

Multiple population breeding for uncertain climatic futures with *Alnus rubra*: ecological genetics and selection experiments

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Abstract: In a case study with red alder (*Alnus rubra* Bong.) we develop multiple breeding populations to cope with uncertainty in the response of genotypes to environmental changes. Genetic parameters and geographic variation in adaptive traits were studied to tailor breeding populations to specific climatic environments. Orthogonal clines were identified in bud break and growth cessation with spatial statistical analysis, implying that it is not possible to cope with effects of climatic warming by simply shifting provenances to new locations. Instead climatic warming may require the development of genotypes with novel combinations in adaptive traits. Selection targets for bud break and leaf abscission for six breeding populations were derived that cover current and possible future climatic conditions. Genetic parameters for adaptive traits were estimated, and it was confirmed that selection targets for the proposed breeding populations could be met in one generation. Heritabilities for the date of bud break and leaf abscission were moderately high (0.41 to 0.54) and genetic correlations implied that selection for advanced bud break and delayed growth cessation will positively influence growth traits.

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 (Bilger 1992). 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 (Wang and Perry 1958; Perry and Wang 1960; Sharik and Barnes 1976). In regions with mild winters, for example, Cannell and Smith (1986) and Kramer (1994) demonstrated that climatic warming regularly causes a chilling deficit and therefore a delayed bud burst, resulting in failure to utilize favorable growing conditions in earlier springs. In other regions, where chilling requirements are far exceeded by winter temperatures, Murray *et al.* (1989) and Hänninen (1991) showed that climatic warming would force bud burst at an earlier date and could increase the risk of frost injuries in spring.

Designing a breeding strategy for a species that takes effects of climate change into account requires knowledge of clinal variation in adaptive traits, genetic parameters for adaptive traits, and the response in phenological traits to warming for a sample of populations from the region of interest. Such data is partly available for red alder in British Columbia (Hamann *et al.* 1998, 2000). 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 elements of uncertainty. Multiple population breeding has been suggested for such a situation (Namkoong *et al.*, 1988; Eriksson *et al.* 1993). Coverage of future climatic conditions may be accomplished by simply assigning new deployment targets for multiple populations, or it may require the development of several populations with novel combinations in adaptive and growth traits.

In this report we develop a multiple population breeding strategy intended to cope with possible effects of climatic warming, given existing provenance data and incomplete information on phenotypic response to climate change. We derive which trait combinations are most likely required for current and possible future climates in British Columbia, and test if selection targets could be met within one generation of breeding.

Methods

Phenology

Data were collected in a provenance trial of red alder covering its natural range in British Columbia including some sources from Oregon and Alaska. (Hamann 1999). Monthly height measurements from 100 trees for each of the 65 provenances over the period of one year were evaluated to examine differences in growth patterns among provenances during the second growing season. 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. The experimental design of the provenance trial is described in the next section.

A model of geographic variation in bud break and leaf abscission was developed with the kriging method, which yields smooth varying surfaces of best linear unbiased predictions of provenance performance over the geographic range of the species. The program GSTAT by Pebesma and Wesseling (1998) and the GIS software IDRISI (Clarke Labs 1999) was used to fit variogram models for kriging and to generate maps of predicted values. Methodological details are described in Hamann *et al.* (2000).

Genetic testing

Genetic parameters were estimated based on half-sib families of a provenance trial, and full-sib families from a selection experiment. The provenance trial was laid out as a 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. Individual heritabilities and genetic correlations were calculated based on family within provenance variance components following standard procedures.

Families for the second experiment were generated from the above provenance trial using a restricted index selection (Kempthorne and Nordskog 1959), where one or two traits were advanced while keeping the others constant. Three populations were generated by advancing exclusively seedling height, date of leaf abscission or date of bud break. In three more populations every combination of two traits was advanced simultaneously. Each population

consisted of eight male and eight female trees mated in a disconnected four parent factorial design to generate 32 families per population. Offspring was planted in a randomized complete block design with each family represented by one offspring per block using eight replications. Because of variable success in obtaining offspring from controlled crosses (420 offspring of 1536 required) the unbalanced data were evaluated with the mixed model procedure of the SAS statistical software package (SAS Institute 1997) according to the following model:

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

where Y is the measurement of seedling m in block i from population j , female parent k and male parent l ; μ is the overall mean; B , P , $M(P)$ and $F(P)$ are the effects of block, population, and male and female within populations, respectively. Individual heritabilities were calculated based on the mean of male and female family variance components. Standard errors of heritabilities were estimated according to the delta-method (Lynch and Walsh 1998, Appendix 1).

Results and discussion

Ecological genetics

Analysis of geographic patterns in bud break shows that coastal provenances in the southern part of British Columbia break bud later than inland sources (Fig. 1) conforming to typical maritime patterns (Campbell and Sugarno 1979, Myking and Heide 1995). 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.

Leaf abscission occurs earlier in northern provenances and thus at longer critical photoperiods than southern sources (Fig. 2). As in most temperate trees, growth cessation in alder is primarily controlled by the shortening of the photoperiod, since in colder northern environments favorable growing conditions end at longer photoperiods than in southern environments (Perry 1971; Morgenstern 1996). Leaf abscission has been shown to be a reliable indicator for growth cessation in red alder, being highly correlated with growth

late in the season (Hamann 1999). The reason is that alder exhibits indeterminate growth patterns and young leaves that are formed late in the season will not drop readily.

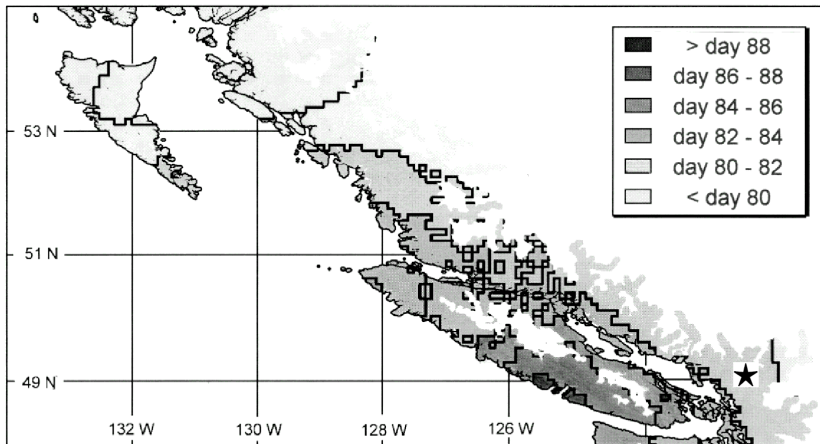


Figure 1. Date of bud break predicted for red alder provenances when grown at a southeastern location (★). Contours are drawn at intervals of approximately 0.25 standard deviations.

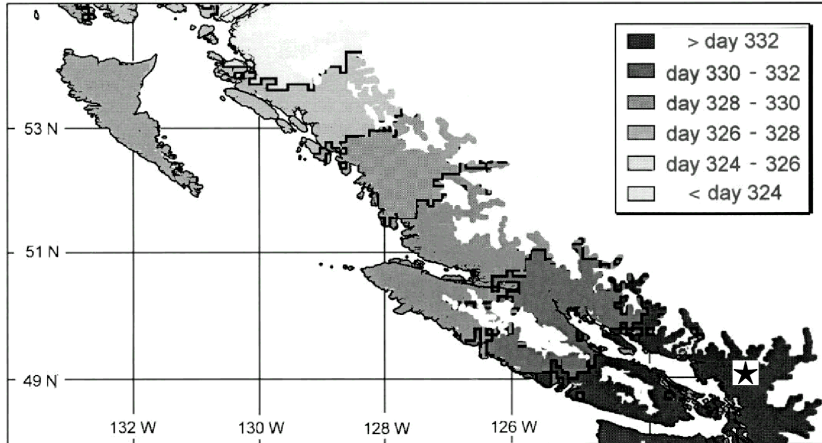


Figure 2. Date of leaf abscission predicted for red alder provenances when grown at a southeastern location (★). Contours are drawn at intervals of approximately 0.25 standard deviations.

Analysis of growth rates throughout the season also indicates that synchronization of growth initiation and growth cessation with the available growing season has important effects on growth. When northern provenances are transferred to a southern site with favorable environments in fall, premature growth cessation appears to be a disadvantage compared to local sources (Fig. 3). In addition, provenances sampled from a very far northern location showed reduced growth during the summer months (Fig. 3, Alaska).

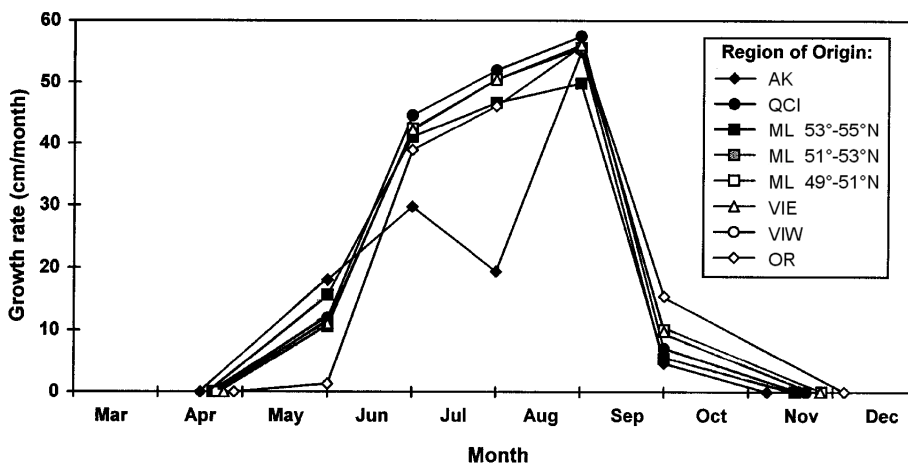


Figure 3. Growth rates during the second growing season for provenances summarized by region of origin (AK, Alaska; ML, mainland British Columbia; QCI, Queen Charlotte Islands; VIE Vancouver Island East; VIW, Vancouver Island West; OR, Oregon).

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. However, provenances that cease growth later than local sources (Fig. 3, Oregon) exhibit severely retarded growth rate during the first 30 days after bud break. Active growth late in the season may expend resources 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.

Early leaf abscission as well as late bud break were also shown to be correlated with reduced height and biomass at the end of the growing season (Hamann *et al.* 1998). These observations are good circumstantial evidence that the traits bud break and leaf abscission are relevant indicators for adaptive traits

in red alder, and can be used for tailoring breeding populations to specific climatic environments.

Breeding populations

For current climatic conditions we delineated three breeding zones for British Columbia, which ensures that transfer of seed does not result in a reduction of growth traits larger than 10% relative to a local source (Hamann *et al.* 2000). In red alder a 10% change in growth or survival is associated with approximately 8 days change in the date of growth cessation and 4 days in the date of bud break. (Hamann *et al.* 1998). Assuming that either shift in phenology could cause the 10% reduction in growth, these values were used as conservative thresholds, where the use of a new breeding population over another would be justified under a scenario of uniform climatic warming.

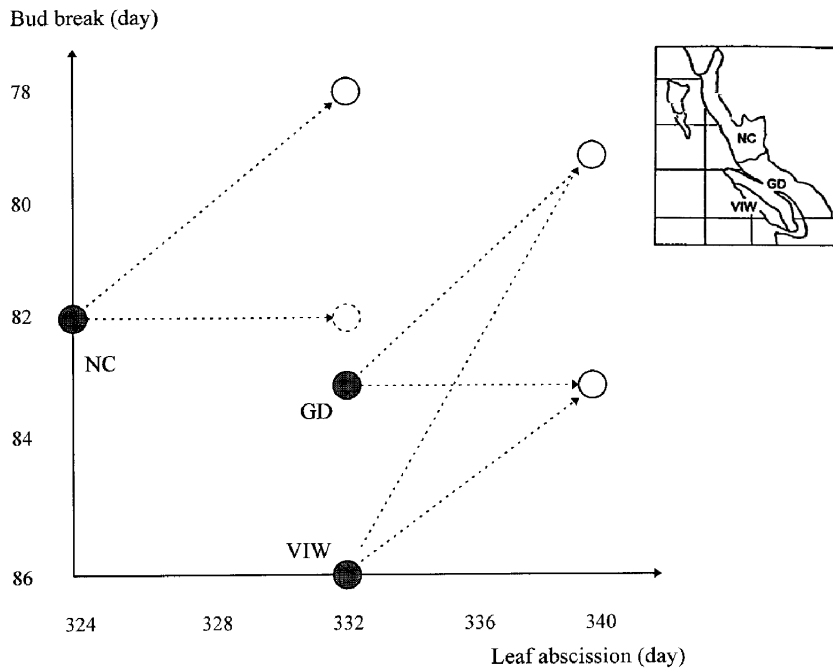


Figure 4. Proposed multiple breeding populations for current (dark circles) and possible future (light circles) climatic conditions (NC, British Columbia north of 51°N latitude; GD, Georgia Depression; VIW, Vancouver Island Westcoast).

Since there is a simple linear cline over latitude and the environmental cue for growth cessation is independent of climate change itself, identification of selection targets for growth cessation is straightforward. A delayed date of bud break by 8 days for all populations would allow that longer favorable growing conditions in fall can be utilized (Fig. 4).

The situation for the date of bud break is more ambiguous, since the exact effect of climatic warming on growth initiation is unknown. The sources from southern coastal British Columbia showed the highest dormancy stability and are most likely to suffer delayed bud break due to a chilling deficit. Selecting alternatively for 4 and 8 days of advanced bud burst in the VIW-breeding population could compensate for this effect. For the other populations with less dormancy stability, the effect of climate warming is likely to be neutral or less pronounced. Alternatively, bud break is not advanced or it is advanced by only 4 days (Fig. 4).

Genetic testing

Heritabilities for bud break and leaf abscission based on half-sib as well as full-sib progeny tests suggests that adaptive traits and seedling height are under moderate genetic control (Tab. 1 and 2).

Table 1. Estimated individual heritabilities with standard errors for traits based on half-sib offspring in a provenance trial

| | Height | Bud break | Leaf abscission |
|------------------------|-------------|-------------|-----------------|
| Heritability (h^2) | 0.35 (0.04) | 0.43 (0.04) | 0.54 (0.04) |

Table 2. Estimated genetic variances and individual heritabilities with standard errors for traits based on full-sib offspring of controlled crosses

| | Height | Bud break | Leaf abscission |
|--------------------------|-------------|-------------|-----------------|
| Additive Variance V_A | 249 (27.1) | 8.66 (1.01) | 20.22 (2.81) |
| Dominance Variance V_D | 0.64 (1.12) | 1.16 (2.34) | 10.16 (5.35) |
| Heritability h^2 | 0.46 (0.21) | 0.47 (0.22) | 0.41 (0.21) |

Poor success in generating offspring in the selection experiment did not allow precise estimates of realized gains from selection (reported in Hamann 1999). However, delaying leaf abscission by 8 days would require a selection intensity of approximately 1.9. Similarly, advancing the date of bud break by 4 days would require a selection intensity of approximately 1.3. Both could be

achieved in current test plantations. Advancing the date of bud break by 8 days would require two breeding cycles.

Table 3. Genetic correlations (upper right) and phenotypic correlations (lower left) estimated from half-sib offspring of a provenance trial.

| | Height | Bud break | Leaf abscission |
|-----------------|--------|-----------|-----------------|
| Height | - | -0.38 | 0.42 |
| Bud Break | 0.02 | - | 0.08 |
| Leaf abscission | -0.21 | 0.32 | - |

As expected, growth traits will be positively influenced by selecting for an advanced date of bud break or a delayed date of leaf abscission, presumably due to a longer growing season. Further, the date of leaf abscission and the date of bud break are genetically uncorrelated (Tab. 3).

Summary and recommendations

Red alder showed a typical latitudinal trend in growth cessation and conforms to maritime patterns in bud burst phenology. Southern and coastal sources exhibited the highest dormancy stability, implying that these populations are most likely to experience a chilling deficit due to climatic warming. Under this hypothesis, a greater risk of frost damage due to climatic warming is not expected for red alder. In fact, unusual hardiness of coastal species and provenances has been observed after an exceptionally warm winter (van der Kamp and Worrall 1990). Allowing an advanced date of bud break and a delayed date of growth cessation to varying degrees in breeding populations is expected to enhance growth rates of genotypes by utilizing a longer available growing season under the scenario of climate warming.

References

- Bilger, B. 1992: Global warming. Chelsea House Publishers, New York
- 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. and Smith, R.I. 1986: Climatic warming, spring bud burst and frost damage on trees. *J. Appl. Ecol.* 23: 177-191
- Clarke Labs 1999: Idrisi GIS and Image Processing. Release 3.2. Worcester, Massachusetts
- Eriksson, G., Namkoong, G. and Roberts, J.H. 1993: Dynamic gene conservation for uncertain climatic futures. *For. Ecol. Manage.* 62: 15-37

- Hamann, A. 1999: Utilization and Management of red alder genetic resources in British Columbia. Ph. D. Dissertation, University of British Columbia, Vancouver, B. C.
- Hamann, A., Koshy, M., Namkoong, G., and Ying, C.C. 2000: Genotype \times environment interactions in *Alnus rubra*: developing seed zones and seed transfer guidelines with spatial statistics and GIS. *For. Ecol. Manage.* 136: 107-119
- 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
- Hänninen, H. 1991: Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ.* 14: 449-454
- Kempthorne, O. and Nordskog, A.W. 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 Environ.* 17: 367-377
- Lynch, M. and Walsh, B. 1998: Genetics and analysis of quantitative traits. Sinauer Associates, Inc., Sunderland, Massachusetts, pp. 807-821
- 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
- Myking, T. and Heide, O.M. 1995: Dormancy release and chilling requirements of buds of latitudinal ecotypes of *Betula pendula* and *B. pubescens*. *Tree Physiol.* 15: 697-704
- Namkoong, G., Kang, H.C. and Brouard, J.S. 1988: Tree Breeding: Principles and Strategies. Springer Verlag, New York
- Pebesma, E.J. and Wesseling, C.G. 1998: Gstat, a program for geostatistical modeling, prediction and simulation. *Computers Geosci.* 24: 17-31
- 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 diverse populations of yellow birch (*Betula alleghaniensis*) and sweet birch (*B. lenta*). *Can. J. Bot.* 54: 2122-2129
- van der Kamp B.J. and Worrall, J. 1990: An unusual case of winter bud damage in British Columbia interior conifers. *Can. J. For. Res.* 20: 1640-1647
- 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