52	4	67	40	15	51	33	19	46	37
70	43	25	31	58	13	24	6	60	55	10	73
16	79	61	76	22	49	69	42	78	1	64	28
Rep 1, Block 5			Rep 1, Block 6			Rep 1, Block 7			Rep 1, Block 8		
36	72	27	47	2	38	5	50	59	66	75	21
81	18	63	29	20	65	77	14	23	3	39	30
45	54	9	56	11	74	41	68	32	12	57	48
Rep 1, Block 9			Rep 2, Block 1			Rep 2, Block 2			Rep 2, Block 3		
44	62	8	49	52	47	15	10	14	21	22	19
35	17	26	53	50	46	12	17	11	20	26	23
53	80	71	54	48	51	16	13	18	25	24	27
Rep 2, Block 4			Rep 2, Block 5			Rep 2, Block 6			Rep 2, Block 7		
80	75	77	57	59	56	33	28	32	69	66	71
76	74	79	62	55	61	29	35	31	64	70	65
81	73	78	63	58	60	34	30	36	68	67	72
Rep 2, Block 8			Rep 2, Block 9			Rep 3, Block 1			Rep 3, Block 2		
1	4	3	37	40	39	12	49	19	70	40	3
5	2	9	41	44	38	72	2	62	10	63	20
6	7	8	43	42	45	32	42	79	50	33	80
Rep 3, Block 3			Rep 3, Block 4			Rep 3, Block 5			Rep 3, Block 6		
30	16	37	6	53	23	1	31	61	46	29	39
26	67	9	64	13	74	41	71	21	18	59	69
60	47	77	43	57	36	81	51	11	25	8	76
Rep 3, Block 7			Rep 3, Block 8			Rep 3, Block 9			Rep 4, Block 1		
54	14	44	17	78	27	15	45	22	76	11	3
24	65	4	48	7	38	52	5	66	19	52	44
75	34	55	58	28	68	35	56	73	68	36	60
Rep 4, Block 2			Rep 4, Block 3			Rep 4, Block 4			Rep 4, Block 5		
27	56	8	20	12	45	70	24	37	55	26	50
51	25	40	1	69	34	13	5	29	31	18	42
16	64	32	58	53	77	62	81	48	66	7	74
Rep 4, Block 6			Rep 4, Block 7			Rep 4, Block 8			Rep 4, Block 9		
23	80	28	25	57	9	6	71	22	2	21	10
47	15	4	17	73	49	63	14	30	78	35	67
39	61	72	33	65	41	79	46	38	54	43	59
Rep 5, Block 1			Rep 5, Block 2			Rep 5, Block 3			Rep 5, Block 4		
37	49	80	53	75	7	48	2	61	27	77	31
6	56	18	41	10	29	14	64	26	15	3	46
34	68	21	22	72	60	45	33	76	43	62	65
Rep 5, Block 5			Rep 5, Block 6			Rep 5, Block 7			Rep 5, Block 8		
42	8	70	38	19	35	71	40	24	67	5	39
30	23	11	16	57	50	9	28	59	55	17	36
73	58	54	69	4	81	12	74	52	79	20	51
Rep 5, Block 9			Rep 6, Block 1			Rep 6, Block 2			Rep 6, Block 3		
1	47	32	40	53	19	31	23	9	38	51	13
44	25	63	5	18	78	10	44	79	73	3	26
66	13	78	65	61	30	56	69	48	34	59	72

Rep 6, Block 4			Rep 6, Block 5			Rep 6, Block 6			Rep 6, Block 7		
11	24	45	35	1	39	76	6	54	33	12	55
46	67	80	70	49	60	16	62	28	43	47	22
57	32	7	74	14	27	66	20	41	8	68	81
Rep 6, Block 8			Rep 6, Block 9			Rep 7, Block 1			Rep 7, Block 2		
75	25	58	42	4	29	25	53	3	44	5	58
2	50	15	17	63	21	14	42	67	16	21	33
37	36	71	64	52	77	56	28	81	46	72	74
Rep 7, Block 3			Rep 7, Block 4			Rep 7, Block 5			Rep 7, Block 6		
47	6	31	29	54	26	65	35	63	73	18	20
17	59	19	40	1	79	37	51	12	48	32	60
70	45	75	57	68	15	76	7	23	4	71	43
Rep 7, Block 7			Rep 7, Block 8			Rep 7, Block 9			Rep 8, Block 1		
34	62	22	24	77	36	27	41	2	61	12	44
64	11	50	49	10	61	55	30	52	27	6	73
9	78	39	38	66	8	13	69	80	29	67	50
Rep 8, Block 2			Rep 8, Block 3			Rep 8, Block 4			Rep 8, Block 5		
59	1	42	56	19	33	3	41	24	20	14	57
22	65	16	13	54	7	35	58	18	8	52	37
48	36	80	77	39	71	47	64	79	72	78	31
Rep 8, Block 6			Rep 8, Block 7			Rep 8, Block 8			Rep 8, Block 9		
30	25	62	43	26	5	34	17	40	55	9	15
10	68	51	11	75	63	2	60	23	21	53	38
74	45	4	49	28	69	81	46	66	70	32	76
Rep 9, Block 1			Rep 9, Block 2			Rep 9, Block 3			Rep 9, Block 4		
71	16	23	53	37	4	22	2	70	14	36	69
45	3	78	11	66	33	18	28	57	73	7	40
55	49	29	59	27	79	44	77	51	21	47	62
Rep 9, Block 5			Rep 9, Block 6			Rep 9, Block 7			Rep 9, Block 8		
41	48	8	43	24	56	32	6	65	13	61	9
15	19	34	17	30	1	26	81	10	46	75	35
63	74	67	76	50	72	39	52	58	68	20	42
Rep 9, Block 9			Rep 10, Block 1			Rep 10, Block 2			Rep 10, Block 3		
5	12	31	41	12	70	68	63	31	37	54	3
80	38	25	26	36	4	2	39	24	32	17	69
54	60	64	78	46	56	73	16	53	22	61	74
Rep 10, Block 4			Rep 10, Block 5			Rep 10, Block 6			Rep 10, Block 7		
44	81	20	21	50	8	27	5	47	77	6	11
59	15	64	60	13	65	10	34	76	25	35	72
7	49	30	28	45	79	57	71	42	48	40	55
Rep 10, Block 8			Rep 10, Block 9								
58	19	9	33	1	18						
14	29	43	67	23	62						
66	51	80	38	52	75						

Note: Rectangle represents a 2 tree row plot of a half sib family.

Derivation of incomplete block design from mutually orthogonal latin squares for Alaska trial (rows of 1, 1+9, 1+9+9 ... are added to latin squares to obtain treatment numbers).

B1 B2 B3 B4 B5 B6 B7 B8 B9

R1	1	2	3	4	5	6	7	8	9
	10	11	12	13	14	15	16	17	18
	19	20	21	22	23	24	25	26	27
	28	29	30	31	32	33	34	35	36
	37	38	39	40	41	42	43	44	45
	46	47	48	49	50	51	52	53	54
	55	56	57	58	59	60	61	62	63
	64	65	66	67	68	69	70	71	72
	73	74	75	76	77	78	79	80	81

R2	1	10	19	28	37	46	55	64	73
	2	11	20	29	38	47	56	65	74
	3	12	21	30	39	48	57	66	75
	4	13	22	31	40	49	58	67	76
	5	14	23	32	41	50	59	68	77
	6	15	24	33	42	51	60	69	78
	7	16	25	34	43	52	61	70	79
	8	17	26	35	44	53	62	71	80
	9	18	27	36	45	54	63	72	81

Mutually orthogonal latin squares

R3	1	2	3	4	5	6	7	8	9
	11	12	10	14	15	13	17	18	16
	21	19	20	24	22	23	27	25	26
	31	32	33	34	35	36	28	29	30
	41	42	40	44	45	43	38	39	37
	51	49	50	54	52	53	48	46	47
	61	62	63	55	56	57	58	59	60
	71	72	70	65	66	64	68	69	67
	81	79	80	75	73	74	78	76	77

0	1	2	3	4	5	6	7	8
1	2	0	4	5	3	7	8	6
2	0	1	5	3	4	8	6	7
3	4	5	6	7	8	0	1	2
4	5	3	7	8	6	1	2	0
5	3	4	8	6	7	2	0	1
6	7	8	0	1	2	3	4	5
7	8	6	1	2	0	4	5	3
8	6	7	2	0	1	5	3	4

R4	1	2	3	4	5	6	7	8	9
	12	10	11	15	13	14	18	16	17
	20	21	19	23	24	22	26	27	25
	34	35	36	28	29	30	31	32	33
	45	43	44	39	37	38	42	40	41
	53	54	52	47	48	46	50	51	49
	58	59	60	61	62	63	55	56	57
	69	67	68	72	70	71	66	64	65
	77	78	76	80	81	79	74	75	73

0	1	2	3	4	5	6	7	8
2	0	1	5	3	4	8	6	7
1	2	0	4	5	3	7	8	6
6	7	8	0	1	2	3	4	5
8	6	7	2	0	1	5	3	4
7	8	6	1	2	0	4	5	3
3	4	5	6	7	8	0	1	2
5	3	4	8	6	7	2	0	1
4	5	3	7	8	6	1	2	0

R5

1	2	3	4	5	6	7	8	9
13	14	15	16	17	18	10	11	12
25	26	27	19	20	21	22	23	24
32	33	31	35	36	34	29	30	28
44	45	43	38	39	37	41	42	40
47	48	46	50	51	49	53	54	52
63	61	62	57	55	56	60	58	59
66	64	65	69	67	68	72	70	71
78	76	77	81	79	80	75	73	74

0	1	2	3	4	5	6	7	8
3	4	5	6	7	8	0	1	2
6	7	8	0	1	2	3	4	5
4	5	3	7	8	6	1	2	0
7	8	6	1	2	0	4	5	3
1	2	0	4	5	3	7	8	6
8	6	7	2	0	1	5	3	4
2	0	1	5	3	4	8	6	7
5	3	4	8	6	7	2	0	1

R6

1	2	3	4	5	6	7	8	9
14	15	13	17	18	16	11	12	10
27	25	26	21	19	20	24	22	23
35	36	34	29	30	28	32	33	31
39	37	38	42	40	41	45	43	44
49	50	51	52	53	54	46	47	48
60	58	59	63	61	62	57	55	56
70	71	72	64	65	66	67	68	69
74	75	73	77	78	76	80	81	79

0	1	2	3	4	5	6	7	8
4	5	3	7	8	6	1	2	0
8	6	7	2	0	1	5	3	4
7	8	6	1	2	0	4	5	3
2	0	1	5	3	4	8	6	7
3	4	5	6	7	8	0	1	2
5	3	4	8	6	7	2	0	1
6	7	8	0	1	2	3	4	5
1	2	0	4	5	3	7	8	6

R7

1	2	3	4	5	6	7	8	9
15	13	14	18	16	17	12	10	11
26	27	25	20	21	19	23	24	22
29	30	28	32	33	31	35	36	34
40	41	42	43	44	45	37	38	39
54	52	53	48	46	47	51	49	50
57	55	56	60	58	59	63	61	62
68	69	67	71	72	70	65	66	64
79	80	81	73	74	75	76	77	78

0	1	2	3	4	5	6	7	8
5	3	4	8	6	7	2	0	1
7	8	6	1	2	0	4	5	3
1	2	0	4	5	3	7	8	6
3	4	5	6	7	8	0	1	2
8	6	7	2	0	1	5	3	4
2	0	1	5	3	4	8	6	7
4	5	3	7	8	6	1	2	0
6	7	8	0	1	2	3	4	5

R8

1	2	3	4	5	6	7	8	9
16	17	18	10	11	12	13	14	15
22	23	24	25	26	27	19	20	21
36	34	35	30	28	29	33	31	32
42	40	41	45	43	44	39	37	38
48	46	47	51	49	50	54	52	53
59	60	58	62	63	61	56	57	55
65	66	64	68	69	67	71	72	70
80	81	79	74	75	73	77	78	76

0	1	2	3	4	5	6	7	8
6	7	8	0	1	2	3	4	5
3	4	5	6	7	8	0	1	2
8	6	7	2	0	1	5	3	4
5	3	4	8	6	7	2	0	1
2	0	1	5	3	4	8	6	7
4	5	3	7	8	6	1	2	0
1	2	0	4	5	3	7	8	6
7	8	6	1	2	0	4	5	3

R9

1	2	3	4	5	6	7	8	9
17	18	16	11	12	10	14	15	13
24	22	23	27	25	26	21	19	20
30	28	29	33	31	32	36	34	35
43	44	45	37	38	39	40	41	42
50	51	49	53	54	52	47	48	46
56	57	55	59	60	58	62	63	61
72	70	71	66	64	65	69	67	68
76	77	78	79	80	81	73	74	75

0	1	2	3	4	5	6	7	8
7	8	6	1	2	0	4	5	3
5	3	4	8	6	7	2	0	1
2	0	1	5	3	4	8	6	7
6	7	8	0	1	2	3	4	5
4	5	3	7	8	6	1	2	0
1	2	0	4	5	3	7	8	6
8	6	7	2	0	1	5	3	4
3	4	5	6	7	8	0	1	2

R10

1	2	3	4	5	6	7	8	9
18	16	17	12	10	11	15	13	14
23	24	22	26	27	25	20	21	19
33	31	32	36	34	35	30	28	29
38	39	37	41	42	40	44	45	43
52	53	54	46	47	48	49	50	51
62	63	61	56	57	55	59	60	58
67	68	69	70	71	72	64	65	66
75	73	74	78	76	77	81	79	80

0	1	2	3	4	5	6	7	8
8	6	7	2	0	1	5	3	4
4	5	3	7	8	6	1	2	0
5	3	4	8	6	7	2	0	1
1	2	0	4	5	3	7	8	6
6	7	8	0	1	2	3	4	5
7	8	6	1	2	0	4	5	3
3	4	5	6	7	8	0	1	2
2	0	1	5	3	4	8	6	7

Appendix 7. Alaska provenance information

Label	Provenance name	Lat	Long
1-20	Ketchikan	55.42	131.71
21-40	Petersburg	56.56	132.61
41-60	Sitka	57.04	135.29
61-80	Juneau	58.54	134.81

Appendix 8. Layout of selection experiment at Surrey

Block 1											
449	BL6 x BL8	405	BH1 x BH2	539	H8 x L5	82	B1 x B3	418	BH4 x BH1	296	H5 x L6
568	H8 x H5	448	BL6 x BL8	489	H2 x H2	335	BL2 x BL2	141	H8 x L5	307	H5 x L6
147	L2 x H2	556	H8 x L7	396	B8 x H5	509	H4 x B3	437	BL6 x BL6	88	O6 x O6
239	EL1 x EL4	153	H8 x L6	219	LH8 x LH7	137	H8 x L5	128	H8 x H5	196	H8 x H5
247	EL3 x EL2	197	H8 x H5	195	H8 x L8	124	H2 x B4	463	EL3 x EL3	233	LH8 x LH7
39	L7 x L8	10	BH1 x BH2	596	LH5 x LH5	162	H8 x L7	57	L4 x L3	494	H3 x B2
258	EL3 x EL2	287	H4 x H3	72	O5 x O7	65	O3 x O3	607	LH5 x LH8	488	H2 x H2
Block 3											
563	H8 x H5	411	BH1 x BH4	373	B5 x B8	253	EL3 x EL2	189	H8 x L8	59	H4 x B1
302	H5 x L6	345	O6 x O5	433	BL8 x BL7	231	LH8 x LH7	443	BL6 x BL8	43	L6 x L8
514	H4 x H1	400	B8 x H7	158	H8 x H7	473	H1 x B4	214	EL2 x EL3	572	L2 x H1
168	H8 x L7	383	B6 x H7	534	H8 x L5	148	H8 x L6	228	LH8 x LH7	269	EL3 x EL3
291	H5 x L6	579	L3 x L2	342	BH5 x BH7	1	B5 x H7	45	LH5 x LH5	550	H8 x L6
42	L6 x L8	337	BL5 x BL8	25	B5 x B6	613	LH7 x LH5	277	O3 x O3	567	H8 x H5
471	EL8 x EL6	522	H6 x L8	602	LH5 x LH5	620	H8 x L8	266	O6 x O7	526	H7 x H5
Block 5											
406	BH1 x BH2	324	BL3 x BL2	450	BL6 x BL8	530	H8 x L5	576	L2 x L2	511	H4 x B3
155	H8 x L6	559	H8 x L8	403	B8 x B5	298	H5 x L6	439	BL6 x BL7	130	H8 x H5
350	B2 x B3	67	O3 x O3	476	H2 x B4	570	H8 x H5	317	H4 x H4	459	EL1 x EL4
221	LH8 x LH7	369	B5 x B7	235	LH8 x LH7	210	EL3 x EL4	198	H8 x H5	249	EL3 x EL2
497	H3 x B3	309	H5 x L6	96	O6 x O7	164	H8 x L7	420	BH4 x BH1	33	L6 x L6
74	O6 x O5	50	LH6 x LH6	541	H8 x L5	18	B6 x H7	260	EL3 x EL2	598	LH5 x LH5
359	B5 x H8	366	B5 x B6	391	B6 x B6	518	H4 x H1	416	BH4 x BH1	590	L7 x L8
Block 7											
467	EL3 x EL4	408	BH1 x BH2	441	BL6 x BL7	371	B5 x B7	513	H4 x B3	543	H8 x L5
332	BL5 x BL7	561	H8 x L8	321	H4 x H1	381	B6 x H7	90	O3 x O1	532	H8 x L5
354	B5 x H5	452	BL6 x BL8	143	H8 x H6	132	H8 x H5	478	H2 x B4	62	L3 x L2
133	L2 x H1	431	BL8 x EL8	205	EL2 x EL2	166	H8 x L7	300	H5 x L6	548	H8 x L6
226	LH8 x LH7	346	O8 x O8	262	EL3 x EL2	185	H8 x L8	251	EL3 x EL2	200	H8 x H5
76	O6 x O5	98	O6 x O7	275	O3 x O3	49	LH4 x LH4	22	B5 x B5	600	LH5 x LH5
610	L6 x L7	611	LH7 x LH5	14	B8 x H7	289	H5 x H5	146	L2 x H2	284	H3 x B4
Block 9											
536	H8 x L5	385	B6 x H7	445	BL6 x BL8	54	L3 x L3	4	B6 x B6	64	B2 x L1
160	H8 x H7	552	H8 x L6	516	H4 x H1	101	O3 x O2	618	LH7 x LH6	340	BL8 x EL8
565	H8 x H5	339	BL5 x BL8	170	H8 x L7	85	O6 x O6	622	H8 x L8	127	H8 x H5
293	H5 x L6	304	H5 x L6	441	BL6 x BL7	48	LH5 x LH5	605	LH5 x LH5	232	LH8 x LH7
312	H1 x H4	271	EL3 x EL3	150	H8 x L6	204	EL2 x EL2	241	O3 x O2	38	L7 x L8
23	B7 x H7	102	O4 x O4	560	H8 x L8	28	B5 x B6	123	H2 x B4	624	H8 x L8
8	BH1 x BH1	224	LH8 x LH7	191	H8 x L8	36	L7 x L8	595	LH5 x LH5	53	LH5 x LH6

Block 2						
540 H8 x L5	438 BL6 x BL6	248 EL3 x EL2	83 B1 x B8	538 H8 x L5	334 BL2 x BL2	
557 H8 x L7	129 H8 x H5	574 L2 x H2	308 H5 x L6	295 H5 x L6	344 O4 x O4	
496 H3 x B3	597 LH5 x LH5	393 B6 x B6	163 H8 x L7	218 LH8 x LH7	306 H5 x L6	
220 LH8 x LH7	589 L7 x L8	367 B5 x B6	94 O6 x O7	194 H8 x L8	462 EL3 x EL3	
154 H8 x L6	297 H5 x L6	125 H2 x B4	234 LH8 x LH7	378 B6 x H5	172 H8 x L7	
323 H3 x H2	66 O3 x O3	336 BL2 x BL2	109 O6 x O8	259 EL3 x EL2	139 H8 x L5	
529 H8 x L5	458 EL1 x EL4	569 H8 x H5	575 L2 x L2	609 LH6 x LH5	326 BL6 x BL6	
Block 4						
551 H8 x L6	507 H4 x B1	444 BL6 x BL8	474 H1 x B4	229 LH8 x LH7	26 B5 x B6	
472 EL8 x EL8	292 H5 x L6	580 L3 x L2	104 O6 x O8	254 EL3 x EL2	604 LH5 x LH5	
535 H8 x L5	303 H5 x L6	424 BL1 x BL1	149 H8 x L6	573 L2 x H1	3 B6 x B6	
412 BH1 x BH4	398 B8 x H5	356 B5 x H7	169 H8 x L7	134 H8 x L5	621 H8 x L8	
515 H4 x H1	384 B6 x H7	564 H8 x H5	159 H8 x H7	35 L7 x L8	46 LH5 x LH5	
84 O6 x O6	270 EL3 x EL3	100 O3 x O2	202 BL8 x BL8	190 H8 x L8	617 LH7 x LH6	
92 O3 x O1	278 H6 x H6	93 O4 x O3	215 EL2 x EL3	282 H3 x B2	107 O6 x O8	
Block 6						
224 LH8 x LH7	531 H8 x L5	498 H3 x B3	142 H8 x H6	451 BL6 x BL8	477 H2 x B4	
542 H8 x L5	547 H8 x L6	407 BH1 x BH2	236 LH8 x LH7	180 O6 x O8	131 H8 x H5	
199 H8 x H5	370 B5 x B7	404 B8 x B6	328 BL5 x BL6	310 BH5 x BH6	519 H4 x H4	
61 L3 x L2	212 EL3 x EL4	56 L4 x L3	250 EL3 x EL2	40 LH1 x LH1	261 EL3 x EL2	
512 H4 x B3	30 L8 x L6	19 B6 x H7	75 O6 x O5	299 H5 x L6	353 B4 x B1	
274 O3 x O3	51 LH6 x LH6	283 H5 x L7	97 O6 x O7	165 H8 x L7	447 BL6 x BL8	
599 LH5 x LH5	320 H4 x H1	585 L6 x L6	13 B8 x H7	508 H4 x B3	365 B5 x B6	
Block 8						
77 O6 x O5	382 B6 x H7	453 BL6 x BL8	362 B5 x B5	481 H2 x B4	520 H5 x H7	
167 H8 x L7	260 EL3 x EL2	333 BL5 x BL7	533 H8 x L5	549 H8 x L6	578 L3 x L2	
612 LH7 x LH5	265 O6 x O7	91 O3 x O1	311 H1 x B2	263 EL3 x EL2	322 H4 x H1	
544 H8 x L5	423 BH5 x BH6	372 B5 x B8	301 H5 x L6	15 B8 x H7	593 LH4 x LH4	
327 B5 x H6	42 L6 x L8	242 EL4 x EL4	252 EL3 x EL2	562 H8 x L8	227 LH8 x LH7	
442 BL6 x BL7	157 H8 x H7	521 H6 x L5	276 O3 x O3	601 LH5 x LH5	201 H8 x H5	
554 H8 x L6	16 BH1 x BH3	587 L7 x B8	426 BL2 x EL2	592 L8 x B6	58 L5 x B7	
Block 10						
314 H4 x B3	294 H5 x L6	487 H2 x H2	415 BH4 x BH1	341 BL2 x BL1	553 H8 x L6	
145 L2 x H2	428 BL5 x BL8	305 H5 x L6	86 O6 x O6	171 H8 x L7	566 H8 x H5	
161 H8 x H7	272 EL3 x EL3	446 BL6 x BL8	138 H8 x L5	245 EL3 x EL2	537 H8 x L5	
151 H8 x L6	319 H7 x H5	52 LH5 x LH6	260 EL3 x EL2	594 LH5 x LH5	55 L4 x L3	
358 B5 x H8	493 H3 x B2	364 B5 x B6	230 LH8 x LH7	435 BL8 x BL8	103 O4 x O4	
37 L7 x L8	5 B6 x B6	193 H8 x L8	231 LH8 x LH7	256 EL3 x EL2	517 H4 x H1	
7 BH1 x BH1	11 B7 x H5	614 LH7 x LH8	623 H8 x L8	152 H8 x L6	87 O6 x O6	

Note: Label number and parents are given (female x male).

Appendix 9. Information on selected parents

Parent	Row	Block	Prov	Fam	Tree
0-F1	250	2	35	2	3
0-F2	170	1	31	4	1
0-F3	53	2	36	2	2
0-F4	188	3	55	3	2
0-F5	160	3	4	1	2
0-F6	182	4	19	5	1
0-F7	196	1	29	0	1
0-F8	201	4	45	5	4
0-M1	162	2	69	0	5
0-M2	222	2	33	3	3
0-M3	232	3	46	2	4
0-M4	278	3	41	3	4
0-M5	244	2	15	1	1
0-M6	74	3	28	3	4
0-M7	260	2	39	2	1
0-M8	93	3	33	4	5
B-F1	1	1	12	1	1
B-F2	13	4	40	2	2
B-F3	96	4	16	4	3
B-F4	101	1	15	2	2
B-F5	293	3	44	1	1
B-F6	208	1	33	5	1
B-F7	309	3	24	4	1
B-F8	291	4	13	2	2
B-M1	249	1	17	1	1
B-M2	251	3	45	5	5
B-M3	11	3	39	4	1
B-M4	131	4	34	4	2
B-M5	141	3	29	0	5
B-M6	81	2	23	3	2
B-M7	41	3	49	5	3
B-M8	167	3	56	4	1
EL-F1	178	2	31	2	1
EL-F2	235	1	32	2	5
EL-F3	276	4	31	3	5
EL-F4	231	1	32	1	5
EL-F5	136	1	23	5	4
EL-F6	265	3	19	5	3
EL-F7	203	2	29	0	2
EL-F8	71	3	67	0	3

Note: Position of parents in
Surrey plantation are given.
M = male, F = female.

EL-M1	274	2	59	5	3
EL-M2	100	2	61	4	1
EL-M3	260	3	34	5	2
EL-M4	222	1	41	5	4
EL-M5	94	1	27	3	4
EL-M6	206	2	42	2	1
EL-M7	280	3	41	2	4
EL-M8	117	3	38	0	5
BH-F1	300	2	6	1	5
BH-F2	317	1	47	4	1
BH-F3	203	3	31	4	5
BH-F4	111	2	43	2	4
BH-F5	60	3	32	5	4
BH-F6	152	2	9	3	1
BH-F7	44	2	18	3	5
BH-F8	275	1	19	3	3
BH-M1	239	2	13	5	4
BH-M2	130	3	52	5	2
BH-M3	13	3	39	3	3
BH-M4	262	2	39	5	1
BH-M5	248	2	35	5	5
BH-M6	93	2	24	2	4
BH-M7	60	2	12	1	3
BH-M8	37	1	11	1	3
BL-F1	203	4	44	2	2
BL-F2	216	1	28	4	2
BL-F3	297	3	12	4	1
BL-F4	147	1	18	2	5
BL-F5	213	4	68	2	2
BL-F6	69	3	9	3	3
BL-F7	61	4	29	0	2
BL-F8	205	4	44	1	2
BL-M1	148	2	56	5	5
BL-M2	199	3	13	1	1
BL-M3	93	4	11	1	4
BL-M4	312	4	62	2	3
BL-M5	13	3	39	3	5
BL-M6	85	3	10	0	5
BL-M7	135	3	20	3	1
BL-M8	36	3	8	2	2
H-F1	107	1	2	0	5
H-F2	241	1	13	5	5
H-F3	94	2	24	3	3
H-F4	20	2	40	3	5

H-F5	221	1	41	4	5
H-F6	303	1	55	5	2
H-F7	305	1	55	3	1
H-F8	152	2	9	3	3
H-M1	144	2	34	1	1
H-M2	82	4	41	1	5
H-M3	313	3	35	3	3
H-M4	50	1	36	4	4
H-M5	305	3	24	3	3
H-M6	166	4	35	1	5
H-M7	224	1	41	3	4
H-M8	210	1	33	2	1
L-F1	118	1	64	4	2
L-F2	17	1	62	3	5
L-F3	273	4	56	4	2
L-F4	110	2	43	5	1
L-F5	140	4	58	2	3
L-F6	113	2	43	4	2
L-F7	68	4	26	1	3
L-F8	88	4	67	0	5
L-M1	243	3	68	1	5
L-M2	170	2	8	2	5
L-M3	224	4	53	1	1
L-M4	86	2	65	4	1
L-M5	5	4	18	5	2
L-M6	124	4	63	4	1
L-M7	220	3	23	3	4
L-M8	169	3	56	2	5
LH-F1	94	2	24	3	1
LH-F2	265	1	24	2	1
LH-F3	25	2	53	5	4
LH-F4	292	2	64	3	1
LH-F5	194	1	57	2	1
LH-F6	2	2	55	4	3
LH-F7	144	1	25	3	2
LH-F8	83	4	41	4	4
LH-M1	124	4	63	4	5
LH-M2	4	2	55	1	5
LH-M3	25	3	53	2	3
LH-M4	42	2	18	2	5
LH-M5	185	3	59	5	1
LH-M6	103	2	61	2	2
LH-M7	243	1	13	2	1
LH-M8	119	4	24	4	4

Appendix 10. Layout of B. C./Idaho provenance trial at Surrey

Block 1				
78	15	6	12	27
8	30	84	59	67
98	50	94	62	44
91	80	73	38	29
13	20	49	63	57
99	96	90	92	97
23	25	76	71	70
93	75	95	82	81
51	31	2	45	26
77	42	66	55	79
4	35	22	21	14
53	61	74	83	86
10	1	16	46	37
32	28	19	11	5
65	41	43	58	48
3	24	87	54	69
34	64	47	7	68
33	100	88	89	17
52	60	40	56	72
9	39	36	18	85
Block 2				
31	97	50	71	8
15	87	62	22	41
17	29	51	70	88
3	60	39	81	96
94	78	61	20	40
86	69	49	12	33
92	65	45	32	13
76	54	42	25	2
89	68	57	21	38
77	63	6	46	30
100	27	48	72	10
83	55	19	36	1
18	67	75	34	9
84	53	43	26	5
98	37	73	58	23
82	66	14	28	47
4	99	35	80	56
74	7	24	44	11
52	95	59	93	85
91	64	90	79	16

Block 3				
4	86	62	41	27
12	17	35	48	78
25	31	44	90	65
16	36	57	99	77
81	60	46	23	7
14	95	73	33	53
88	67	10	29	43
20	97	76	58	38
2	82	61	42	24
18	92	71	50	34
5	84	59	40	22
13	93	70	52	30
9	80	68	32	55
19	45	94	72	63
100	28	51	74	87
21	98	39	64	79
1	26	49	85	66
11	47	91	75	56
3	96	54	83	8
6	15	37	69	89
Block 4				
17	89	71	57	39
32	46	64	98	84
2	42	14	85	65
8	24	93	80	50
13	34	82	49	67
27	40	58	94	72
15	95	30	51	69
22	37	61	100	81
1	86	63	47	16
91	74	54	28	4
3	99	62	36	19
10	97	25	76	48
6	92	78	59	26
83	87	68	20	43
73	23	77	55	35
12	90	66	44	31
5	88	60	45	29
9	38	96	75	53
7	70	52	18	33
41	21	11	79	56

Block 5				
5	47	16	31	6
70	95	80	67	96
49	8	32	2	19
53	100	79	64	93
44	4	14	23	36
58	87	97	66	77
82	98	92	73	60
25	51	37	18	10
56	99	88	69	78
22	30	1	9	17
12	20	28	38	43
75	83	94	91	57
41	33	3	15	26
89	76	46	71	59
48	13	27	39	7
54	62	90	72	81
50	34	24	42	11
84	55	63	68	86
52	61	65	74	85
45	21	29	40	35

Note: Rectangle represents a 4 tree row plot of a half sib family.

Appendix 11. Idaho/B. C. provenance information

Label	Provenance name
1	Clearwater river, Idaho
2	Clearwater river, Idaho
3	Clearwater river, Idaho
4	Clearwater river, Idaho
5	Clearwater river, Idaho
6	Clearwater river, Idaho
7	Clearwater river, Idaho
8	Clearwater river, Idaho
9	Clearwater river, Idaho
10	Clearwater river, Idaho
11	Sandpoint, Idaho
12	Sandpoint, Idaho
13	Sandpoint, Idaho
14	Jordan River, V. I.
15	Sandpoint, Idaho
16	Jordan River, V. I.
17	Sandpoint, Idaho
18	Sandpoint, Idaho
19	Sandpoint, Idaho
20	Sandpoint, Idaho
21	Sandpoint, Idaho
22	Sandpoint, Idaho
23	Jordan River, V. I.
24	Clearwater river, Idaho
25	Clearwater river, Idaho
26	Clearwater river, Idaho
27	Clearwater river, Idaho
28	Clearwater river, Idaho
29	Clearwater river, Idaho
30	Sandsplit, Q.C. I.
31	Sandsplit, Q.C. I.
32	Sandsplit, Q.C. I.
33	Sandsplit, Q.C. I.
34	Sandsplit, Q.C. I.
35	Sandsplit, Q.C. I.
36	Sandsplit, Q.C. I.
37	Sandsplit, Q.C. I.
38	Sandsplit, Q.C. I.
39	Sandsplit, Q.C. I.
40	Sandsplit, Q.C. I.
41	Sandsplit, Q.C. I.
42	Sandsplit, Q.C. I.
43	Sandsplit, Q.C. I.
44	Sandsplit, Q.C. I.
45	Sandsplit, Q.C. I.
46	Sandsplit, Q.C. I.
47	Sandsplit, Q.C. I.
48	Sandsplit, Q.C. I.
49	Sandsplit, Q.C. I.
50	Sandsplit, Q.C. I.

51	Sandsplit, Q.C. I.
52	Sandsplit, Q.C. I.
53	Sandsplit, Q.C. I.
54	Sandsplit, Q.C. I.
55	Jordan River, V. I.
56	Jordan River, V. I.
57	Jordan River, V. I.
58	Jordan River, V. I.
59	Jordan River, V. I.
60	Jordan River, V. I.
61	Jordan River, V. I.
62	Jordan River, V. I.
63	Jordan River, V. I.
64	Jordan River, V. I.
65	Jordan River, V. I.
66	Jordan River, V. I.
67	Jordan River, V. I.
68	Jordan River, V. I.
69	Jordan River, V. I.
70	Jordan River, V. I.
71	Jordan River, V. I.
72	Jordan River, V. I.
73	Jordan River, V. I.
74	Jordan River, V. I.
75	Jordan River, V. I.
76	Jordan River, V. I.
77	Jordan River, V. I.
78	Menzies Bay, V. I.
79	Menzies Bay, V. I.
80	Menzies Bay, V. I.
81	Menzies Bay, V. I.
82	Menzies Bay, V. I.
83	Menzies Bay, V. I.
84	Menzies Bay, V. I.
85	Menzies Bay, V. I.
86	Menzies Bay, V. I.
87	Menzies Bay, V. I.
88	Menzies Bay, V. I.
89	Menzies Bay, V. I.
90	Menzies Bay, V. I.
91	Menzies Bay, V. I.
92	Menzies Bay, V. I.
93	Menzies Bay, V. I.
94	Menzies Bay, V. I.
95	Menzies Bay, V. I.
96	Menzies Bay, V. I.
97	Menzies Bay, V. I.
98	Menzies Bay, V. I.
99	Menzies Bay, V. I.
100	Menzies Bay, V. I.

Lat	Long
Menzies Bay	
50.07	125.23
Jordan River	
48.41	124.02
Sandsplit	
53.71	131.4
Clearwater River	
48.17	116.18
Sandpoint	
45.51	115.42