Genetic adaptation of aspen (*Populus tremuloides*) populations to spring risk environments: a novel remote sensing approach

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Abstract: This study investigates geographic patterns of genetic variation in aspen (*Populus tremuloides* Michaux.) spring phenology with the aim of understanding adaptation of populations to climatic risk environments and the practical application of guiding seed transfer. We use a classical common garden experiment to reveal genetic differences among populations from western Canada and Minnesota, and we present a novel method to seamlessly map heat-sum requirements from remotely sensed green-up dates. Both approaches reveal similar geographic patterns: we find low heat-sum requirements in northern and high-elevation aspen populations, allowing them to take full advantage of a short growing season. High heat-sum requirements were found in populations from the central boreal plains of Saskatchewan and Alberta, and populations from Minnesota exhibit moderately low heat-sum requirements for budbreak. Analysis of corresponding climate normal data shows that late budbreak is strongly associated with the driest winter and spring environments, which suggests selection pressures for late budbreak due to both frost and drought risks in early spring. We therefore caution against long-distance seed transfer of Minnesota provenances to the boreal plains of Alberta and Saskatchewan. Although such transfers have been shown to increase tree growth in short-term field tests, this planting material may be susceptible to exceptional spring droughts.

Résumé : Les auteurs ont étudié les patrons géographiques de la variation génétique de la phénologie printanière du peuplier faux-tremble (*Populus tremuloides* Michaux.) dans le but de mieux comprendre l'adaptation des populations aux risques environnementaux liés au climat et les implications pratiques pour guider le transfert des semences. Une expérience classique en plantation comparative a permis de révéler les différences génétiques entre les populations de l'ouest du Canada et celles du Minnesota. De plus, les auteurs présentent une nouvelle méthode permettant de cartographier de façon continue les exigences en sommes de température à partir des dates d'apparition du feuillage déterminées par télédétection. Les deux approches ont révélé des patrons géographiques similaires : des exigences faibles en sommes de température ont été notées pour les populations de peuplier faux-tremble situées au nord et à haute altitude, leur permettant de profiter pleinement de la courte saison de croissance. Des exigences élevées en sommes de température ont été notées pour les populations des plaines boréales du centre de la Saskatchewan et de l'Alberta, alors que les populations du Minnesota avaient des exigences modérément faibles en sommes de température pour le débourrement. L'analyse des données de la normale climatique correspondante démontre que le débourrement tardif est fortement associé aux conditions environnementales reliées aux hivers et aux printemps les plus secs, ce qui indique qu'il y a des pressions de sélection pour le débourrement tardif en raison des risques de gel et de sécheresse tôt au printemps. Les auteurs déconseillent donc le transfert sur de longues distances des semences des provenances du Minnesota vers les plaines boréales de l'Alberta et de la Saskatchewan. Même s'il a été démontré que de tels transferts augmentent la croissance des arbres dans les tests au champ de courte durée, ce matériel de plantation pourrait être sensible à des sécheresses printanières exceptionnelles.

[Traduit par la Rédaction]

Introduction

Phenology is the study of timing of recurring phases of plant development throughout the year. Phenological phases include important adaptive traits such as the onset of frost hardiness, budbreak, bud set, flowering, and fruiting (e.g., Rathcke and Lacey 1985). The timing of budbreak in trees is adaptive in temperate regions, balancing the need to avoid damage due to late spring frosts while maximizing the use of the available growing season (e.g., Lechowicz 1984; Leinonen and Hanninen 2002). Early budbreak could cause loss of flowers, frost damage to leaves, or even mortality. A late start, on the other hand, may lead to a competitive disadvantage in growth or failure to produce seeds if growing seasons are short.

The timing of budbreak is one of the most sensitive and direct biological responses to temperature, where temperature is measured as thermal time (e.g., Hunter and Lecho-

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wicz 1992). The heat-sum requirement for budbreak is typically calculated as degree-days: average daily temperature values above a certain threshold are added until a phenological event occurs. The threshold value that yields the highest correlations with budbreak normally ranges between 0 and 5 °C for temperate trees (e.g., Hunter and Lechowicz 1992; Snyder et al. 1999). Another factor that may influence the timing of budbreak is a fall chilling requirement (e.g., Campbell and Sugano 1975). This mechanism is prevalent under maritime climates, requiring a certain amount of chilling degree-days (accumulated temperatures below a certain threshold) before accumulating degree-days toward the heat-sum requirement starts. A chilling requirement prevents premature heat-sum accumulation and budbreak if fall and winter temperatures are unusually mild.

In wide-ranging species, different populations typically have different heat-sum requirements and different chilling requirements, which can be interpreted as adaptations to local climate conditions. This geographic differentiation in adaptive traits is of practical relevance to guide the movement of planting stock for reforestation and to select genotypes in tree improvement programs (e.g., Campbell 1974; Rehfeldt 1983). For example, if genotypes are selected based on short-term trials, better growth may be the result of risking late spring and early fall frost damage due to an extended growing season. Ideally, genotypes that show lower adaptive risks while maintaining superior growth would be preferred as planting stock for reforestation programs. It is therefore important to evaluate and control both adaptive and growth traits in tree improvement programs.

The development of plantation-based forestry and tree improvement programs for aspen (*Populus tremuloides* Michaux.) in western Canada is relatively recent, driven by hardwood demand from oriented strand board mills. Although there is a small-scale common garden experiment for the species in eastern Canada (Brissette and Barnes 1984), the first systematic genetic trial series to study geographic structure of genetic variation in aspen was established in 1998 throughout the boreal plains of western Canada, and early results have shown large increases in tree growth if planting material is moved north or northeast (Brouard and Thomas 2002). However, no information exists on genetic variation in adaptive traits. Here we evaluate one of the 1998 provenance trials for patterns of geographic variation in heat-sum requirements for budbreak to reveal adaptive mechanisms to spring risk environments. We ask the following questions. What are the geographic patterns in variation in heat-sum requirements for budbreak and what do these reveal about adaptive mechanisms to spring risk environments? Does the observed increase in tree growth through movement of planting stock come at the expense of increased exposure to late spring frost events or other adaptive disadvantages?

In addition to the classical, sample-based common garden trial approach, we also test a novel method to seamlessly map geographic patterns of genetic variation in heat-sum requirements of aspen populations. Because the timing of budbreak is under strong control of a single environmental variable, we hypothesize that a uniform experimental environment is not needed to reveal genetic differences among populations for this trait. Instead, we propose to use interpo-

lated daily climate data from weather stations to calculate the required heat sum for budbreak of aspen populations in situ. The date of budbreak of natural populations in western Canada is observed through remote sensing using data from NASA's Terra satellite, which is freely available and widely used to monitor the green-up date of deciduous vegetation (e.g., White and Nemani 2006).

Methods

Provenance trial data

We measured the date of budbreak at the provenance trial series established by an industry cooperative consisting of members of the Western Boreal Aspen Corporation and Alberta Pacific Forest Industries in 1998, which include plant material from 43 open-pollinated bulked seed lots originating from British Columbia to Minnesota (Fig. 1). Provenances were planted in a randomized complete block design with six replications, and five-tree row plots within blocks serve as experimental units. Between 4 May and 2 June 2009, we evaluated 1126 trees planted at the Athabasca test site (54°43′11″N, 113°17′08″W) for the timing of budbreak. Over this time period, trees were scored on a seven-level bud development scale (0, dormant; 1, buds swelling; 2, buds breaking; 3, leaves extending 1 cm; 4, leaves extending 2 cm; 5, leaves extending 3 cm; 6, leaves fully extended) at 10 dates. We calculated least squares means and standard errors of budbreak date for provenances with the GLM procedure of the SAS statistical software package (SAS Institute Inc. 2008). The response variable was the Julian date at which a bud development score of 3 was reached. If this score was not recorded for an individual tree, the date was estimated through linear regression of the previous and subsequent score (above and below 3).

Remote sensing data

The date of budbreak of natural populations in western Canada was inferred by means of the Enhanced Vegetation Index (EVI) from the Moderate Resolution Imaging Spectroradiometer (MODIS) of NASA's Terra satellite. We used the 16-day interval 500 m resolution EVI product (Gao et al. 2008), which was obtained through the MODIS-for-NACP data products Web site (NASA 2008). Annual green-up dates for each grid cell were determined with the TIMESAT software package, using the adaptive Savitzky–Golay function to fit EVI values as a function of Julian date (Jonsson and Eklundh 2004). Although, in principle, only 1 year of remote sensing data is necessary to calculate heat-sum requirements, the Savitzky–Golay function fitted to a temporally coarse 16-day interval product is not expected to result in a very accurate heat-sum estimate for a single year. We therefore processed 5 years of remote sensing data (2001 to 2005) and calculated an average required heat sum with a standard error of the estimate for each grid cell.

MODIS–EVI data for North America was cropped to the study area and filtered for grid cells that primarily contained aspen populations. For the filtering, we explored several options: the Alberta Vegetation Inventory database (Alberta Sustainable Resource Development (ASRD) 2005), 25 m resolution land cover data for western Canada (Wulder et al. 2008), and 30 m resolution land cover data for the United

Fig. 1. Location of the provenance trial, collection location of provenances, and the aspen species distribution inferred from deciduous forest cover. The inset shows the match between remotely sensed deciduous forest cover (top) and aspen frequencies in forest inventory data (bottom). Summarized as average freqency at 500 m resolution (grid in inset), both frequency maps appear nearly identical.
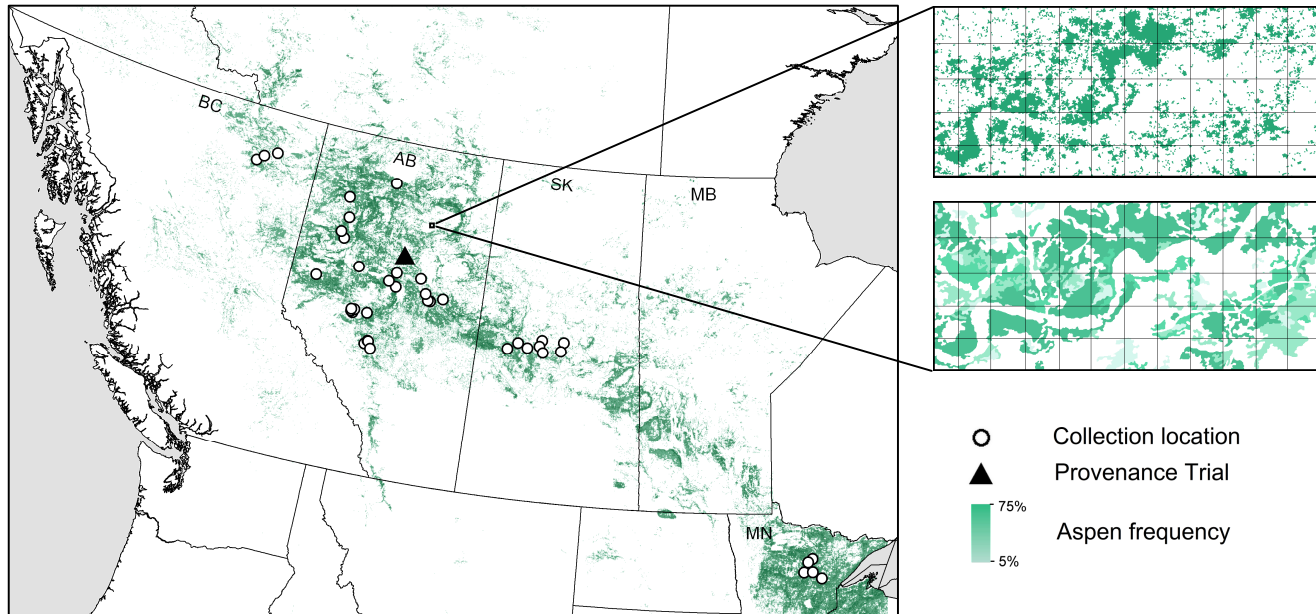
States (Homer et al. 2007). Summarized at the native 500 m resolution of MODIS–EVI data, the deciduous land cover data could almost perfectly reproduce aspen frequency data from Alberta's forest inventory database. This is plausible because aspen is by far the most predominant deciduous forest species throughout the study area, accounting for 75% to 95% of deciduous forest in the ecological regions of the study area. After confirming a satisfactory match of remotely sensed deciduous forest cover data and aspen forest inventory data (example shown in Fig. 1), we used deciduous forest cover as a proxy for aspen frequency over the entire study area. For subsequent analysis, only grid cells of the 500 m MODIS–EVI data set that contained at least 40% aspen cover were evaluated. This value was a compromise between acceptable aspen representation in individual MODIS–EVI grid cells and loss of regional data coverage where aspen is less frequent. The application of different threshold values from 30% to 70% did not fundamentally change the results, but high thresholds led to regional loss of data coverage, primarily in Saskatchewan.

### Degree-day and heat-sum calculations

Daily mean temperature data from approximately 4300 weather stations for Canada were purchased as a customized data set from the Meteorological Service of Canada (MSC) (2007). Daily climate data for Minnesota were obtained from the US Historical Climatology Network (Easterling et al. 2009). Temperature data from the weather station nearest to the field trial (Athabasca, station 3060L20, 7 km distance) were used to calculate daily heat sums for the provenance trial location. Interpolated data for all weather stations were used to calculate daily heat sums for the years 2001 to 2005 for all MODIS–EVI grid cells with at least 40% aspen cover. We used a thin-spline interpolation method implemented with the G3GRID procedure of SAS (SAS Institute

Inc. 2008) and a subsequent lapse rate based elevation adjustment (Hamann and Wang 2005; Wang et al. 2006). Interpolated grids of daily mean temperatures were transformed to accumulated degree-days with DATA steps in SAS using a threshold of 0 °C, which best correlates with the timing in aspen spring phenology in western Canada (Beaubien and Johnson 1994). From this degree-day data set, we extracted the heat-sum value that corresponded to the remotely sensed Julian day of green-up for the years 2001 to 2005 in MODIS–EVI data. The required heat sum for budbreak obtained from either remote sensing data or from the common garden experiment is a genetic property of aspen populations (i.e., it theoretically does not vary from year to year). However, variation does arise due to imperfect MODIS–EVI-based green-up estimates and errors in interpolated temperature data. Calculating heat-sum values for multiple years from 2001 to 2005 allows us to calculate a mean and standard error for the required heat-sum estimate.

Statistical analysis

To aid in the interpretation of geographic patterns of genetic variation in heat-sum requirements, we used 15 biologically relevant climate variables for the 1961–1990 climate normal, which we interpreted as a proxy for long-term climate conditions to which populations are adapted. This climate normal data was obtained through the ClimateBC and ClimatePP software packages (Wang et al. 2006; Mbogga et al. 2009) to investigate associations between long-term local climate conditions and required heat sum for budbreak. To simplify the analysis of associations between climate variables and required heat sum of provenances, we employed a principal component analysis of 1961–1990 climate normal variables obtained for the 43 provenance collection locations. Principal component analysis was implemented with

Fig. 2. (A) Heat-sum requirements inferred from remote sensing. The inset shows 500 m grid data interpolated to a coarse resolution for better visualization of geographic patterns. (B) Heat sum inferred from a common garden experiment (also displayed in A). Symbols represent different ecological regions: △, BC taiga plains; diamond with cross, AB northern boreal plains; □, AB lower Rocky Mountain foothills; open diamond, AB central boreal plains; ○, SK central boreal plains; ▽, MN boreal shield.
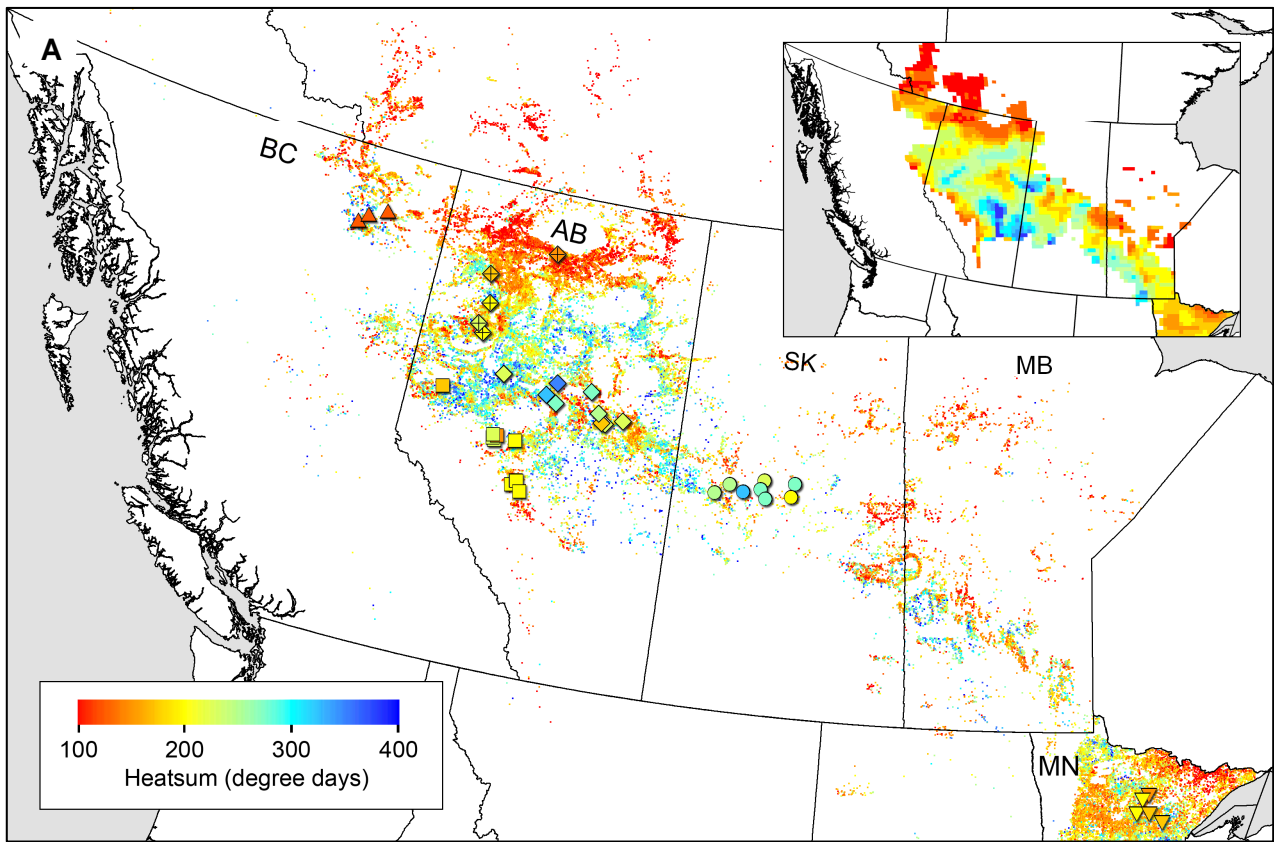
the PRINCOMP procedure of SAS (SAS Institute Inc. 2008). After visually determining linearity of the relationships among climate variables, their principal components (PCs), and budbreak data (some variables were log-transformed to obtain a linear relationship), we used Pearson's correlation coefficients to quantify the strength and direction of the associations.

We further tested how well heat-sum values estimated from remote sensing data correspond to values obtained through the common garden experiment. For this purpose, we report Pearson's correlation coefficients of required heat sum determined for 43 provenances with MODIS–EVI grid cell that contains more than 40% aspen within a given radius (we tested 1, 3, 5, 10, 30, and 50 km). Alternatively,

Fig. 3. Correlation between heat sum observed in provenance collections and nearby Enhanced Vegetation Index (EVI) grid cells. Only high-level geographic summaries (averages by ecological region) are significant ($p = 0.003$).
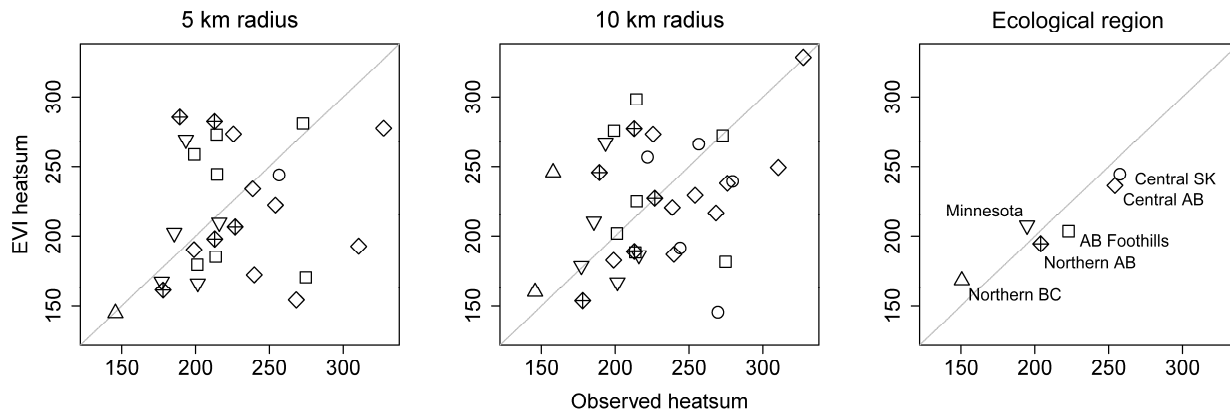
we correlated regional averages of grid cells and provenances, where data were summarized by "ecosections" of the National Ecological Framework for Canada (Selby and Santry 1996) and corresponding "level 4" delineations of the US Ecoregion System (Omernik 1995). The provenance sample locations were not randomly chosen, but structured into six regions of interest: the aspen habitat of the Alberta (AB) foothills, the boreal plains of Saskatchewan (SK) and AB, the northern boreal plains of AB, the taiga plains of northwestern British Columbia (BC), and the boreal shield of Minnesota (MN). To obtain regional summaries of remote sensing data corresponding to these groups of provenance samples, we used all grid cells within the ecosections that also contained the provenance samples (between two and six ecosections per sampling region). We subsequently refer to these aggregates of ecosections representing a group of provenance samples as "ecological regions."

Results

Provenance differences in budbreak

When planted in a common garden, provenances from western Canada showed a large range of heat-sum requirements for budbreak ranging from approximately 145 to 325 degree-days above 0 °C (Fig. 2A). For the spring climate of 2009 at the Athabasca planting site, the corresponding dates of budbreak between the earliest and the latest provenances differed by 24 days (Fig. 2B). Provenances from northern British Columbia had by far the earliest budbreak, with a heat-sum requirement of 150 degree-days, followed by provenances from northern Alberta and the Rocky Mountain foothills (approximately 200 degree-days). The latest budbreak was observed in provenances from the central boreal plains of Alberta and Saskatchewan (around 260 degree-days). This northeastern to southwestern cline was reversed for Minnesota provenances, with an average heat-sum requirement of approximately 200 degree-days. For the replicate trees of provenances, the standard error of the least squares means estimate of heat-sum requirement was on average 7.2 degree-days, which corresponds to an average standard error of the estimated date of budbreak of 0.9 days.

Remotely sensed heat-sum requirements

Approximately similar geographic patterns of heat-sum requirement were observed through an analysis of remote sensing data and corresponding daily climate data (Fig. 2A). Populations from northern British Columbia and northern Alberta showed by far the lowest heat-sum requirements, with values between 125 and 200 degree-days. Additional patterns that were not apparent in the provenance samples are very high heat-sum requirements along the southern fringe of the central boreal plains, where aspen parkland transitions to dry grassland ecosystems. There is also a region of low heat-sum requirements in central Alberta that breaks the pattern of a simple latitudinal cline. We further see a pronounced reversal of the latitudinal cline towards Minnesota, with average heat-sum requirements of 200 degree-days in both the provenance and remote sensing data. The standard error of the estimate of required heat sum for green-up was 41 degree-days, averaged across all 500 m grid cells. This corresponds to an average standard error of 4.8 days for the estimated day of green-up throughout the study area for 2001–2005 climate conditions. Mapping the error estimates for individual grid cells did not reveal any spatial patterns in the value of standard errors (data not shown).

Though broad geographic patterns seem to correspond to results from the common garden trial, we did not observe significant correlations between heat-sum requirements of provenances and the remotely sensed data points in the vicinity (Fig. 3). Only when heat-sum values were averaged at the level of ecological regions for both remotely sensed data and provenance samples did we obtain a good correlation of heat-sum values estimated from field observations and remote sensing data ($R^2 = 0.91$, $p = 0.003$).

Heat-sum requirements and long-term climate

To interpret geographic patterns in required heat sum for budbreak as adaptations to spring risk environments, we focus on the statistically more precise provenance data first. Geographic patterns of 15 climate variables of provenance collection locations can be reduced to three independent dimensions with principal component analysis (Table 1). The first component (PC 1), with an eigenvalue of 6.6, explains

Table 1. Principal component analysis of 15 climate normal variables at provenance collection locations.

Climate variable	PC 1	PC 2	PC 3
Mean annual temperature (°C)	0.28	0.26	–0.20
Mean warmest month temperature (°C)	–0.03	**0.43**	0.12
Mean coldest month temperature (°C)	**0.35**	–0.08	–0.20
Continentality (°C)	–0.29	0.24	0.21
Mean annual precipitation (mm)[a]	**0.34**	0.11	0.22
Mean summer precipitation (mm)[a]	**0.35**	0.06	0.12
Mean winter precipitation (mm)[a]	0.22	0.20	**0.41**
Precipitation as snow (mm)[a]	0.09	–0.27	**0.43**
Annual heat–moisture index (°C/mm)[a]	–0.25	0.07	**–0.46**
Summer heat–moisture index (°C/mm)[a]	**–0.35**	0.10	–0.03
Winter heat–moisture index (°C/mm)[a]	**0.32**	–0.12	**–0.47**
Chilling degree-days < 0 (°C × days)	**–0.34**	–0.05	0.26
Growing degree-days > 5 (°C × days)	0.00	**0.43**	0.07
Beginning of frost-free period (day)	0.01	**–0.40**	0.19
End of frost-free period (day)	0.10	**0.41**	0.00

Note: The highest correlations (eigenvectors) of the original climate variables with principal components (PCs) are indicated in bold.

[a]Values are $\log_{10}$-transformed.

Table 2. Pearson correlations among required heat sum for budbreak of provenances and long-term climate (1961–1990 normals) at collection locations. Correlations with principal components of climate variables (Table 1) are also included.

Climate variable	r
Mean annual temperature (°C)	0.02
Mean warmest month temperature (°C)	–0.12
Mean coldest month temperature (°C)	–0.02
Continentality (°C)	–0.03
Mean annual precipitation (mm)[a]	–0.25
Mean summer precipitation (mm)[a]	–0.19
Mean winter precipitation (mm)[a]	–0.41**
Precipitation as snow (mm)[a]	–0.30*
Annual heat–moisture index (°C/mm)[a]	0.41**
Summer heat–moisture index (°C/mm)[a]	0.10
Winter heat–moisture index (°C/mm)[a]	0.31*
Chilling degree-days < 0 (°C × days)	–0.06
Growing degree-days > 5 (°C × days)	–0.10
Beginning of frost-free period (day)	–0.18
End of frost-free period (day)	0.02
PC 1	–0.13
PC 2	–0.01
PC 3	–0.51***

Note: PC, principal component. Significance values, not adjusted for multiple inference, are indicated as follows: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

[a]Values are $\log_{10}$-transformed.

43% of the total variation in climate variables and distinguishes cold and dry from warm and moist environments. This component primarily represents summer precipitation and winter temperatures, as indicated by the eigenvectors (Table 1). The second, independent component (PC 2), with an eigenvalue of 5.3, explains 36% of the variation and primarily represents variables related to growing-season temperature. The last component (PC 3), with an eigenvector above unity (2.1), represents winter precipitation or dryness and explains 15% of the variation. Cumulatively, 94% of the variation in climate variables is accounted for by these components.

Pearson's correlation coefficients between heat-sum requirements of provenances and the long-term climate data at their collection locations suggest that provenances from locations with the driest winter conditions break bud latest (Table 2). Interestingly, PC 3 has a higher correlation coefficient with heat-sum requirements than any individual climate variable. Because of spatial autocorrelations in interpolated climate normal data, we did not statistically analyze associations with grid cells of remotely sensed heat-sum values, which were determined with interpolated climate data as well. It is notable, however, that heat-sum requirements correspond to precipitation patterns mapped by Alberta Environment (2005): dry aspen parklands at the southern fringe of the boreal forest have high heat-sum requirements, and an area in central Alberta along a storm track that originates in the Rocky Mountains and crosses Alberta in a southwestern to northeastern direction has low heat-sum requirements (Fig. 2A).

Discussion

Geographic patterns of genetic variation

Within-species latitudinal or elevational clines in required heat sum for budbreak are common and can be interpreted as balancing survival adaptation versus capacity adaptation, i.e., the risk of frost damage versus the effective use of the growing season (e.g., Lechowicz 1984; Leinonen and Hanninen 2002). Northern and high-elevation origins usually flush earlier for a given heat sum, i.e., capacity adaptation takes relative precedence over survival adaptation under a restricted growing season. Although there are exceptions, this pattern generally holds true for many temperate tree species from North America and Europe, e.g., red alder (*Alnus rubra* Bong.; Hamann et al. 1998), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.; Kuser and Ching 1980), Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco; Campbell 1974), whitebark pine (*Pinus albicaulis* Engelm.; Bower and Aitken 2008), ericaceous shrubs (Reader 1983), eastern white pine (*Pinus strobus* L.; Li et al. 1997), European beech (*Fagus sylvatica* L.; von Wuehlisch et al. 1995), or Scotts pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.) (Beuker 1994).

The geographic patterns of genetic variation for aspen in this study partially conform to this expectation. The most northern provenances of aspen clearly show the lowest heat-sum requirements (Fig. 2A). This trend, however, does not hold true for Minnesota and some areas in central Alberta, and consequently, the correlation of budbreak with PC 2, which represents growing season length, approaches zero. We should therefore reject the adaptive balance of minimum frost damage versus maximizing growing season utilization as the exclusive evolutionary cause of different heat-sum requirements in aspen. Instead, we need to interpret PC 3, representing winter precipitation and dryness, as possible evolutionary driver for the timing of budburst.

White et al. (1979) point us to a plausible explanation: in their study, Douglas-fir provenances from areas with summer drought conditions break bud early, as it is highly

advantageous for these populations to complete growth before they are limited by drought. In our study, the opposite is the case: late budbreak for provenances from the central boreal plains is advantageous because the growing season starts only when summer rains commence, typically in late April. Both drought conditions and risk of frost damage in early spring appear to select for high heat-sum requirements and late budbreak. In contrast, Minnesota populations are under the influence of eastern weather systems with relatively high winter precipitation and increased spring precipitation starting in March. Taking the risk of an earlier budbreak is again offset by utilizing favorable early spring growing conditions.

Implications for genetic resource management

The common garden trial that we evaluated in this study for the timing of budbreak is part of a larger series of clonal, progeny, and provenance trials of an industrial tree improvement program. Early results from these trials suggest that movement of seed sources in northern and northwestern directions or to higher elevations generally results in substantial increases in growth relative to the local sources (Brouard and Thomas 2002). Most dramatic are the results of long-distance transfers of Minnesota provenances to the central boreal plains of Saskatchewan and Alberta, with gains in height and diameter growth of up to 40% relative to local sources in provenance trials. Does this increase in tree growth come at the expense of increased exposure to late spring frost events or other adaptive disadvantages?

This study suggests that movement of seed from central Alberta sources northward and to higher elevations does not expose planting material to late spring frosts. The transferred planting material would in fact break bud later than the local high-elevation or northern sources because they have higher heat-sum requirements. Long-distance transfer from Minnesota to the central boreal plains of Saskatchewan and Alberta, on the other hand, would carry an increased risk of spring frost damage and potential exposure to exceptional drought conditions in early spring. We therefore caution against long-distance seed transfer of Minnesota provenances to the boreal plains of Alberta and Saskatchewan. Although results from short-term trials are promising, these sources could be at risk from exceptional frosts and drought events in early spring, whereas local sources are still protected through dormancy.

An exception to this conclusion may be an area of central Alberta along the jet stream storm track, where precipitation is high (Alberta Environment 2005, their fig. 8), and where the local aspen population also has similarly low heat-sum requirements (Fig. 2A, inset). This region roughly corresponds to the forest management area of Alberta Pacific Forest Industries and, incidentally, also corresponds to the area where test plantations of Minnesota provenances have shown by far the highest field performance (compared with all other test sites and all other provenances).

Our findings raise new questions and working hypotheses that suggest the evaluation of genetic variation in other adaptive traits. (*i*) Given our conclusion that seed sources from central Alberta may be transferred north and to higher elevation without increased risk of spring frost damage, does the transferred planting material match local sources with re-

spect to fall and midwinter cold hardiness? (*ii*) Are provenances from the central boreal plains better adapted to drought conditions than Minnesota sources in general? (*iii*) Does the increase of tree growth of Minnesota provenances come at the expense of mortality risks due to frost or drought exposure, and are these risks acceptable in a short-rotation plantation forestry setting? The first two questions can be addressed through straightforward physiological studies in laboratory settings. The third question requires exposure of provenances to rare climatic events in long-term field testing. Maintenance of the current trial series over the next decades will therefore provide valuable data and may increase our confidence in using long-distance seed transfer for operational plantation forestry with aspen.

Validation of the remote sensing approach

Although the statistical validation of remote sensing results with an independent provenance data set did not yield a convincing result, we find the current results exciting and promising. The difficulties of ground-truthing coarse resolution remote sensing data with point observations are well known (e.g., Fisher and Mustard 2007; Fisher et al. 2007). In this study, we compare provenance samples with 500 m grid cells that may contain hundreds or thousands of aspen trees. In addition, there is a variable contribution of other tree species, understory vegetation, and other vegetation classes that may be present in each grid cell. A reasonable correlation among ground data and remote sensing data when summarized at the level of ecological regions (Fig. 3) suggests that large-scale geographic patterns in remote sensing data may be interpreted with some confidence. However, random error and complex composition of individual pixels make interpretation of variation at small scales meaningless. For example, we would not suggest that seed collectors should target a particular raster cell to find sources with high heat-sum requirements.

Despite random errors at small scales, the remote sensing approach appears to be a promising approach to comprehensively map patterns of genetic variation. To our knowledge, this is the first time that geographic patterns of genetic variation in any trait have been revealed for all populations of a species across a large study area. An equivalent result from a sample-based approach would require a large effort involving the collection of many hundreds or thousands of samples. Could this approach be applied to detect genetic variation in other species and in other traits? In this study, we selected a trait that has a strong remote sensing signature (deciduous green-up) in the regionally most abundant tree species (aspen). Finding enough informative grid cells for less frequent species would likely require finer resolution remote sensing products such as 30 m Landsat data and more careful filtering of pixels with high-quality forest inventory data (Fisher and Mustard 2007; Fisher et al. 2007). This would likely also apply for species such as conifers that have a less pronounced green-up signal.

Net primary productivity, green-up date, and green-down date are all routinely estimated from MODIS–EVI and other remote sensing products, but an important condition for detecting population differences is that the trait of interest needs to be under reasonably strong control of a single or few environmental variables, and that the values of these

variables can be estimated for all locations. This is certainly the case for the timing of leaf abscission or bud set, which in temperate tree species is primarily under day-length (and, in some cases, temperature) control. We think that trying to detect population differences in net primary productivity under severe regional multiyear drought conditions may also be an interesting research subject. In this case, a single environmental variable may temporarily become the overriding environmental factor controlling net primary productivity, whereas under normal conditions, many confounding factors that influence productivity would make the detection of genetic variation in response to any individual variable impossible.

Acknowledgements

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