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Genetic adaptation of aspen populations to spring risk environments: a novel remote sensing approach

by

Haitao Li

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Abstract

This study investigates geographic patterns of genetic variation in aspen spring phenology to understanding how tree population adapts to climatically risk environments. These finding suggest rules to guide seed transfer between regions. I use a classical common garden experiment to reveal genetic differences among populations from western Canada and Minnesota, and present a novel method to seamlessly map the heatsum required for remotely sensed green-up. Both approaches reveal two major geographic patterns: northern and high elevation aspen populations break bud earlier than sources from the boreal plains, and late budbreak is strongly associated with the driest winter and spring environments. This suggests selection pressures for late budbreak due to both frost and drought risks in early spring, and we therefore caution against transfer of seed to droughtprone regions of the boreal plains. Although such transfers have been shown to increase plantation productivity in short-term tests, non-local planting material may be susceptible to exceptional spring droughts.

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1. Introduction

Phenology is the study of timing of recurring phases of biological 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 Lechowicz 1992). The heatsum requirement for budbreak is typically calculated as degree-days: average daily temperature values above a certain threshold are added until the date of a phenological event. The threshold value that yields the highest correlations with budbreak normally ranges between 0 and 5°C for temperate trees (Hunter and Lechowicz 1992, McMaster and Wilhelm 1997, Snyder et al. 1999, Beaubien and Freeland 2000). Another factor that may influence the timing of budbreak is a fall chilling requirement (e.g. Campbell and Sugano 1975, Murray et al. 1989). 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 heatsum requirement starts. A chilling requirement prevents premature heatsum accumulation and budbreak if fall and winter temperatures are unusually mild.

In wide-ranging species, different populations typically have different heatsum 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 strandboard mills (Li 1995). 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 productivity increases if planting material is moved north or northeast (Brouard and Thomas 2002, Gylander et al. unpublished manuscript). However,

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no information exists on genetic variation in adaptive traits. In this thesis I evaluate one of the 1998 provenance trials for patterns of geographic variation in heatsum requirements for budbreak to reveal adaptive mechanisms to spring risk environments. Does the observed increase in productivity 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, I also test a novel method to seamlessly map geographic patterns of genetic variation in heatsum requirements of aspen populations. Because the timing of budbreak is under strong control of a single environmental variable, I hypothesize that a uniform experimental environment is not needed to reveal genetic differences among populations for this trait. Instead, I propose to use interpolated daily climate data from weather stations to calculate the required heatsum 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. Sakamoto et al. 2005, White and Nemani 2006).

2. Literature Review

2. 1. Science of phenology

Phenology is a term derived from the Greek word *phaino* meaning to show or to appear. The term refers to the study of repeatable phenomena and their reasons

and is usually applied to the life stages of plants and animals. Plant phenology studies recurring biological phases of species, biotic and abiotic causes, and the interrelation of phases within or among species (Leith 1970, Rathcke and Lacey 1985). For spring phenology, these traits refer to flowering, budburst, or leaf unfolding. Timing of spring phenology and its relationships to environmental variations, especially inter-annual climate variation and long-term climate change, are a major research focus (Menzel 2003, Chuine et al. 2004). Results have been applied in agriculture to determine timing of planting and harvesting in order to achieve the maximum crop yield (e.g. Sakamoto et al. 2005), and have also been used to determine optimal timings of applying pesticide and herbicide (e.g. Moola and Mallik 1998). In forest management, tree phenology has been used to estimate forest productivity (e.g. Goetz and Prince 1996), and to optimize adaptation of planting stock for reforestation to their planting environments (e.g. Campbell 1974, Rehfeldt 1983). In addition, plant phenology is considered the key element that affects the carbon balance of terrestrial ecosystems (e.g. Gill et al. 1998).

Phenological events, such as budburst or first bloom, are statistically described by timings of their occurrence, duration, and synchrony (Rathcke and Lacey 1985). Recording phenology events has a long history with perhaps the oldest observation records in Japan dating back to the 13th century (Menzel and Dose 2005) and in Europe dating back to the Swedish biologist Carolus Linnaeus and a British landowner Robert Marsham who started systematic phenology observations in the 18th century (Lechowicz 2001). In North America, Thomas Jefferson started the earliest systematic phenology observations in 1776

(Schwartz et al. 2006), followed by Thomas Mikesell a century later between 1883 and 1921, and he recorded about 25 species during that period of time (Lechowicz 1995). These historical recordes still contribute to current research (Sparks and Carey 1995). Today, research involving phenological observations is often carried out with the help of extensive plant phenological observation networks that have been established across the world, such as Encyclopedia of Life and Project BudBurst (van Vliet et al. 2003). Beside field observation, digital cameras (Richardson et al. 2009), aerial photography (Carreiras et al. 2006), and satellite imagery (Reed et al. 1994, Sellers et al. 1995, Fisher and Mustard 2007) have been used to study of phenology.

2.2. Environmental control of budburst

Temperature controls plants' respiration and growth, and is also the primary driver of the timing of spring phenological events. These include bud burst, flowering, fruiting, and leaf senescence in many temperate plant species (Penuelas and Filella 2001, Menzel 2003, Morin et al. 2009).Temperature accumulated over time, also referred to as heatsum, determines the rate of spring development of plants. Heatsum is calculated as the accumulation of degree-days up to the date of a phenological event. Degree-days are also referred to as heat units, thermal units, or day degrees. Generally, degree-days sum average daily temperature values above a minimum temperature threshold over a predetermined active period (Hunter and Lechowicz 1992, Ghelardini et al. 2006). For example, for budburst, the active period starts with the end of winter dormancy and ends with leaf flush. Temperatures that surpass a minimum threshold value, often ranging between 0

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and 5°C are accumulated as degree days. Using heatsum as predictor, Reaumur successfully predicted the occurrence of a phenological stage more than 200 years ago (Lechowicz 2001). He suggested heatsum is relatively invariable for species and could be used to predict a future phenological event of the same or similar kind (Reaumur cited in Lechowicz 2001). Phenological events in one species could therefore also be used to predict a subsequent phenological event of practical importance in another species if that second event requires a somewhat higher heatsum (Sharpe and Demichele 1977, Johnson and Thornley 1985).

In a predictive heatsum model, there are generally two parameters that can be varied to maximize the accuracy of predicting a phenological event: the minimum threshold above which degree day values are accumulated and the beginning of the active period, or start date, where heatsum accumulation is initiated. Yang et al. (1995) summarized four most commonly used approaches to estimate the value of these variables: smallest standard deviation method, linear regression model, iteration method, and the triangle method. The main idea of these approaches was to approximate model parameters with regression or iteration method based on the field-measured phenological data. Snyder et al. (1999) found that the results from iteration method usually provid the smallest root mean square error (RMSE) in most cases, indicating that this is a better approach. Temperatures exceeding 0°C and 10°C can be used to infer dormancy release and determine the start date of heatsum accumulation, but often the start date is arbitrarily (or iteratively) determined with values ranging from January 1st or March 1st (Perry 1971). Many studies have determined 0°C or 5°C as the optimal minimum temperature threshold for calculating degree day values across a wide range of temperate

species (Snyder et al. 1999). Heide (1993) has determined a threshold value of 1°C for aspen, but generally, a threshold value of 0°C provides good predictive accuracy for most northern tree species (Ring et al. 1983, Snyder et al. 1999). After setting the minimum temperature threshold, the required heatsum for a phenological event can be calculated by summing all the effective temperatures from a start date to the date of the event. This computation is also called thermal time model (Reader 1983, Delahaut 2003).

A modification of the thermal time model includes negative temperature accumulation below a certain threshold (often 0°C). These so called chilling degree-days are required in many tree species to release winter dormancy of buds and seeds temperate area (Campbell and Sugano 1975, Murray et al. 1989). A chilling requirement prevents premature bud burst or germination of seeds due to heatsum accumulated in fall and winter. Therefore chilling requirements are usually highest in species or populations of species that occur in maritime climates with mild winter conditions that could result in premature forcing (Cannell and Smith 1986). If experimental data on dormancy release as a function of chilling degree-days are available, this information can be incorporated in thermal time models: the start date of heatsum accumulation is the date where chilling requirements are satisfied. An important source of error in predictions of models that include chilling requirements is that unusually warm winter temperatures that do not satisfy the chilling requirement lead to an indefinite delay of the start date for heatsum accumulation. In reality, some delay of dormancy release does in fact take place and implicitly leads to a higher observed heatsum requirement for budburst (Leinonen and Hanninen 2002).

2.3. Spring phenology as an adaptive trait

Timing of phenological event is considered to be the result of an evolutionary adaptation of plants to their environments, especially for those grown in extreme environments such as cold temperature or less moisture (Perry 1970). Abiotic factors usually have straightforward impacts on plant phenology. In temperate regions frost would cause damage in spring and fall to plants that do not time their growing cycle well with the frost-free period (Leinonen and Hanninen 2002, Jonsson et al. 2004, Vitasse et al. 2009). Other factors, such as precipitation and soil moisture (Reich 1995, Kramer et al. 2000, Beaulieu et al. 2002) or changes in the duration of the photoperiod (Partanen et al. 1998) may also have an influence on plant phenology. Even biotic factors may be evolutionary causes for the timing of phenological events. For example, the population dynamics of pollinators can determine the optimal timing of flowering, and variations in the population size of seed predators can influence the optimal timing of fruiting for reproductive success (Elzinga et al. 2007, Kolb et al. 2007). Even though biotic factors may be the ultimate cause for the timing of a biological event, abiotic factors are usually the proximate cause or triggers (Hamann 2004).

In seasonal, temperate regions the adaptive process of plant phenology can be described as a balance between the survival adaptation and capacity adaptation (Howe et al. 2000, Leinonen and Hanninen 2002). The optimal timing of bud flush, for example, is determined by a tradeoff between avoiding late spring frost damage (survival adaptation) and utilizing favorable growing conditions in spring

(capacity adaptation). Capacity adaptation is ultimately linked to survival and is therefore a trait that can be under evolutionary selection. For example, a delayed bud break could potentially cause the plants from failing to produce seeds or fruits to increasing the chance of mortality to competition by better adapted individuals (Billington and Pelham 1991). The optimal timing of phenological events may differ for different life forms, different ages, different species, and for different populations within a species. Differences in the optimal timing may arise due to different microclimate conditions, regional differences in climate variability, and long term growing season conditions. For example, an herbaceous plant or seedling is more vulnerable to frost pockets than a mature tree and may therefore break bud later. To give another example, populations in high elevation or cold northern ecosystems may take a greater risk of frost damage in spring and fall to take full advantage of the short growing season (Lechowicz 1984, Leinonen and Hanninen 2002).

Even at the population or individual level, phenological traits would not be considered fixed genetic effects. In fact, the adaptive value of phenological traits usually lies in the flexible response to biotic or abiotic environment. This ability is defined as phenotypic plasticity (Via and Lande 1985, Agrawal 2001). Spring phenology may change according to the temperature, light, soil nutrition and other environmental factors. These environmental factors can also result in a somewhat more permanent plastic response, influencing size of buds and the morphological and physiological properties of leaves (de Kroon et al. 2005). Longevity of trees coupled with phenotypic plasticity should allow individuals and population to survive a few decades of adverse environmental conditions. Meanwhile,

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recombination may produce genotypes that are better adapted to the new environmental regime (Hamrick 2004). Genetic variation in phenotypic plasticity itself can be considered an evolutionary result of plant adaptation to the environmental heterogeneity (Jelinski 1997). There is further evidence that phenotypic are under stronger selection pressures than most other traits (Spitze 1993), and gene flow among differently adapted populations appears to be responsible for high genetic diversity in phenology traits in most species (McKay et al. 2005). Thus landscape-scale pattern of genetic variation in phenological traits is seldom determined by one factor, but is instead a balance between natural selection and gene flow. Strong environmental differentiation leads to strong divergent selection pressures, but short geographic distances, for example along elevational gradients, increases genetic diversity at the population level (Spichtig and Kawecki 2004).

2.4. Detecting genetic variation in phenology

Field observation of phenological traits is the traditional way to compare the timing of phenology events among species, but it is less suitable to detect differences among genotypes within a species because the observed differences might be confounded by environmental variation. To eliminate the environmental factors experiments can be carried out, where populations of a species are replicated by means of cuttings or seedlings and grown in a common garden experiment, also referred to as progeny trial (if seed sources covering a significant portion of the species range are grown together) (Campbell 1986, Beaulieu et al. 2004). The essence of the provenance trials is to compare phenological and

growth traits of different genotypes within or among species from different sites in an identical experimental environment (often a greenhouse, growth chamber, or carefully prepared field site), with a systematic experimental design that accounts for random site variation (Kawecki and Ebert 2004, Whitham et al. 2006).

When plants of different provenances are grown together under the same conditions, phenotypic variation is expected to reflect underlying genetic variation caused by the adaptation to local environmental conditions at the origin of the seed source. It should be kept in mind, however, that the failure to detect genetic differences among populations in a common garden trial does not mean that genotypes are identical. Genetic differences may be revealed under one set of environmental conditions, but not under another. Therefore, provenance trials are typically replicated over several environments. Testing multiple replicated genotypes over multiple environments makes provenance trial series an expensive research approach, especially for tree species where trials have to be maintained for many years.

As an alternative to common garden experiments, advances in molecular techniques show promise to detect genetic differences related to phenological traits (Erickson et al. 2004). Genetic variations can be detected by several methods such as molecular genetic marker and quantitative traits locus (QTL) mapping (Gonzalez-Martinez et al. 2006). Phenological traits usually show stronger correlations with genetic marker data than other quantitative traits, and population differentiation can be achieved that is similar to results from common garden experiments (Hall et al. 2007). However, genetic variation in molecular

marker data are specific to the genotypes included in any specific study and are likely to be poorly correlated with phenological variation observed in different populations (McKay and Latta 2002, McKay et al. 2005). Also, marker techniques alone cannot be used to detect which gene affects the phenotypes without field observation data (Whitham et al. 2006). Therefore, provenance trials are still the main method used for investigating geographic variation in phenological traits.

2.5. Phenology and forest management

Many tree species have large geographic ranges and usually show profound geographic variation in adaptive traits (Howe et al. 2003). These traits, which include phenological characteristics, are important factors to be considered in the movement of planting stock for reforestation and in genetic tree improvement programs. For example, if genotypes are selected for growth traits in short-term experiments, adaptive traits may be sub-optimal. Consequently, the better growth may be the result of risking late spring and early fall frost damage for an extended growing season (Brissette and Barnes 1984). Therefore, phenotypes with high mortality risk due to susceptibility to frost damage or drought may not be a suitable choice for reforestation. Ideally, we should use genotypes that show lower adaptive risks while maintaining superior growth.

It is generally difficult to experimentally or empirically link phenological trait variation to fitness of populations. For example, while we can determine genetic variation in heatsum requirement for the timing of bud flush with common garden

experiments, it is difficult to say whether a particular heatsum value is adaptively optimal for a particular location. Instead, we usually simply make the assumption that populations are optimally adapted to their source environments. Based on this assumption of local optimality, we can then select planting stock for reforestation that has similar adaptive traits compared to the local sources. This method has been used to create guidelines of seed transfers and to delineate seed zones (Kleinschmit et al. 2004, Savva et al. 2007, Bower and Aitken 2008). The objective of limiting seed movement in reforestation is to ensure that planting stock is not mal-adapted to environmental conditions of the planting site. Preferably such guidelines should be expressed through straight-forward rules that can be implemented by forestry practitioners. For example, northern provenances of Norway spruce (*Picea abies*) and scots pine (*Pinus sylvestris*) have earlier budburst and should therefore not be used planting environments further south to avoid late spring frost damage (Beuker 1994, Leinonen and Hanninen 2002).

An important challenge for forest management that increases the need for understanding the adaptive value of phenological traits is anthropogenic climate change. Considerable climate warming has been observed around the world and the trend is predicted to continue for the next century (IPCC 2007). In western Canada, climate warming in mean annual temperature of approximately 0.7° C and decreases in mean annual precipitation of approximately 15% have been observed over the last 25 years, exceeding climate change projections from most general circulation models (Mbogga et al. 2009). An important climate change adaptation strategy to mitigate climate change impacts that has been proposed and implemented in some jurisdictions is to move planting stock to higher elevations

and latitudes further north to compensate for climate warming (Marris 2009, McKenney et al. 2009). For such transfers, the assumption of local optimality is meaningless, and we now have to understand instead the adaptive value of the timing of phenology in order to provide scientifically well supported seed transfer guidelines.

2.6. Remote sensing of phenology

To overcome the logistical limitations of traditional phenological field observations, remote sensing was introduced to study green-up and green-down of vegetation over large geographic areas (Reed et al. 2003, Schwartz et al. 2006). Remote sensing is the acquisition of information by using information contained in electromagnet bands of different spectral wavelength from sensors that are typically located on satellites (Elachi and Zyl 2006). The advantages of remote sensing include its ability to repetitively acquire large scale and synoptic phenology information (Botta et al. 2000, Fisher and Mustard 2007, White et al. 2009). Considering the differences between traditional phenology and remotely sensed phenology, researchers have introduced the term "land surface phenology" to refer to variation in vegetated land surface observed from synoptic sensors (de Beurs and Henebry 2005, Reed et al. 2009). Land surface phenology provides aggregate information that relates to the timing of vegetation growth, senescence, and dormancy, and it also reflects surficial phenomena at seasonal and interannual time scales.

In recent years satellite imageries with high spatial, spectral, and temporal resolution have become available. These images are mainly from satellite based sensors including Landsat ETM+, MODIS, RADARSAT, Hyperion, and QuickBird, and for some sensors cover the whole world periodically (Raney et al. 1991, Cohen et al. 2003, Thenkabail et al. 2004, Toutin 2004). Moreover, some of these data, such as MODIS and Landsat ETM+, are free for the public and have been extensively used in various research fields. The spatial resolution of remotely sensed imageries most commonly used to monitor land surface phenology is moderate to coarse (500m to 25km) (Botta et al. 2000). Few researchers use high spatial resolution imagery for this purpose due to the lower temporal resolution that is usually available from high resolution sensors (Fisher and Mustard 2007). In addition, there are limitations in the amount of data that can be processed with imagery collected in recurring intervals at high resolution (Drake et al. 2003, Kimball et al. 2004).

Reliably detecting the amount of green vegetation is always the fundamental basis to monitor land surface phenology. Key for this detection is the reflectance characteristic of the plant leaves, particularly the spectral features of chlorophyll and water contained in leaves (Myneni et al. 1995). Chlorophyll absorbs solar radiation with wavelength between 0.43 and 0.45 μm (blue) and between 0.65 and 0.66 μm (red) to conduct photosynthesis in a healthy green leaf. Between these two spectral bands, there is a characteristic gap of low absorption and high reflectance around 0.55 μm. Water in leaf cells, on the other hand, has a high reflectance between 0.74 and 1.00 μm (near-infrared) (Woolley 1971, Hunt and

Rock 1989).The canopy therefore appears relatively dark in the red absorption bands of chlorophyll and relatively bright in near-infrared.

In contrast, soil and water do not absorb solar radiation at the same blue and red bands as chlorophyll does. Further, clouds and snow have high reflectance at visible light and near-infrared, and absorb infrared radiation at around 1.50 μm. Therefore, they are rather bright in the red and quite dark in the near-infrared band. Because the ratio between near-red and infrared red band is considerably higher for vegetation than for soil, water and clouds, the sources of background noises, it can be used to distinguish and quantify the density of vegetation. This is the fundamental idea for all vegetation indexes (Jensen 2005), and rather than reflectance, vegetation indices are more commonly used in remote sensing of land surface phenology. Furthermore, vegetation indices can also be used to identify drought stress and plant health according to the reflectance change at near-infrared and infrared (Hunt and Rock 1989, Running et al. 1989, Zarco-Tejada et al. 2003, Asner et al. 2004).

The Normalized Difference Vegetation Index (NDVI) is one of the most widely used vegetation indices. This index involves only two parameters: the reflectance of near infrared band (NIR) and the reflectance of red band. NDVI has been proven to perform better in distinguishing vegetation from soil (Richardson and Wiegand 1977). NDVI values theoretically range from -1.0 to 1.0, and vegetation covered area has positive NDVI value that usually range from 0.3 to 0.8. Clouds and snow fields are characterized by negative values of this index. Oceans, lakes and rivers have a low reflectance in both NIR and red bands, and thus result in

very low positive or even slightly negative NDVI values. Soils generally exhibit a NIR spectral reflectance somewhat larger than the red, and tend to also generate rather small positive NDVI values (around 0.1 to 0.2). Although NDVI is a good index to represent vegetation phenology, the index is affected by the local seasonal atmospheric conditions such as the aerosols and clouds (Kobayashi and Dye 2005).

In order to correct this problem, the Enhanced Vegetation Index (EVI) was developed to optimize the vegetation signal by reducing atmosphere influences and enhancing its sensitivity to high biomass area (Huete et al. 2002). The index utilizes a band in the blue spectrum between 0.45 and 0.495 μm to calibrate the reflectance of the red and near infrared bands. Therefore, EVI uses three spectrum bands: the red, the near-infrared, and the blue. It requires three sets of coefficients: a soil adjustment coefficient L, two aerosol calibration coefficients (C1 and C2) derived by using the blue band to correct the atmospheric influences in the red and near-infrared band, and the last one is gain factor (G) which is used to modify the whole EVI computation equation. Huete et al (1997) empirically determined the values of these coefficients as L=1, C1=6, C2 = 7.5, and G = 2.5. Compared to NDVI, an advantage of EVI is that it does not as easily reach the saturation point when LAI is high (Huete et al. 2002). Assuming there is a time-series remotely sensed data set, and NDVI and EVI are separately used to detect when the vegetation produces the most biomass in a year, NDVI will generally result in an earlier date than EVI because NDVI value saturate at a lower biomass level than EVI does. Moreover, EVI was found to perform better in the heavy

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aerosol conditions and soil/vegetation background (Miura et al. 2001, Xiao et al. 2003).

In addition to EVI, some indices were specifically developed for the purpose to study plant phenology in far northern and southern regions: Normalized Difference Water Index (NDWI) (Delbart et al. 2005) and Normalized Difference Snow Index (NDSI) are capable of distinguishing snow cover particularly well (Salomonson and Appel 2004). In addition, the Fraction of Photosynthetically Active Radiation (fPAR) has been successfully used to monitor land surface phenology (Ahl et al. 2006).

The date of a phenological event is usually inferred from remotely sensed time series data by fitting a mathematical function to vegetation index values observed over time. For instance, a sharp increasing of NDVI is related to the onset of significant photosynthetic activity (Reed et al. 1994, Doktor et al. 2009). To locate a phenological event on the fitted vegetation index curve, therefore, is one of the key tasks when studying land surface phenology. There are three general methods available for this task: threshold, mathematical, and hybrid. In the threshold method, the date of phenological events is determined by the day when the vegetation index value reaches a given threshold. Filtering or smoothing of input data is not required for this method. For example, the date of bud burst is determined by NDVI exceeding 0.2 or 0.3 (White and Nemani 2006). The second method assumes a mathematical function or a suite of functions to locate a phenological event. For example, Reed et al. (1994) developed a delayed moving average method (DMA). Roerink et al. (2000) proposed a method based on fast

Fourier transformations (FFT), where the greenup date occurs at the point of maximum increase on the NDVI profile. The quadratic method, developed by de Beurs and Henebry (2005, 2008), is a linear quadratic regression model between NDVI and growing degree days. The hybrid method generates a fitted curve, e.g. a Gaussian curve, and then determined the phenological date with a threshold (White et al. 2009). Jonsson and Eklundh (2002) developed a suite of filter and smoothing functions to estimate the greenup date, including Savitzky-Golay filter, least-squares fitted Gaussian, and logistic smooth functions. They combined these functions into a software package called TIMESAT (Jonsson and Eklundh 2004).

Overall, the satellite-derived metrics correspond well with the ground-observed phenology (Studer et al. 2007, Doktor et al. 2009). However, research also found satellite-derived date is always earlier than field observation. Studer et al. (2007) and Zhang (2004) suggested that it was caused by the sensitivity of NDVI to low LAI. Snow (Studer et al. 2007) and heterogeneous vegetation cover (Doktor et al. 2009) are also the major factors influencing the date of spring phenology derived from satellite imageries. Remotely sensed phenology has been successfully related to interannual climatic variations (Los et al. 2001, Stockli and Vidale 2004). But long-term trends related to global climate change appear to be different among studies. Reed (2006) found a trend toward earlier starts of season in limited areas, and a trend toward later end of season in areas of New England and southeastern Canada. Piao et al. (2007) showed that there is no overall continental trend toward earlier spring under global warming scenarios, but Zhou et al. (2001) found a strong continental trend of greenup dates getting earlier.

Across large geographic areas, the spatial variability of land surface phenology reflects primarily climatic variability (Jenkins et al. 2002, Schwartz et al. 2002, Fisher et al. 2007). Although climatic factors significantly correlate with phenological timing, climatic variation is not equivalent to phenotypic variation. Therefore, land surface phenology cannot be directly used to differentiate geographic variations among phenotypes. For example, timing of budburst is mainly determined by heatsum, and required heatsum usually shows a latitudinal trend that increases from north to south when elevation is not considered (Leinonen and Hanninen 2002). Therefore, timing of budburst may show a reduced latitudinal cline when observed from satellite-derived data that reflects the confounded effects of geographic trends in climate and heatsum requirements of plants. To my knowledge, no research has been conducted to disentangle these effects.

2.7. Limitations of land surface phenology

Studies that compare remotely sensed land surface phenology with ground observations have shown variable results. There are a large number of potential sources of errors that influence the strength of the correlation between remote sensing data and ground observations: (1) variability in atmospheric conditions, (2) temporal and spatial variability in soil moisture and snow melt, (3) the composition and type of vegetation, (4) the resolution of remote sensing data, (5) the corresponding density of ground data, (6) the type and temporal resolution of remote sensing data, and (7) the mathematical parameter used to define a phenological event.

To give some examples from the literature for these sources of error: Kobayashi and Dye (2005) found that local and seasonal variability in atmospheric conditions such as the aerosols and clouds influnced 15-day composite NDVI values by up to 10%. DeBeurs and Henebry (2004) found that delayed snow-melt due to cold and wet winter conditions can significantly delay the NDVI-based estimate of green-up of local vegetation compared to wet/warm years. Wilson and Meyer (2007) showed that different vegetation types had unique seasonal and annual reflectance signatures, some of which correlated well with ground observations but others did not. Fisher and Mustard (2007) demonstrate that spatial variability in 500m resolution satellite data is considerably smoothed, a potential source of error when comparing point observations on the ground and with satellite data. Further, complex species or community composition cannot be captured in remote sensing data and did not allow successful linkage of satellite observations to ground data (Fisher et al 2007).

Secondly, the way in which remote sensing data is collected and processed can be a source of multiple types of errors. Phenology studies usually rely on multi-day composite data (7 to 16 days), which has the advantage that cloudy days can be excluded for each interval, but which introduces a temporal error (Huete et al. 2002, Gao et al. 2008). Further, phenology is usually described by means of mathematical function that is fitted to time series data. The beginning and end of growing season are defined as the point where the rate of change in a remotely sensed vegetation index is maximal (Jonsson and Eklundh 2004). These parameters are inherently associated with an additional error of a mathematical

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estimate and depending on the vegetation type, and they may not exactly correspond to green-up observed on the ground. Although one-season or one-year data can theoretically be used to identify a phenological event, three or more years of data are required to fit reliable functions to time series data (Jonsson and Eklundh 2004).

2.8. Life histories of aspen

Trembling aspen or quaking aspen (*Populus tremuloides* Michx.) is a widespread tree species in North America. Aspen is a fast-growing pioneer species that can be found from northern Alaska and Yukon to Mexico, and grows on many soil types and under various climatic conditions throughout its range (Burns and Honkala 1990). Aspen is most frequent in the central boreal plains of western Canada, where it is an important source of wood for pulp and oriented stranded board industries in western Canada (Li 1995). Aspen is a wind-pollinated and wind-dispersed species with high fecundity and long-distance dispersal capability (Mitton and Grant 1996). Seedling requires favorable moisture and light conditions for establishment (Romme and Despain 1989), and the species generally establishes well from seed after fire disturbance on bare ground if adequate moisture is available (Jelinski 1997, Kay 1993).

Aside from sexual reproduction, aspen is capable of vegetative reproduction from rood suckers. Where aspen is already established, this is the predominant mode of reproduction after disturbance (Barnes 1966). Individual aspen trees usually live around 70-150 years in North America, but the clone from which trees originate

by means of root suckers may be as old as 10,000 years (Madsen 1996). Clonal propagation can be an effective survival strategy for aspen if environmental conditions are adverse for extended periods of time and prevent reproduction through seedlings (Cook 1979, Tissue and Nobel 1988). On the other hand, clones by definition do not adapt to changing environments (without natural selection taking place), although somatic mutations may contribute to accumulating favorable mutations to adapt new environments (Jelinski and Cheliak 1992, Whitham and Slobodchikoff 1981). Patterns of genetic diversity in neutral allozyme loci or molecular markers further imply that clones are shorter-lived and sexual reproduction is more prevalent under favorable conditions for seedling establishment (Jelinski and Cheliak 1992, Cheliak and Dancik 1982, Lund et al. 1992, Namroud et al. 2005).

3. Methods

3.1. Provenance trial data

The date of budbreak was measured in a provenance trial established by an industry cooperative consisting of members of the Western Boreal Aspen Corporation and Alberta Pacific Forest Industries in 1998, which includes 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 6 replications, and 5-tree row plots within blocks serve as experimental units. Between May 4th and June 2nd 2009, I 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 at 10 dates on a 7-level bud development scale (Fig. 2: 0, dormant; 1, buds swollen; 2, buds broken; 3, leaves appeared; 4, scales opened; 5, scales lost and leaves folded; 6, leaves fully extended). I calculated least squares means (to adjust for missing values) and standard errors of budbreak date for provenances with the GLM procedure of the SAS statistical software package (SAS Institute 2008). The response variable was the Julian date where 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).

3.3. 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, which is freely available and one of the best options to estimate the green-up date of vegetation (White and Nemani 2006). I used the 16-day interval 500m resolution EVI product (Gao et al. 2008), which was obtained through the MODIS-for-NACP data products website (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 one year of remote sensing data is necessary to calculate heatsum requirements, the Savitzky–Golay function fitted to a temporally coarse 16-day interval product is not expected to result in a very accurate heatsum estimate for a single year. I therefore processed 5 years of

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remote sensing data (2001 to 2005) and calculated an average required heatsum 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 I explored several options: the Alberta Vegetation Inventory database (ASRD 2005), 25m resolution land cover data for western Canada (Wulder et al. 2008), and 30m resolution land cover data for the United States (Homer et al. 2007). Summarized at the native 500m 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) I used deciduous forest cover as a proxy for aspen frequency over the entire study area. For subsequent analysis, only grid cells of the 500m MODIS/EVI dataset 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.

3.4. Degree day and heatsum calculations

Daily mean temperature data from approximately 4300 weather stations for Canada were purchased as a customized dataset from the Meteorological Service of Canada (MSC 2007). Daily climate data of 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 ID 3060L20, 7km distance) were used to calculate daily heatsums for the provenance trial location. Interpolated data for all weather stations were used to calculate daily heatsums for the years 2001-2005 for all MODIS/EVI grid cells with at least 40% aspen cover. I used a thin-spline interpolation method implemented with the G3GRID procedure of the SAS statistical software package (SAS Institute 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 dataset I extracted the heatsum value that corresponded to the remotely sensed Julian day of green-up for the years 2001 to 2005 in MODIS/EVI data. The required heatsum 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 greenup estimates and errors in interpolated temperature data. Calculating heatsum values for multiple years from 2001 to 2005 allows us to calculate a mean and standard error for the required heatsum estimate.

3.5. Statistical analysis

To aid the interpretation of geographic patterns of genetic variation in heatsum requirements, I used 15 biologically relevant climate variables for the 1961-1990 climate normal, which is used 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 heatsum for budbreak. To simplify the analysis of associations between climate variables and required heatsum of provenances, I employed a principal component analysis of 1961-1990 climate normal variables obtained for the 43 provenance collection locations. Principal component analysis was implemented with the PRINCOMP procedure of the SAS statistical software package (SAS Institute 2008). After visually determining linearity of the relationships among climate variables, their principal components and budbreak data (some variables were log-transformed to obtain a linear relationship), I used Pearson correlation coefficients to quantify the strength and direction of the associations.

I further tested how well heatsum values estimated from remote sensing data correspond to values obtained through the common garden experiment. For this purpose I report Pearson correlation coefficients of required heatsum determined for 43 provenances with MODIS/EVI grid cell that contains more than 40% aspen within a given radius (I tested 1km, 3km, 5km, 10km, 30km, 50km). Alternatively, I correlated regional averages of grid cells and provenances, where data was summarized by "Ecosections" of the National Ecological Framework for

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Canada (Selby and Santry 1996), and corresponding "Level 4" delineations of the United States Ecoregion System (EPA 2007). The provenance sample locations were not randomly chosen, but structured into six regions of interest (aspen habitat of the AB Foothills, the boreal plains of SK and AB, the northern boreal plains of AB, the taiga plains of northwest BC, and the boreal shield of MN). To obtain regional summaries of remote sensing data corresponding to these groups of provenance samples, I used all grid cells within the ecosections that also contained the provenance samples (between two and six ecosections per sampling region). I subsequently refer to these aggregates of ecosections representing a group of provenance samples as "ecological regions".

4. Results

4.1. Provenance differences in budbreak

When planted in a common garden, provenances from western Canada showed a large range of heatsum requirements for budbreak ranging from approximately 145 to 325 degree days above 0°C (Fig. 3A). 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. 3B). Provenances from northern British Columbia had by far the earliest budbreak with a heatsum 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 northeast to southwest cline

was reversed for Minnesota provenances with an average heatsum requirement of approximately 200 degree days. There was also considerable variation of heatsum values for provenance within regions. The boreal plains regions of central Alberta and Saskachewan had the largest range of approximately 200 degree days, while the regions Minnesota and northern British Columbia had smaller ranges of heatsum values, 175 and 150 degree days, respectively. For the replicate trees of provenances, the standard error of the least squares means estimate of heatsum 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.

4.2. Remotely sensed heatsum requirements

Approximately similar geographic patterns of heatsum requirement were observed through an analysis of remote sensing data and corresponding daily climate data (Fig. 3A). Populations from Northern British Columbia and northern Alberta showed by far the lowest heatsum requirements with values between 125 and 200 degree days. Additional patterns that were not apparent in the provenance samples are very high heatsum 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 heatsum requirements in central Alberta that breaks the pattern of a simple latitudinal cline. The spatial patterns of required heatsum tend to be homogeneous in north British Columbia and Alberta, and Minnesota while they are more complex in central Alberta and Saskatchewan, reflecting the variance in heatsum values that was found in provenance data. I further see a pronounced reversal of the latitudinal cline towards Minnesota with average

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heatsum requirements of 200 degree days in both the provenance and remote sensing data. The standard error of the estimate of required heatsum for green-up was 41 degree-days, averaged across all 500m 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).

While broad geographic patterns seem to correspond to results from the common garden trial, I did not observe significant correlations between heatsum requirements of provenances and the remotely sensed data points in the vicinity (Fig. 3). Significant correlations among field observations and remote sensing data only emerged when heatsum values were averaged at the level of ecological regions for both remotely sensed data and provenance samples (R^2=0.91, p=0.003).

4. 3. Heatsum requirements and long-term climate

To interpret geographic patterns in required heatsum for budbreak as adaptations to spring risk environments, I 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 with an Eigenvalue of 6.6 explains 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 with an Eigenvalue of 5.3 explains 36% of the variation, and primarily represents variables related to growing season temperature. The last component 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 correlation coefficients between heatsum 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, Principal Component 3 has a higher correlation coefficient with heatsum requirements than any individual climate variable. Because of spatial autocorrelations in interpolated climate normal data, I did not statistically analyze associations with grid cells of remotely sensed heatsum values, which were determined with interpolated climate data as well. It is notable, however, that heatsum requirements correspond to precipitation patterns mapped by Alberta Environment (2005): dry aspen parklands at the southern fringe of the boreal forest have high heatsum requirements, and an area in central Alberta along a storm-track that originates in the Rocky Mountains and crosses Alberta in southwest to northeast direction heatsum requirements are low (Fig. 4).

5. Discussion

5.1. Geographic patterns of genetic variation

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Within-species latitudinal or elevational clines in required heatsum 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 heatsum, 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 (Hamann et al. 1998), western hemlock (Kuser and Ching 1980), Douglas-fir (Campbell 1974), whitebark pine (Bower and Aitken 2008), ericaceous shrubs (Reader 1983), eastern white pine (Li et al. 1997), European beech (von Wuehlisch et al. 1995), or Scotts pine and Norway spruce (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 heatsum requirements (Fig. 3A). This trend, however, does not hold true for Minnesota and some areas in central Alberta, and consequently the correlation of budbreak with Principal Component 2, which represents growing season length, approaches zero. Therefore, the adaptive balance of minimum frost damage versus maximizing growing season utilization should be rejected as the exclusive evolutionary cause of different heatsum requirements in aspen. Instead, Principal Component 3 representing winter precipitation and dryness needs to be interpreted as possible evolutionary driver of budburst.

White et al. (1979) point 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 this 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 starting in late April. Both drought conditions and risk of frost damage in early spring appear to select for high heatsum 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.

5.2. Implications for genetic resource management

The common garden trial that I 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 north and north-west direction 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 heatsum 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. I 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, while 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 (Figure 8 in Alberta Environment 2005), and where local aspen population also has similarly low heatsum requirements (Fig. 3A, 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 to all other test sites and compared to all other provenances).

The findings raise new questions and working hypotheses that suggest the evaluation of genetic variation in other adaptive traits: (1) 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 respect to fall and mid-winter cold hardiness? (2) Are provenances from the central boreal plains better adapted to drought conditions than Minnesota sources in general? (3) 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 straight forward 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.

5.3. Validation of the remote sensing approach

Although the statistical validation of remote sensing results with an independent provenance dataset did not yield a convincing result, I 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 I compare provenance samples with 500m 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

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summarized at the level of ecological regions (Fig. 5) 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, I would not suggest that seed collectors target a particular raster cell to find sources with high heatsum requirements.

Despite random errors at small scales, remote sensing appears to be a promising approach to comprehensively map patterns of genetic variation. To my 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 I 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 30m 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 that have a less pronounced green-up signal, such as conifers.

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 budset, which in temperate tree species is primarily under day-length (and in some cases temperature) control. I think that trying to detect population differences in net primary productivity under severe regional multi-year 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.

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Table 1. Principal component analysis of 15 climate normal variables at provenance collection locations. The highest correlations (Eigenvectors) of the original climate variables with principal components (PCs) are indicated in bold font.

| Climate variable	PC 1	PC 2	PC 3
Mean annual temperature (°C)	0.28	0.26	-0.20
Mean warmest month temp. (°C)	-0.03	**0.43**	0.12
Mean coldest month temp. (°C)	**0.35**	-0.08	-0.20
Continentality (°C)	-0.29	0.24	0.21
Mean annual precipitation (mm)[1]	**0.34**	0.11	0.22
Mean summer precipitation (mm)[1]	**0.35**	0.06	0.12
Mean winter precipitation (mm)[1]	0.22	0.20	**0.41**
Precipitation as snow (mm)[1]	0.09	-0.27	**0.43**
Annual heat:moisture index (°C/mm)[1]	-0.25	0.07	**-0.46**
Summer heat:moisture index (°C/mm)[1]	**-0.35**	0.10	-0.03
Winter heat:moisture index (°C/mm)[1]	**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

[1] $\log_{10}$ transformed

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

Climate variable	r
Mean annual temperature (°C)	0.02
Mean warmest month temp. (°C)	-0.12
Mean coldest month temp. (°C)	-0.02
Continentality (°C)	-0.03
Mean annual precipitation (mm)[1]	-0.25
Mean summer precipitation (mm)[1]	-0.19
Mean winter precipitation (mm)[1]	-0.41 **
Precipitation as snow (mm)[1]	-0.30 *
Annual heat:moisture index (°C/mm)[1]	0.41 **
Summer heat:moisture index (°C/mm)[1]	0.10
Winter heat:moisture index (°C/mm)[1]	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
Principal Component 1	-0.13
Principal Component 2	-0.01
Principal Component 3	-0.51 ***

Note: [1] $\log_{10}$ transformed; significance values not adjusted for multiple inference are indicated as: * $p<0.05$, ** $p<0.01$, *** $p<0.001$
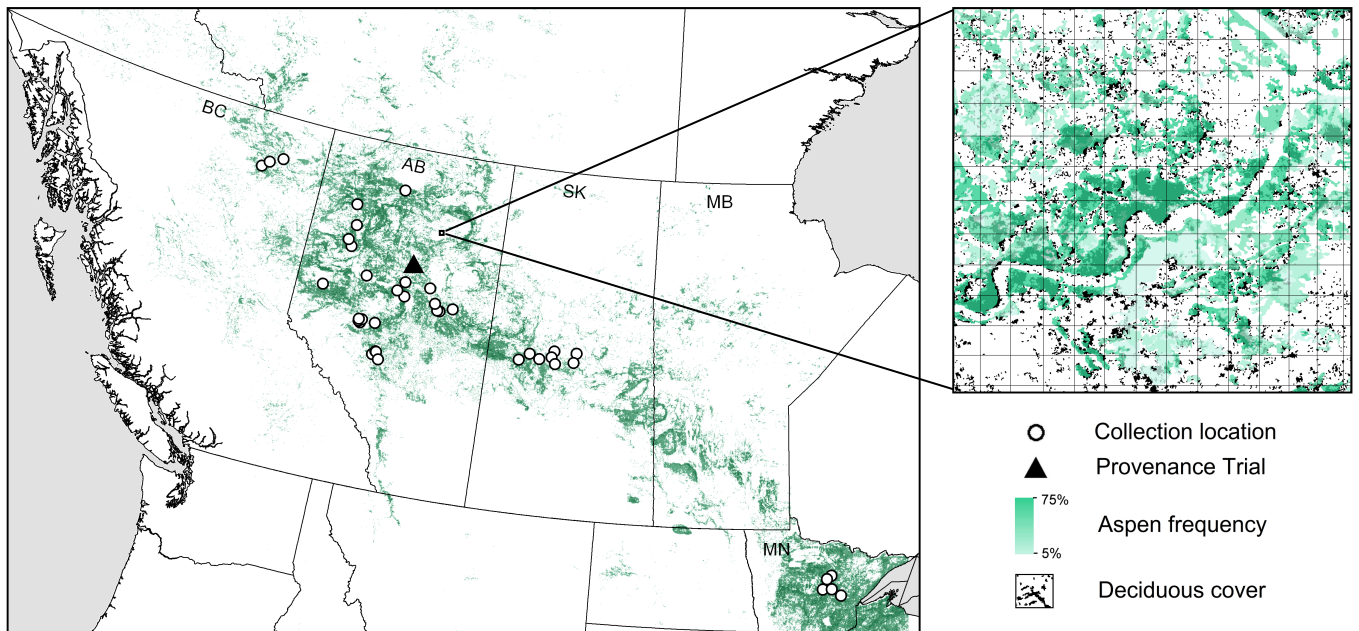
Fig. 1. Location of the provenance trial, collection location of provenances, and the aspen species distribution inferred from deciduous forest cover. The inset shows the match between aspen frequencies in forest inventory data (shades of green) overlayed as a transparent layer on remotely sensed deciduous forest cover. Summarized at 500m resolution (grid in inset) both frequency maps appear near identical.
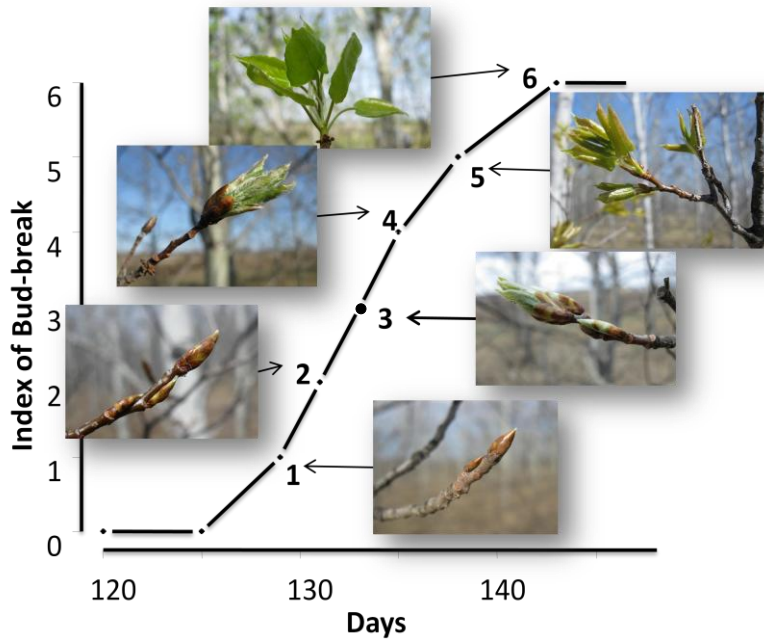
Fig. 2. Score of bud development on 7-level scale: 0, dormant; 1, buds swollen; 2, buds broken; 3, leaves appeared; 4, scales opened; 5, scales lost and leaves folded ; 6, leaves fully extended.
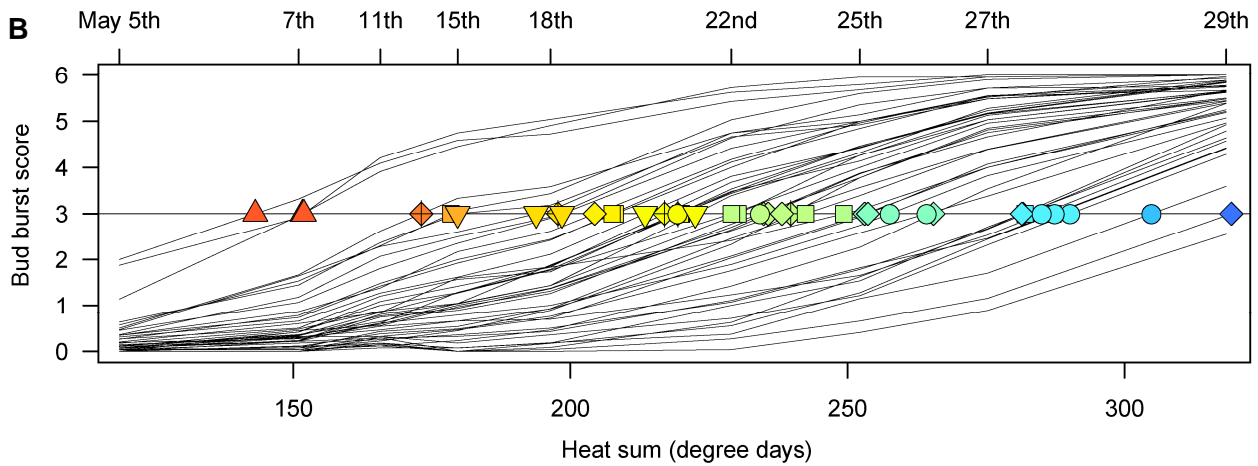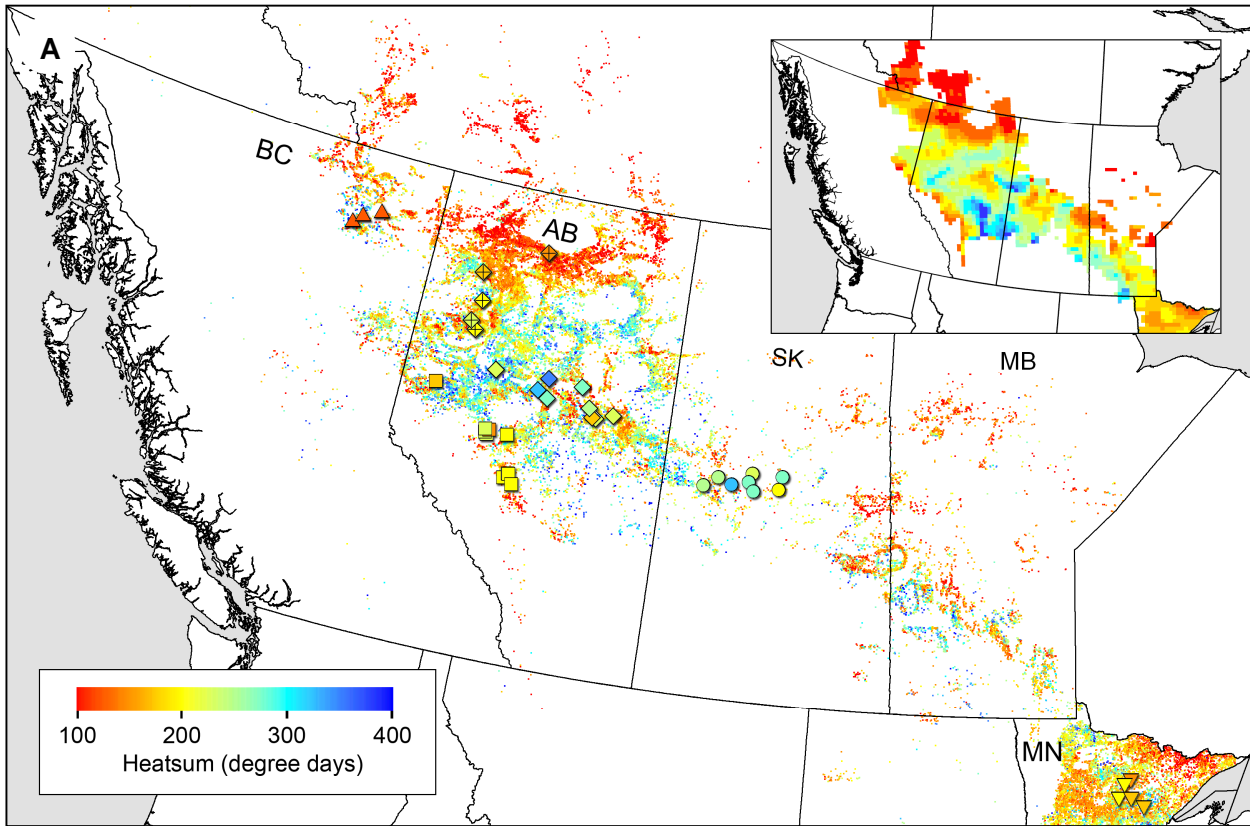
Fig. 3. (A) Heatsum requirements inferred from remote sensing. The inset shows 500m grid data interpolated to a coarse resolution for better visualization of geographic patterns. (B) Heatsum inferred from a common garden experiment (also displayed in A). Symbols represent different ecological regions: △ BC taiga plains, ⬙ AB northern boreal plains, □ AB lower rocky mountain foothills, ◇ AB central boreal plains, ○ SK central boreal plains, ▽ MN boreal shield.
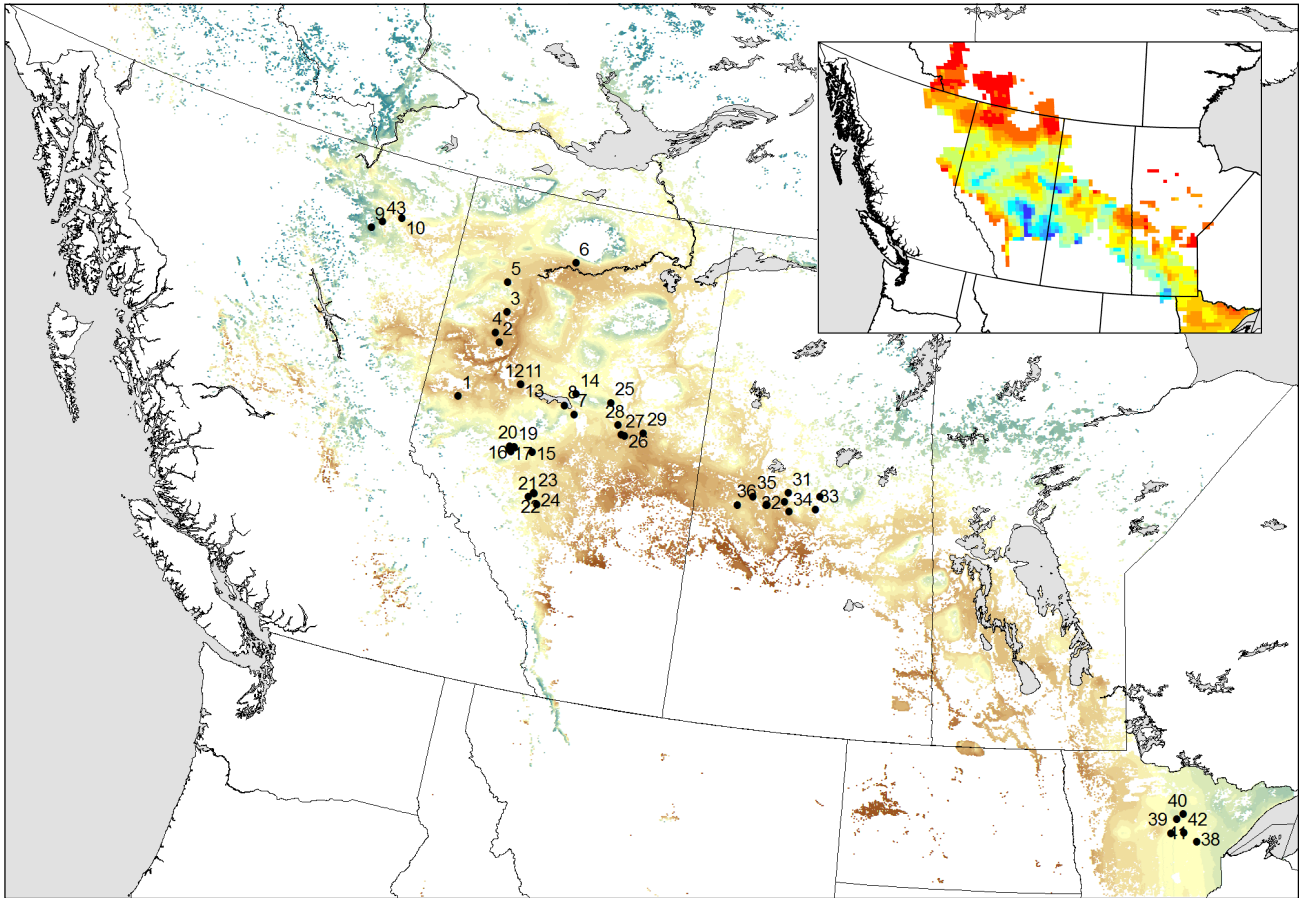
Fig. 4. Annual heat:moisture index (**brown** = dry, **blue** = moist), and required heatsum of aspen provenances for bud break inferred from remote sensing (inset as in Fig 3). Although a statistical analysis of correlations is not valid because of spatial autocorrelations, the geographic pattern appears to be very similar, corroborating correlations between climate variables and provenance data (Table 1).
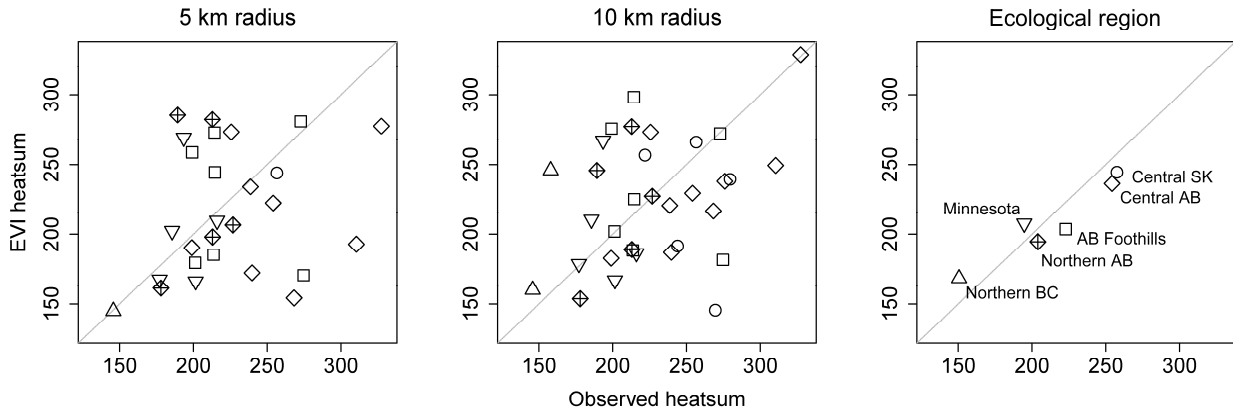
Fig. 5. Correlation between heatsum observed in provenance collections and nearby EVI grid cells. Only high-level geographic summaries (averages by ecological region) are significant (p=0.003).