

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

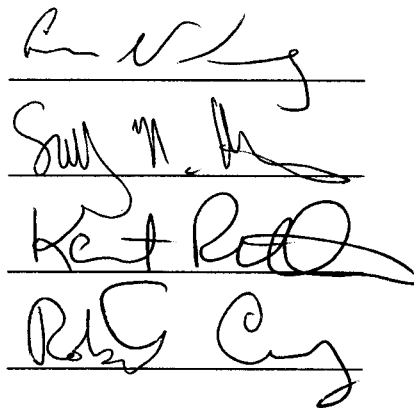
A thesis submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

in

The Faculty of Graduate Studies

(Department of Forest Science; Faculty of Forestry)

We accept this thesis as conforming to the required standard



The image shows four handwritten signatures, each written above a horizontal line. From top to bottom, the signatures are: 1. A cursive signature that appears to be 'C. V. G.'. 2. A cursive signature that appears to be 'Sally M. H.'. 3. A cursive signature that appears to be 'Kent R. D.'. 4. A cursive signature that appears to be 'R. G. C.'.

The University of British Columbia

July 1999

© Andreas Hamann, 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 genecology, 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	38
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 × 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 × 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.	Conclusions	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 estimats	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 (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). 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