University of Alberta

Genetic variation in lodgepole pine and interior spruce: adaptation to climate and implications for seed transfer

by

Katharina Julie Liepe

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Abstract

This thesis investigates genetic variation of two commercially important conifers in western Canada, interior spruce and lodgepole pine. The goals were to quantify genetic diversity and geographic structure, to describe multitrait adaptation to local climates, and to use this information for the development of seed zones for Alberta and British Columbia. The study is based on common garden experiments in growth chambers simulating multiple environments. Genetic differences in phenology, frost hardiness and seedling growth were assessed for approximately 250 seed sources. The results show that 85% of the trait variation was found within populations of both species, while only 15-20% of the among-population variation (or 2-3% of the total variation) could be interpreted as multitrait adaptations to different macroclimatic regions. A key finding of this study is a remarkable degree of genetic diversity in climate-related adaptive traits, implying enough evolutionary capacity to adapt to new environmental conditions. Our results indicate that the current seed zones system can be simplified, especially in Alberta. No more than 20 seedzones for each, lodgepole pine and interior spruce, are required to guide reforestation across Alberta and British Columbia, substantially reducing logistics for seed management.

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1. Introduction

Temperate and boreal forest ecosystems of western Canada provide more than 60% of Canada's harvest volume, with lodgepole pine (*Pinus contorta*) and interior spruce (*Picea glauca*, *P. engelmannii* and their hybrids) being the most important forestry species (Canadian Forest Service, 2013). Approximately 220 million seedlings of these two species are planted annually in the interior of British Columbia and in Alberta. Climate change threatens these ecosystems and their economic benefits through direct impacts or insect mediated damage. Mountain pine beetle destroyed more than 50% of all lodgepole pine by volume, affecting about 18 million hectare of pine forest (BC Ministry of Forests, 2013). Other insect pests have caused significant damage as well in recent years: spruce budworm infection peaked in 2001 at 1.6 million hectare of affected or dead spruce forests (Westfall, 2001) and spruce bark beetles reached a maximum in 2003 with approximately 300,000 hectare of damage (Westfall & Ebata, 2012). The fungal disease Dothistrohma needle blight, another endemic disease, has caused unprecedented losses of lodgepole pine stands in northwestern British Columbia (Welsh *et al.*, 2009); the greatest extent of visible damage from aerial surveys was in 2008 with 50,000 hectare (Westfall & Ebata, 2012).

These impacts were often plausibly linked to climate change. Lack of cold snaps in fall and winter allow insect larvae to better survive winter conditions (Carroll *et al.*, 2006), and trends toward moister and warmer summers favor the spread of fungal diseases (Woods, 2011, Woods *et al.*, 2005). In addition, direct climate impacts have been documented with unprecedented heat and drought conditions being the primary causes of forest dieback at the southern fringe of the boreal forests (Allen *et al.*, 2010). According to aerial surveys in this area, 20% of all aboveground biomass represents dead trees killed due to a severe drought in 2001-2002 (Michaelian *et al.*, 2011), and Peng *et al.* (2011) documented increased mortalities for all frequent boreal tree species over the last two decades.

These climate change impacts are associated with warming trends significantly higher than the global average (IPCC, 2007). Western boreal forest ecosystems have experienced increases in mean annual temperature of approximately 1.5°C (IPCC, 2007), and regional changes in precipitation of ±15% in western Canada over the last several decades (Mbogga *et al.*, 2009). The observed warming trends in mean annual temperature match or exceed projections by general circulation models for the 2020s (Hamann *et al.*, 2013). Under moderate emission scenarios (A1B), warming in western Canada is predicted to continue to around 3°C (IPCC, 2007), which raises concerns that forest health and productivity may be compromised even more in the future (Aitken *et al.*, 2008, McKenney *et al.*, 2009).

Millar *et al.* (2007) propose several strategies how resource managers may cope with climate change related challenges to forest management. Resistance and resilience strategies may be applied to highly valued resources and aim at maintaining or restoring current ecosystems if possible. Alternatively, they propose to facilitate transitions to new ecosystems that are a more appropriate match to changed climate conditions. This may involve human assisted migration of species, which has been the subject of much controversy in conservation biology (Marris, 2009, McLachlan *et al.*, 2007). However, in the context of forestry, assisted migration could be restricted to the movement of populations within a species range or somewhat beyond the leading edge, which is less controversial (Aubin *et al.*, 2011, Gray *et al.*, 2011). In reforestation programs for commercial species it has been proposed as a key forest management strategy to maintain forest health and productivity (McKenney *et al.*, 2009, Pedlar *et al.*, 2012, Wang *et al.*, 2006).

Assisted migration of planting stock representing locally adapted populations requires knowledge of ecological genetics of species. For commercial trees, a substantial body of research is available about adaptation of their populations to local environmental conditions (e.g., Morgenstern, 1996). Those genetic differences are reflected in seed zones and seed transfer guidelines that restrict movement of genetic material in reforestation programs (Ying & Yanchuk, 2006). Local adaptations of forest trees are revealed by provenance trials, where seeds are collected throughout the range of a species and grown at one or more test sites, ideally representing the range of planting environments of interest. Forest geneticists have established and maintained large and systematic provenance trial series since the 1950s, with the goal of identifying superior genotypes for reforestation. These trials have emerged as useful climate change laboratories, first noted by Matyas (1994) and Carter (1996). By testing populations from a range of source climates across a range of recipient climates, provenance tests can reveal effects of climatic maladaptation under realistic forest plantation settings.

Based on growth and survival data from provenance tests across multiple environments, response functions for different genotypes or provenances have been developed, which allow predictions of population performance under both current and expected future climates (e.g., O'Neill *et al.*, 2008a, Rehfeldt *et al.*, 2001, Wang *et al.*, 2010). Wang *et al.* (2006) predicted productivity gains of 14-36% among 16 forest management areas of British Columbia by matching optimally adapted populations to planting sites. General transfer guidelines, for example, the movement of 100-300m up in elevation, varying by species and seed planning zone, have been proposed as a climate change adaptation strategy for British Columbia (O'Neill *et al.*, 2008b, Snetsinger, 2009).

In addition to long-term field trials, common garden experiments are often carried out with seedlings or saplings in controlled environments to assess genetic variation in adaptive traits that are not always revealed under field conditions. Adaptive traits include the timing of budbreak and growth cessation, responsible for the synchronization of the growing period with the available growing season. The timing of budbreak is typically controlled by genetically controlled chilling and heatsum requirements (Hannerz, 1999), while photoperiod tracking mechanisms control the timing of budset (e.g., Ekberg *et al.*, 1979). The timing of budbreak and budset is often a trade-off between maximizing use of the available growing season and avoiding frost damage from rare late frosts in spring or early frosts in fall (Leinonen & Hanninen, 2002). Similarly, the onset and degree of cold hardiness in living tissue and wood properties are important adaptations to winter severity and length (Howe *et al.*, 2003, Schreiber *et al.*, 2013). To develop assisted migration prescriptions to address future climate change, it is necessary to assure that when moving planting stock to new geographic locations, their adaptive traits are still appropriate for the current and future environmental conditions at these new planting locations.

Here, we contribute an experimental study to assess geographic variation in adaptive traits. We have to know whether a species can be treated as a genetically more or less homogeneous unit, or whether it consists of many, locally adapted populations. Furthermore, the degree of within-population genetic diversity will indicate whether unmanaged populations have the capacity to adapt by means of natural selection. We investigate patterns of genetic adaptation to local climates and genetic diversity within populations based on a comprehensive sample of approximately 250 commercial seedlots for each of lodgepole pine and interior spruce collected throughout British Columbia and Alberta. Growth and adaptive traits are assessed at the seedling stage and subsequently genetic variation is mapped with a constrained clustering approach that delineates genetically homogeneous populations based on geographic and climatic criteria. The resulting groups are intended to be used for the delineation of seed zones to ensure forest health and productivity. We further quantify within- and among-population diversity using several variance partitioning approaches. This analysis provides a first assessment of the adaptive potential present on the landscape, and we discuss management options for seed transfer to maintain forest health and productivity under current and projected future climate.

2. Literature review

2.1. Climate change in western Canada

Anthropogenic climate change is an established global phenomenon threatening ecosystems, their services and products. Over the last century (1906-2005) global surface temperatures rose on average 0.74°C, with 1998 and 2005 being the warmest years on record since 1850 (IPCC, 2007). The number of frost days reduced in mid latitudes, cold nights became rarer and warm nights more frequent (Trenberth *et al.*, 2007). Precipitation increased north of 30°N, and weather extremes, such as heavy precipitation events, became more frequent, while droughts simultaneously became more intense and longer (Trenberth *et al.*, 2007). These warming trends are expected to become stronger in future. By midcentury global climate models (GCM) predict changes of 1.3° to 1.7°C, and predicted changes for the end of the century vary between +1.8° and 3.4°C, depending on the used emission scenario (B1 or A2) (Meehl *et al.*, 2007). Heat waves are expected to become more frequent and more intense, while the number of frost days will further decrease in middle and high latitudes, resulting in increasing growing season lengths (Meehl *et al.*, 2007).

Compared to the global averages, higher latitudes of the Northern Hemisphere have experienced the greatest warming, especially during winter and spring (Solomon *et al.*, 2007). Arctic temperatures increased twice as much as the global average rate over the last 100 years. During the same time period, British Columbia experienced increases in mean annual temperature of 0.7° or 0.8°C (Hamann & Wang, 2006, Mote & Salathé, 2010), with regional increases of 0.8–1.2 °C in the interior and up to 1.2–1.5°C in the extreme south and north of the province (Walker & Sydneysmith, 2008). Temperatures in Alberta increased on average by 1.6°C (Sauchyn & Kulshreshtha, 2008), with about half this increase occurring in the last 25 years (Mbogga *et al.*, 2009). Weather records indicate up to 20% less precipitation in Alberta and up to 10% less in British Columbia, since 1997, with the exception of the Rocky Mountains and a section of coastal British Columbia, where summer precipitation increased by 20% (Mbogga *et al.*, 2009).

These observed trends are expected to continue: winter warming is projected to increase the most in northern latitudes, with minimum temperatures being expected to increase more than the winter average (Christensen *et al.*, 2007). Spittlehouse (2008) predicts temperature increases of 2–5°C in British Columbia by the 2080s. For Alberta, Barrow and Yu (2005) expect changes in mean annual temperature of on average 0–3°C by the 2050s and 3–5°C by the 2080s. Precipitation models give variable results, arising from uncertainties in cyclone behavior (Christensen *et al.*, 2007). Mote and Salathé (2010) estimate little changes in mean precipitation of +1–2% for the Pacific Northwest, but over 60% of the used GCMs predict greater seasonal variation by the 2080s with wetter autumns and winters (+8%) and drier summers (–14%).

2.2. Observed impacts on forest ecosystems

Over the last several decades climate change impacts on forests have been particularly prevalent at the Northern Hemisphere, affecting forest health, as well as the distribution of species, ecosystems and biomes (Davis & Shaw, 2001, Walther *et al.*, 2002). Increasing forest mortality has been observed, with drought being one of the main causes. Allen *et al.* (2010) documented 88 global examples of forest mortality, driven by climatic and water stress since the 1970s. Worrall *et al.* (2013) mapped episodic aspen (*Populus tremuloides*) declines of about 3.2 million hectares across Canada and the United States between 2000-2010 as a consequence of moisture deficits during preceding severe droughts. In the transition of the boreal to forest ecosystems of Alberta and Saskatchewan, aerial surveys have revealed that 20% of the aboveground biomass is represented by dead aspen trees that were killed as result of a severe drought in 2001-2002 (Michaelian *et al.*, 2011). Remaining living trees had an overall decrease of 30%

in radial growth (Hogg *et al.*, 2008). The analysis of Canada's network of permanent sample points and showed increased mortalities for all frequent boreal tree species (*Pinus banksiana, Picea mariana, Picea glauca, Populus tremuloides*) (Peng *et al.*, 2011).

Aside from direct climate impacts, climate change has also allowed forest pests and disease to take hold in ecosystems, where they have not been problematic before. The large outbreak of the mountain pine beetle (*Dendroctonus ponderosae*) in British Columbia, which destroyed more than 18 million hectare lodgepole pine forest since 1999 (BC Ministry of Forests, 2013) and the beetles spread over the Rocky Mountains into Alberta since 2006, have been associated with increasing winter temperatures and lower frequencies of harsh cold snaps, allowing the insect larvae to better survive winter conditions (Carroll *et al.*, 2006, Carroll *et al.*, 2004). Berg *et al.* (2006) found large outbreaks of spruce bark beetle (*Dendroctonus rufipennis*) that affected about 1.2 million hectare forest in Alaska in the 1990s to be related to warming temperatures that increase winter survival and induce summer drought stress to host trees. In British Columbia the outbreak of this bark beetle species shows a lower but still considerable extent, which peaked in 2003 with approximately 300,000 hectare of damage (Westfall & Ebata, 2012). The spruce budworm infestation (*Choristoneura fumiferana*) reached provincial maxima in British Columbia in 2001 with 1.6 million hectare of damaged spruce and true fir forests and in Alberta in 2003 with 580,000 hectare (Canadian Forest Service, 2013). Besides insect pests, the fungal disease

Dothistroma needle blight (*Dothistroma septosporum*) has an increasing effect on lodgepole pine stands in northwestern British Columbia, where the recent widespread infection has been linked to increases in precipitation and summer temperatures that seem to favor the spread of the fungal spores (Welsh *et al.*, 2009, Woods *et al.*, 2005).

2.3. Annual variation in phenology

Phenology studies recurring biological phases of development throughout the year. Alternating periods of growth and dormancy describe the annual development cycle of forest trees, including important adaptive traits, such as the onset of cold acclimation, budset, budbreak, flowering and fruiting, with the latter two being important in mature trees, but not in the seedling phase. Toward the end of the growing season, the growth of forest trees ceases in response to decreasing day length (Aitken & Hannerz, 2001, Ekberg *et al.*, 1979). The overwintering meristem tissues are formed, i.e. trees set buds. Along with growth cessation, a slow cold acclimation process is induced, which is then followed by a more rapid acclimation once freezing temperatures occur (Bigras *et al.*, 2001, Weiser, 1970). Winter dormancy is induced with growth cessation, starting with a rest stage, during which buds remain inactive, restricted by internal physiological factors, even if they are exposed to growth-promoting conditions (Hannerz *et al.*, 2003). The following transition from rest phase to quiescence requires chilling, which is highly variable among populations and genotypes (Campbell & Sugano, 1979, Leinonen, 1996). High chilling requirements are of particular importance under maritime climates, and have been observed, for example, in Sitka spruce (*Picea sitchensis*) (Cannell & Smith, 1983, Leinonen, 1996). They prevent premature heatsum accumulation and budbreak, if fall and spring temperatures are mild. Populations from continental climates have small, if any chilling requirements, which are completed in November-December (Hannerz *et al.*, 2003).

Once chilling requirements are fulfilled, cold deacclimation, dormancy release and the initiation of primary growth depend in general on the accumulation of a genetically determined heatsum (Hannerz, 1999, Howe *et al.*, 2003). In most conifers budbreak and needle emergence indicate the start of active growth. Pine species, however, have been observed to start shoot elongation first, while the emergence of needles occurs later (Norgren *et al.*, 1996, Van Den Berg & Lanner, 1971). The required threshold temperature and duration of warm temperatures for growth initiation varies both among and within populations; however, the timing typically shows much less variation among provenances than growth cessation and budset, when grown under field or controlled conditions (Aitken & Hannerz, 2001). Chuine *et al.* (2001) estimated threshold temperatures for shoot elongation of lodgepole pine to vary between 4.1° and 6.8°C depending on the seed source location.

Shoot elongation initiates the period of active growth. Conifer species from harsh climate typically have fixed growth patterns, where rapid growth occurs at warm temperatures and long photoperiods. Their terminal shoot elongation ceases as early as midsummer, while needle elongation continues much longer (Bigras *et al.*, 2001). Species from milder climates show free growth patterns, describing a simultaneous formation and elongation of new stem units (Lanner, 1976). This growth pattern can often be observed in first-year seedlings (e.g., scots pine (*Pinus sylvestris*)), being a risky habit; however, it may give a competitive advantage in the highly competitive establishment phase (Repo *et al.*, 2001). In subsequent years the free growth pattern changes to fixed growth.

It is essential that the alternation between growth and dormancy is synchronized with the available growing season in such way that the growing season is used effectively, but also that the timing of cold hardening and dehardening minimizes the risk of damage by late and early frosts (Leinonen & Hanninen, 2002). This results in patterns of adaptive variation among and within populations that can be identified through experimental studies.

2.4. Projected maladaptation of populations

Climate warming that began during the twentieth century is projected to continue, provoking concerns that trees could neither be able to migrate nor to adapt fast enough to keep pace with the predicted velocity of environmental change, and with increasing adaptational lag, forest health and productivity could decrease, even local extinction may occur (Aitken *et al.*, 2008, Davis *et al.*, 2005). Trees are long-lived, bound to a single location for their complete lifecycle. Migration is only possible through the dispersal of reproductive material. Postglacial migration rates have been estimated from fossil pollen and range for most species between 50 to 500 m/yr. White spruce migrated up to 250 m/yr, and jack pine (*Pinus banksiana*), a species closely related to lodgepole pine, up to 400 m/yr (Davis, 1981). Estimated postglacial seed dispersal rates from genetic marker evidence are even lower, with distances less than 100 m/yr (McLachlan *et al.*, 2005, Savolainen *et al.*, 2007).

Migration rates that will be necessary to track habitat under climate warming exceed observed postglacial migration rates by far. Loarie *et al.* (2009) suggest rates of 110 m/yr for temperate forest ecosystems and 430 m/yr for the boreal forest ecosystems by modelling the velocity of temperature change, while Malcolm *et al.* (2002) estimate them to be higher than 1000 m/yr in 35% of the biomes in temperate and boreal forest using two global vegetation models. Hamann and Wang (2006) use a bioclimatic envelope modelling approach to predict potential impacts on forest ecosystems and tree species in British Columbia and estimate even greater rates in suitable habitat gain up to 10 km/yr.

Adaptation describes the process that leads to a better degree to which an organism can live and reproduce in a given set of environments that evolves through means of natural selection (Eriksson *et al.*, 2006). Early models of adaptation assumed directional changes toward a new phenotypic optimum for a single trait under selection (Lynch & Lande, 1993). However, nature is more complex, with overall fitness and local adaptation being a function of multiple traits and dependent on population demographics (Aitken *et al.*, 2008, Burger & Lynch, 1995). Different traits including bud phenology, growth and cold adaptation are related and interact. Genetic trait correlations between traits can be positive, but may also be unfavorable, if increased fitness in one trait leads to a correlated response decreasing fitness in another trait, which would slow evolutionary processes (Etterson & Shaw, 2001). In addition, high gene flow from the center to peripheral populations may inhibit adaptation, if it swamps local adaptation of marginal populations by introducing maladapted genes (Franks *et al.*, 2013).

Transplant experiments that consist of multiple population samples, planted on planting sites with a range of climatic conditions, have revealed patterns of local adaptation in forest trees. Significant among-population variation and steep genetic clines along environmental gradients have been observed (reviewed in Morgenstern, 1996), suggesting a narrow climatic adaptation of individual populations for most conifer species that may render many populations maladapted with the continuation of climate change. Especially the synchronization of annual growth and dormancy cycles shows strong local adaptation, which often results in a genetic trade-off between freezing tolerance and height growth (Loehle, 1998). If trees have a genetically determined growing period, which is shorter than the available growing season, and can’t expand it rapidly, they won’t have competitive growth rates. However, if they start growth too early in the spring or end growth to late in the fall, substantial cold injury may be the result (Aitken & Hannerz, 2001).

Evaluating a comprehensive provenance trail series of lodgepole pine in British Columbia (140 range-wide provenances planted at 62 test sites), Rehfeldt *et al.* (1999), and Wang *et al.* (2006) conclude that local populations already lack behind local optimality in terms of growth potential. They were outcompeted by other populations through higher growth vigor and density dependent selection. White spruce populations in Ontario were found to be optimally adapted to the present thermal conditions, but lacking local adaptation regarding moisture conditions (Andalo *et al.*, 2005).

Models that incorporate population adaptation to estimate the future impact of climate change on growth and productivity are generally pessimistic. Response functions for lodgepole pine that are based on provenance trial data predict that productivity will decline 6–9%, compared to current productivity in British Columbia, if the mean annual temperature increases by 4°C and precipitation by 7%, as it is expected for the 2080s (O'Neill *et al.*, 2008a, Wang *et al.*, 2006). Regional differences are projected to be great, with productivity declines of 31-59% in the currently most productive and abundant interior, while northern areas and higher altitudes will experience increases in productivity (O'Neill *et al.*, 2008a). For white spruce, Andalo *et al.* (2005) predicts maximum decreases in growth of 18% for populations in Ontario, if temperatures increase by the same amount, but precipitation decreases by 10%. According to a bioclimatic envelope model of Hamann and Wang (2006), lodgepole pine, white spruce and Engelmann spruce in British Columbia will significantly decrease in frequency (-24%, -10% and -52% by 2055, respectively) and may lose a large portion of their suitable habitat (-9%, -32% and -49% by 2055).

2.5. Potential mitigating factors

Paleoecological evidence indicates that the geographic ranges of tree species have expanded and contracted several times in response to environmental changes since the last glacial age (Schnabel & Hamrick, 1990). For instance, deciduous tree populations along river drainages of the Great Plains of the USA experienced such range fluctuations (Bryson *et al.*, 1970) without apparent loss of genetic diversity (Schnabel & Hamrick, 1990). Some of the largest changes in climate in the Quaternary of +7°C to 12°C within approximately 50 years were greater than any changes projected for the close future, and species didn't go extinct on the global scale in such adverse periods of changing environmental conditions (Botkin *et al.*, 2007, Macdougall, 2006). A unique combination of characteristics may have allowed trees to withstand past environmental changes and may do so in future: phenotypic plasticity, high within-population variation and the potential for high rates of gene flow.

Due to their longevity, trees can't move to avoid stressful conditions. Their first defense against changing environments is acclimation (Nicotra *et al.*, 2010). This ability, called phenotypic plasticity, allows them to persist for many years at a single location, experiencing seasonal as well as year-to-year climatic variation, and enduring periods of adverse environments (Namkong *et al.*, 2000). Some examples of plasticity are temperature regulated timing of leaf unfolding (Kramer, 1995), varying tree-ring size (McLane *et al.*, 2011) and microdensity (Martinez-Meier *et al.*, 2009), expanded root growth due to drought (Guo *et al.*, 2007), shade avoidance mechanisms in response to competition (Schmitt *et al.*, 2003) or light acclimation (Valladares *et al.*, 2002).

Second, trees have high levels of genetic diversity. Reviewing alloenzyme literature including 620 plant species, of which 322 were woody species, Hamrick *et al.* (1992) concluded that woody perennials have remarkably higher within-population genetic diversity, while genetic diversity among populations is approximately 25% of that of annual plants. Molecular studies that quantified within- versus among-population variation confirm the unequal allocation of genetic variation: in sitka spruce (*Picea sitchensis*) 27% of the total variation resides among populations, in lodgepole pine 16% and in white spruce 10% (McKay & Latta, 2002, Merilä & Crnokrak, 2001). Assessing the variation in quantitative traits (height, diameter, shoot and root weight) of mountain hemlock (*Tsuga mertensiana*) for 12 provenances with 10 families each, Benowicz and El-Kassaby (1999) found 5-15% of the variance attributed to among-population variation, while the remaining variance was attributed to intraprovenance variation. These high levels of local genetic diversity are a fuel for evolutionary change, as natural selection operates by sieving from this genetic variation found within populations (Kremer *et al.*, 2012).

Third, high levels of gene flow through pollen and seed dispersal constantly enhance within-population diversity (Hamrick & Nason, 2000). Yeaman and Jarvis (2006) conclude from a strong correlation between regional heterogeneity and genetic variance (r^2 ~20%) that gene flow and heterogeneous selection contribute to the level of genetic variation within populations. Hence, gene flow increases the genetic variance of a population available for selection (Hamrick & Nason, 2000) and may provide preadapted genotypes that facilitate adaptation (Franks *et al.*, 2013, Jump & Penuelas, 2005, Kremer *et al.*, 2012). In a study of fruit flies (*Drosophila melanogaster*) Swindell and Bouzat (2006) emphasize this positive effect, finding that even limited immigration (migration rate=0.05) among a set of isolated lineages increased their adaptive potential by 30–40%.

In addition, the expected warming is likely to have favorable physiological short-term responses that can be attributed to plastic responses. Already established tree populations may react with an earlier budbreak, if genetically determined heatsum requirements are fulfilled earlier in the spring (Aitken & Hannerz, 2001, Hannerz, 1999). As a result growing seasons will expand, favoring the productivity of the boreal forest, as long as water and nutrients are not limited (McLane *et al.*, 2011). Additional heat is likely to enhance photosynthesis by increasing the content of pigments that increase the photosynthetic rate and decreasing the degree of winter inhibition (Saxe *et al.*, 2001). Furthermore, rising CO_2 concentrations may have a fertilizing effect increasing tree growth rates and carbon sequestration in the short term, as the C_3 photosynthesis is not CO_2 saturated yet (Saxe *et al.*, 2001). The Free-Air CO_2 Enrichment (FACE) project investigates the effect of elevated atmospheric CO_2, finding that trees show significant increases in leaf area index and are more responsive to CO_2 concentrations than herbaceous species (Ainsworth & Long, 2005). However, these increases in biomass production may be reduced once soil nutrients become limited (Millard *et al.*, 2007). Elevated CO_2 could also improve the water-use-efficiency and therefore increase the photosynthetic capacity under drought stress (McLane *et al.*, 2011), although the effect might be negligible otherwise (Hamann & Wang, 2006, Saxe *et al.*, 2001).

2.6. Current strategies to match genotypes to environment

Geographic patterns of genetic variation have practical implications for reforestation programs. To ensure that seedlings are well adapted to the growing conditions of the planting site, seed zones and seed transfer guidelines have been developed as common operational tools to guide seed deployment (Morgenstern, 1996). Seed zones define geographical boundaries for the seed transfer and were originally established based on the long-held assumption that local genotypes are optimally adapted to local conditions (Morgenstern, 1996). However, provenance and progeny testing for commercial tree species indicate that local genotypes may not match their climatic optima (Rehfeldt *et al.*, 2002, Rehfeldt *et al.*, 1999, Wang *et al.*, 2006). To fill this lag, seed transfer guidelines were introduced and further developed based on the ‘floating-point’ principle, restricting seed use based on the climatic distance from collection location to planting site (Morgenstern, 1996, Rehfeldt, 1983).

Both operational tools, seed zones and seed transfer guidelines together, aim to improve productivity, to minimize the risk of maladaptation and maintain forest health, and to accommodate administrative and planning realities of reforestation programs (Morgenstern, 1996, Ying & Yanchuk, 2006). Following these principles, but taking the changing environmental conditions into account, operational seed transfer limits are conceptually an optimization process. In western Canada, various analytical methods have been used to improve seed zone delineations (Campbell, 1979, Crowe & Parker, 2005, Hamann *et al.*, 2010, Hamann *et al.*, 2000, O'Neill & Aitken, 2004) and transfer limits (Parker, 1992, Rehfeldt, 1990, Wu & Ying, 2004) based on information becoming available form provenance trials and practical experience. This is a continuous process, if further scientific knowledge or practical experience provides evidence for an improved conservation of the genetic resources, seed zones and transfer limits can be adjusted (Ying & Yanchuk, 2006).

The forest sector in Canada is regulated provincially, with each province having its own regulations for the seed transfer. Alberta and British Columbia have seed zones for the deployment of seed from natural seedlots and species-specific deployment zones for improved seed with higher genetic worth that span larger areas. In Alberta the movement of seeds from natural stands is currently regulated with a system of 74 seed zones in the forested green zone of the province (ESRD, 2009), which are level 4 subdivisions of the hierarchical Natural Regions and Subregions classification (Natural Regions Committee, 2006). Since environmental conditions limit species occurrence to certain areas, approximately 35 zones are in use for lodgepole pine and 45 zones for interior spruce. In general, free seed movement is only possible within each zone (ESRD, 2009). In addition, Alberta is now starting to produce first generation selected seed that can be deployed in nine species-specific zones for interior spruce and six zones for lodgepole pine (ATISC, 2007a, b).

In British Columbia second generation seed orchards produce seed with a higher genetic worth of approximately 15% (Forest Genetics Council of British Columbia, 2012). Throughout the interior orchard seedlots can be deployed in six seed planning zones for interior spruce and eight for lodgepole pine (Snetsinger, 2005). These zones are subdivided in areas of low and high elevation, which results in eleven zones for spruce and 16 zones for pine, representing climatic conditions that require different adaptive trait combinations. Natural seedlots of all species are divided in 24 zones, of which 21 are located within the distribution of interior spruce and lodgepole pine. The deployment of reproductive material for reforestation is allowed either within the zone where seed were collected, or between adjacent seed zones within the same ecological unit (Snetsinger, 2005, Ying & Yanchuk, 2006). However, fixed boundary seed zones are more used as an auxiliary for floating seed transfer, mainly functioning as units for administrative and planning purposes, as the genetic variation appears to be predominantly clinal in most of British Columbia's commercial tree species according to provenance testing (Ying & Yanchuk, 2006).

In response to the recently observed changes in climate, government agencies in Alberta and British Columbia implemented revisions to their seed zones and transfer guidelines based on preliminary scientific data (O'Neill *et al.*, 2008a). The Alberta Government released interim seed transfer guidelines in 2009, allowing upward and northward transfers across adjacent seed zone boundaries within the natural subregion of origin (ESRD, 2009). Even larger seed transfers may be allowed after a case-by-case approval from the Alberta Tree Improvement and Seed Center. Similarly, British Columbia's Ministry of Forests, Lands and Natural Resource Operations released an amendment in the interim allowing an extended upward transfer of 100–300m (based on species and seed planning zone) (O'Neill *et al.*, 2008b, Snetsinger, 2005, 2009).

And the demand for scientific guidance in the review process of provincial standards is steady. In Alberta policymakers and industry representatives ask for science-based guidelines for the distribution of planting material and the conservation of genetic resources facing changing climate (AFGRC, 2007). In British Columbia, the Tree Improvement Branch, conducts research on climate-based seed transfer itself. This includes the recent establishment of the Assisted Migration and Adaptation Trial (AMAT), as a large-scale provenance trial specifically designed to test climatic adaptation in selectively bred seedlots of eleven native timber producing species (O'Neill *et al.*, 2007, O'Neill *et al.*, 2011).

3. Material and methods

3.1. Seed source selection and characterization

Seedlots were selected to spatially and climatically represent all habitat in which the two species occur in British Columbia and Alberta. We obtained 254 commercial bulk seedlots of interior spruce seed and 281 seedlots of lodgepole pine (Fig. 1) through the provincial seed centers that were donated by many agencies. Each seedlot contains open-pollinated seeds from at least ten female trees in British Columbia and at least 30 female trees in Alberta, according to the provincial seed collection guidelines (ESRD, 2009, Snetsinger, 2005).

We use the common name ‘interior spruce’ for a species complex that includes white spruce (*Picea glauca* [Moench] Voss), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and their natural hybrids. The two species are closely related and hybridize extensively where their distributions overlap (De La Torre *et al.*, 2014), typically along altitudinal gradients with Engelmann spruce at higher elevations in British Columbia and the western part of Alberta (Fig. 1). The species complex is collectively managed as interior spruce in forestry.

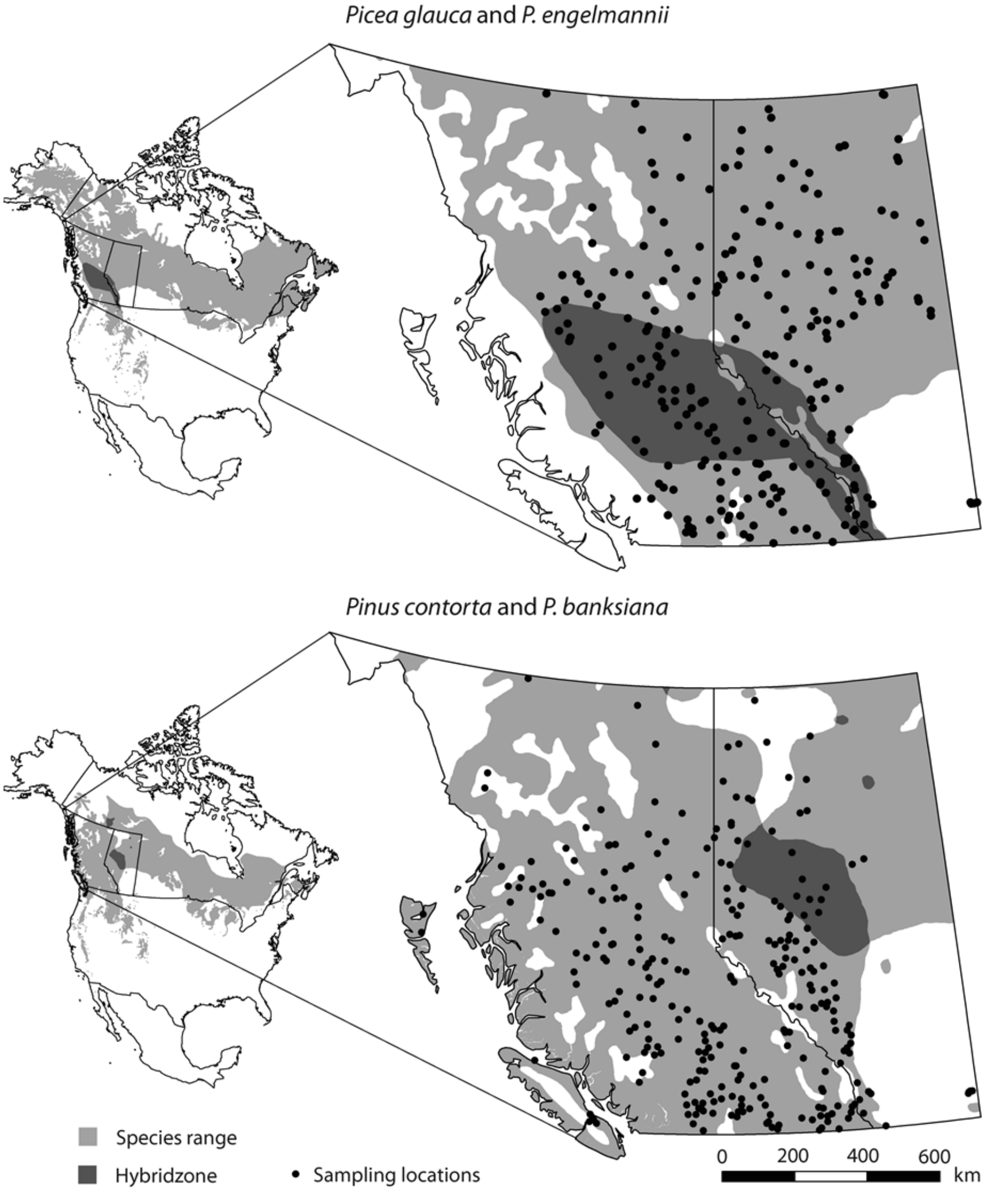

Figure 1. Origin of seed sources for common garden experiments with interior spruce and lodgepole pine. Species distributions and their overlap, representing areas of hybridization, are shown (Critchfield & Little, 1966, Little, 1971). *Picea glauca* and *Pinus banksiana* have boreal range distributions spanning the continent, while the ranges of *Picea engelmannii* and *Pinus contorta* are limited to western North America.

Our lodgepole pine collections focus on the interior variety of the species (*Pinus contorta* Dougl. ex Loud. ssp. *latifolia* [Engelm.] Critchfield). However, we include some samples from the coast (*P. contorta* Dougl. ex Loud. ssp. *contorta*), and some samples from where the species range overlaps with jack pine (*Pinus banksiana* Lamb.) (Fig.1). Lodgepole pine and jack pine may hybridize in north-central Alberta, but the spatial extent and degree of hybridization is still an area of active research (Cullingham *et al.*, 2012).

Seedlots were selected to represent all ecosystems present in British Columbia and Alberta in which the species occurred. Each ecosystem was represented by two to six seedlots depending on the size of the ecosystem and frequency of the species in the ecosystem. We used version 7 of the hierarchical Biogeoclimatic Ecosystem Classification system at the finest delineation of ecosystem “variants” for British Columbia (Meidinger & Pojar, 1991). For Alberta, we used the Natural Regions and Subregions system (Natural Regions Committee, 2006) at the finest level 4, which is approximately equivalent to British Columbia’s ecosystem variants, and hereafter referred to as “variant”. These ecological units are widely applied in resource management, planning and decision making. For analytical purposes we also use higher-level summaries at the level of “ecological zones” in British Columbia, approximately equivalent to “natural subregions” in Alberta.

The seedlots were also characterized climatically using the software package ClimateWNA[1] (Wang *et al.*, 2012), which down-scales climate data from medium-resolution climate grids developed with the parameter-elevation regressions on independent slopes model (Daly *et al.*, 2002). We extracted climate normal data for the 1961-1990 period, which was chosen as a representation of climate prior to a significant anthropogenic warming signal, and because weather station data was most comprehensive for this period. The following biologically relevant climate variables were used in the analysis: mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), continentality (TD, the difference between MWMT and MCMT), degree-days above 5°C (DD>5), degree-days below 0°C (DD<0), mean annual precipitation (MAP), May-to-September precipitation (MSP), precipitation as snow (PAS) and climatic moisture index (CMD), an index representing the sum of the monthly difference between the reference atmospheric evaporative demand and precipitation (Wang *et al.*, 2012).

3.2. Common garden experiments

Four common garden experiments were carried out in walk-in growth chambers (model PGR15 or E-15 from Conviron, Winnipeg) for each species. The four growth chambers had different temperature and moisture regimes. The growing conditions in the different chambers represented climates with mean annual

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[1] ClimateWNA is made freely available at http://cfcg.forestry.ubc.ca/projects/climate-data/climatebcwna/

temperatures of 1°C, 6°C and 11°C, with the warmest temperature regime being divided into two moisture regimes. We do not intend to make inferences on how seedlings respond to these artificial environments, and the growth chambers are therefore not replicated treatments. Rather, we are interested in genotype × environment interactions, induced by different environmental conditions. For analytical procedures and inferences, our growth chamber regimes are therefore equivalent to different provenance test sites in field experiments.

The experimental design in each common garden experiment was an incomplete block design. Incomplete block designs are commonly used in forestry field trials with large numbers of seedlots and a small number of replicates (Williams *et al.*, 2002) and are likewise a suitable design for growth chamber experiments that have limited space, restricting the number of experimental units in a block. Here, we use an α-design algorithm developed by Patterson and Williams (1976) that constructs a resolvable incomplete block design for any number of varieties *v* (seedlots) and block size *k*, so that *v* is a multiple of *k*, giving a high flexibility in the choice of the number of blocks and the number of plots within blocks. In our case, an alpha design was created using Alpha+ (Williams & Talbot, 1993), with four growth chambers (sites). Each growth chamber had 720 seedlings per species that were distributed over eight incomplete blocks with 90 seedlings per block, for a total of 2880 seedlings in each of the interior spruce and lodgepole pine experiments. Therefore, each seedlot was represented by 2–4 seedlings per chamber (mean of 2.5 for lodgepole, 2.8 for interior spruce).

Prior to sowing, seeds were soaked by submersion in distilled H_2O for 24 h, disinfected with a one-minute rinse in 1.5% sodium hypochlorite bleach solution, surface dried and then stratified for approximately 5 weeks at 4°C. Seeds were sown in 49 ml single-tree containers (Stuewe & Sons. Inc.) in a mixture of peat moss (75%) and perlite (25%), and covered with 5–8 mm of 'forestry sand' (Target Products Ltd.) to prevent drying out. Based on germination tests, seed were double or triple sown, and thinned if needed. To induce germination, seed were kept for two weeks in a greenhouse with temperatures of 24/20°C (day/night), moisture was applied by misting (three times a week). The seedlings were then transferred to four different simulated environments in growth chambers, where they were grown for two seasons. During the dormancy period, plant plugs were transplanted into trays (36 × 40 cm, giving each seedling a space of 4 × 4 cm) to allow for more growing space. The soil mixture used in the trays contained peat moss (50%), fine bark (25%) and fine pumice (25%), as it withstands drying out better than the previous soil mixture.

3.2. Growth chamber climate regimes

The temperature regimes for the growth chambers were designed to approximate growing conditions along a north-south climate gradient of the interior plateau of western North America. Seasonal and daily variation in temperature were programmed according to this gradient based on weather station data from Mackenzie, (1°C MAT, 55°N), Williams Lake (3.5°C MAT, 52°N), Merritt, (6°C

MAT, 50°N), Vernon (7.2°C, 50°N), Coeur d'Alene (9.4° MAT, 48°N) and Lewiston, (11°C MAT, 46°N). Monthly averages for these locations were extracted from ClimateWNA (Wang *et al.*, 2012) and interpolated to weekly averages for a period from mid-April to mid-October. This 25 week growing season was used as a baseline climate for the intermediate chamber (6°C). A daily sinusoidal pattern was overlaid on the seasonal variation in two alternating phases: a 3-day warm phase with large temperature variation, mimicking sunny days, and a 4-day cool phase with smaller diurnal fluctuations to mimic cloudy days. The average weekly diurnal variation increased from 12° at the beginning of the growing season to 15°C in the summer, and back to 12°C in the fall. However, daily diurnal variation varied between 8° and 23°C with the smallest values during the cold phases in spring and fall, and the highest values during simulated sunny phases in the summer. An example of the temperature regime for the intermediate chamber (6°C) is provided in Table 1. The climates for the cold (1°C) and warm chambers (11°C) were obtained by adding and subtracting 5°C from the established baseline climate of the intermediate chamber (6°C).

A photoperiod regime equivalent to 54° latitude was applied across all chambers. This represents the central latitude of the two provinces and important commercial forestry areas for lodgepole pine and interior spruce. Photoperiod increased in weekly intervals from 14h in week one to 17 h in week 10 and dropped back to 10:30 h in week 25 (Table 1). The first period of winter dormancy between first and second season was substituted by a compacted six

Table 1. Photo- and thermoperiodic growth chamber regimes of the intermediate chamber (6°C) during the second growing season. Weeks were seven days long, with a 3-day warm phase, followed by a 4-day cold phase. Each day, temperatures varied in a sinusoidal pattern, with maximum temperatures at 1 p.m. (max) and minimum temperatures at 1 a.m. (min).

Week	Photoperiod (h)	Temperature (°C)				
		Weekly average	Warm days		Cold days	
			max	min	max	min
1	13:59	6.1	13.8	1.8	10.8	0
2	14:29	7.2	15.4	2.4	11.9	0
3	15:10	8.1	17.9	2.9	12.9	0
4	15:37	9.2	19.4	3.4	13.9	0.9
5	16:07	10.1	21.4	4.4	13.9	1.9
6	16:29	10.9	23.3	5.3	13.8	2.8
7	16:52	11.7	25.7	5.7	14.2	3.2
8	17:06	12.8	27.3	6.3	14.8	4.8
9	17:14	13.6	29.2	7.2	14.7	5.7
10	17:16	14.4	30.0	8.0	15.0	7.0
11	17:10	15.2	31.3	8.3	16.3	7.3
12	17:00	15.8	31.9	8.9	16.9	7.9
13	16:42	16.1	32.7	9.7	16.7	7.7
14	16:21	16.3	32.9	9.9	16.9	7.9
15	15:51	16.3	32.9	9.9	16.9	7.9
16	15:25	16.2	32.8	9.8	16.8	7.8
17	14:53	15.9	32.0	9.0	17.0	8.0
18	14:25	15.0	31.1	8.1	16.1	7.1
19	13:46	13.8	28.3	7.3	14.3	7.3
20	13:16	12.4	26.9	5.9	12.9	5.9
21	12:42	11.0	25.5	4.5	11.5	4.5
22	12:11	9.6	23.1	4.1	10.6	2.6
23	11:36	8.4	19.3	4.3	9.8	1.8
24	11:06	7.0	17.4	3.4	8.9	0
25	10:31	5.6	15.5	2.5	8.0	0

week chilling period (compared to 27 weeks under natural conditions) with 8 h day length and a constant temperature of 4°C. To more reliably induce dormancy at the end of the second growing season, a five-day period of frost treatments was applied around week 21. Nighttime temperatures were gradually ramped down to –2°C (the coldest setting of the growth chambers) for 2 h on the fifth day of the freezing treatments. Although we could reliably induce dormancy with this temperature and day length regime, it was not possible to simulate realistic frost regimes, which would also rely on appropriate snow cover and soil temperatures.

All treatments were well-watered in biweekly intervals throughout the first season. During the second season seedlings in the warm and dry treatment (11°C dry) were subjected to drought cycles (14 cycles for spruce and 20 for pine), while all other treatments remained well-watered. Consistent water regimes were applied according to tray weights. In spring and fall all pine treatments were watered every five days, while spruce treatments were watered every six days, by adding water until the trays reached a weight of approximately 14 kg for well-watered treatments, and 10 kg for the dry treatments. In the summer well-watered treatments were watered a second time in the middle of each cycle. Following these guidelines, the soil water content of well-watered treatments never dropped below 65% relative to saturation, while the dry treatments experienced a minimum soil water content of 25% relative to saturation. This level had previously been established as corresponding to a soil water potential of –1MPa, a level below which permanent damage starts to appear. In the first season fertilizer was applied with every watering (20-8-20 N-P-K, at 1g/l). During the second season fertilizer was still applied equally across all treatments (20-8-20 N-P-K, at 2g/l to compensate for a decreased frequency), i.e. during the summer well-watered treatments got fertilizer with every second watering, while the drought treatments got fertilizer with every watering.

3.3. Measurements

Height (mm) and root collar diameter (mm) were measured after the second growing season, when seedlings were in dormancy. At the beginning of the second season budbreak was recorded in binary format (yes/no). The observations started earlier in the warm chambers, approximately in week two, whereas the coldest chamber started in week five. For interior spruce, the emergence of needles was recorded and for lodgepole pine the significant swelling and elongation of buds, since it is a better indicator of the start of active growth in this species, while the emergence of needles occurs later (Norgren *et al.*, 1996, Van Den Berg & Lanner, 1971). Budset was measured at the end of the first growing season for lodgepole pine and at the end of the second growing season for interior spruce (due to time constraints). The monitoring of budset started in week 14 at a day length of approximately 16 h, and was recorded in intervals ranging from 3-10 days, depending on the observed rate of budset. The binary data of both budbreak and budset was transformed into a day of season, with the first day of season being equivalent to the first day of the growth chamber season.

Cold hardiness was assessed by artificial freeze testing using the electro-conductivity method described by Hannerz *et al.* (1999) carried out for three freezing temperatures. These test temperatures were chosen based on preliminary tests one week before the full test, aiming for maximum variation of cold injury among populations. The ideal freezing temperatures for lodgepole pine were –10°, –13° and –16°C across all four environments, but different temperatures were chosen for interior spruce: –10°, –13°, –16°C for the cold chamber; –16°, –20°, –24°C for the intermediate chamber; and –10°, –14°, –18°C for the two warm chambers. Only one chamber could be tested per week, hence the different temperatures.

For the freeze testing process, needles were collected, rinsed in distilled water and cut into 5 mm segments (both ends cut). Five needle segments were then placed in each test vial with 0.2 ml of distilled water, and a few grains of silver iodide were added to facilitate ice nucleation. Samples were placed in a programmable Tenney Environmental test chamber (model T20C-3) and held for several hours at 4°C to equilibrate. Control vials were then removed from the chamber and stored at 4°C. After the removal of the control vial, the temperature was reduced at the rate of 4°C/h to the first freeze test temperature, and then held constant for 1 h. Sample vials for that test temperature were removed and placed in a refrigerator at 4°C to thaw. The temperature of the remaining vials was reduced again until the next lower test temperature was reached, and the process was repeated for three test temperatures. After thawing for 2 h in the refrigerator, an additional 3.3 ml of distilled water was added to each vial. Vials were refrigerated at 4°C for approximately 20 h, then placed for 1 h on a gravity shaker at room temperature before conductivity was measured with a digital conductivity meter model 2052 (VWR). The vials were then placed in the environmental chamber at 95°C for three hours to heat kill the samples and remeasured for maximum conductivity.

For the control samples, the same procedure was followed, except that the freezing step was replaced by a refrigerator step (4°C).

An index of injury was calculated for each sample according to Flint *et al.* (1967):

$$(1) \quad I_t = \frac{100(R_t - R_0)}{(1 - R_0)} \quad \text{with} \quad R_t = \frac{L_t}{L_k} \quad \text{and} \quad R_0 = \frac{L_0}{L_d}$$

where I_t is the index of injury (%), R_t is the relative conductance of the sample exposed to freeze temperature t, and R_0 is the relative conductance of the control treatment. L_t is the conductance of leachate from the sample after freezing and L_k is the conductance of the leachate after the heat kill of the sample. L_0 is the conductance of leachate from the unfrozen control and L_d is the conductance of the leachate after the heat kill of the unfrozen control. This calculation results in controls having an implied frost damage of zero. The heat-killed samples are assigned a reference value of 100, representing the complete destruction of the membranes between symplast and apoplast, and the freeze-tested sample normally falls in between these boundaries, representing different degrees of frost damage and subsequent electrolyte leakage.

In order to express frost hardiness as a single variable, the two freeze treatments that resulted in close to 50% average damage were used (the additional third treatment did not improve correlations with climate of the origin of samples). In our case, the two colder freeze temperature assessments were averaged using the least squares means method to account for some missing values. The linear model was implemented with the MIXED procedure of the SAS statistical software package (SAS Institue Inc., 2008) with seedlot, and seedling ID as model effects, and analyzed for each growth chamber separately.

3.5. Statistical analysis

An analysis of variance was conducted for all traits to determine the effect of the experimental design factors (block, location within block specifying whether the seedling is located at border), and to quantify genetic effects (variation among provenances), environmental effects (variation among growth chambers), and their interactions according to the following model:

$$(2)\quad Y_{ijkl} = \mu + G_i + E_j + (G * E)_{ij} + B(E)_{jk} + L(B)_{kl} + e_{ijkl}$$

where Y_{ijkl} is the phenotypic observation of a trait made for the ith genotype (G) grown in the jth environment (E), located in the kth block (B) within environment E and at the lth location (L) within block. $G * E$ represents the genotype by environment interaction (G×E), μ is the overall experimental mean and e the experimental error (residual). All model terms were considered random effects. Variance components and their standard errors were obtained using PROC MIXED with the option COVTEST of the SAS statistical software package (SAS Institue Inc., 2008).

As an alternative variance partitioning approach, we also use multivariate regression tree (MRT) analysis, which is a constrained clustering method that partitions variance in one dataset (trait measurements for provenance) based on criteria of another dataset (climatic or geographic variables of provenance origins) according to De'Ath (2002). This analysis links genetic variation to predictor variables that may be the cause of genetic differentiation. The analysis iteratively partitions the response dataset into two homogeneous groups (similar trait measurements) based on the criteria in the predicting dataset (e.g., cold versus warm, northern versus southern source environments). This analysis was conducted with the *MVpart* package version 1.6-1 (R Development Core Team, 2013).

Prior to this analysis, means of provenances were normalized, i.e. expressed in units of standard deviations from the overall growth chamber mean, and missing values were imputed according to Hamann *et al.* (2010). As predictor variables we use the climatic characterization of the seedlot origins, as well as ecosystem variants. The climatic variables were used to infer adaptation of local populations to their environments, while the same analysis with ecosystem variants as predictors was meant for assembling seed zones that contain similar genotypes. In the latter analysis, the total number of ecosystem variants (approximately 115) was too large to test all possible permutations for candidate splits. Therefore, the analysis was carried out in two steps, first partitioning by zone and subsequently by variant. For conciseness, we do not show results of individual chambers in the regression tree analysis results because the previous variance component analysis revealed low interactions between genotype and environment. Instead, means across all chambers are shown in figures.

4. Results

4.1. Genetic and environmental variation

The analysis of variance indicated that main effects due to different growth chamber environments were large in most cases with values up to 94% in the trait budbreak (Table 2 and 3). (Note that budbreak is directly controlled by temperature and therefore simply reflects different temperature programming of chambers.) Excluding the main effects of the growth chambers, the largest variance component in all traits of both species was the provenance or genotype main effect. The interaction term between genotype and environment (G × E) was substantially smaller for interior spruce (about 12 to 40% of the genotype main effect), and largely absent in lodgepole pine (Table 2 and 3). The experimental design factors block and border generally accounted for little variance, reflecting relatively homogeneous growth chamber environments.

Table 2. Variance components for five phenotypic traits of interior spruce. The components are calculated based on a mixed model, with all factors being considered random effects. Standard errors are given in brackets.

	Variance components (%)				
Source of Variance	Height	Diameter	Budbreak	Budset	Cold injury
Genotype (G)	9.3 (1.3)	11.7 (1.8)	0.5 (0.1)	14.8 (2.1)	36.6 (4.1)
Environment (E)	35.9 (29.7)	13.1 (11.2)	93.3 (76.2)	17.2 (14.2)	0.3 (0.9)
G × E	3.9 (1.2)	3.9 (1.8)	0.2 (0.1)	5.4 (1.9)	4.5 (2.1)
Block (B) within E	3.1 (1.1)	4.0 (1.4)	0.2 (0.1)	0.6 (0.5)	2.4 (1.3)
Location (L) within B	1.4 (0.7)	2.3 (1.1)	0.1 (0.1)	0.0 (0.2)	3.9 (2.0)
Residual	46.4 (1.6)	65.1 (2.4)	5.6 (0.2)	62.0 (2.4)	52.3 (2.3)

Table 3. Variance components for five phenotypic traits of lodgepole pine. The components are calculated based on a mixed model, with all factors being considered random effects. Standard errors are given in brackets.

	Variance components (%)				
Source of Variance	Height	Diameter	Budbreak	Budset	Cold injury
Genotype (G)	11.7 (1.6)	4.2 (1.0)	0.6 (0.1)	21.3 (2.7)	12.0 (1.9)
Environment (E)	28.1 (23.2)	19.3 (15.9)	93.9 (76.7)	1.9 (1.6)	12.5 (11.3)
G × E	2.0 (1.4)	0.0 (0.0)	0.3 (0.1)	0.0 (2.1)	0.0 (0.0)
Block (B) within E	1.5 (0.6)	0.8 (0.5)	0.1 (0.0)	0.2 (0.4)	5.5 (2.3)
Location (L) within B	6.5 (2.6)	2.3 (1.1)	0.0 (0.0)	0.2 (0.3)	2.5 (1.5)
Residual	50.1 (1.8)	73.4 (2.1)	5.1 (0.2)	76.4 (2.9)	67.6 (2.3)

To better evaluate within- versus among-population variance components, we also expressed the genotype main effect as a proportion of the genotype plus the within-population residual variance components (Table 4). The among-population variance was around 10-20% for both species, except for very high genetic differentiation in cold injury of interior spruce (41%). As a typical example of geographic patterns of genetic variation, we display cold injury of lodgepole pine with 15% among- and 85% within-population variation. The map represents the average cold injury for each seedlot across all four chambers (Fig. 2). Although a latitudinal gradient is clearly visible, it is also notable that very susceptible seedlings can be found in the far north, subarctic ecosystems of Alberta, while extremely hardy individuals can be found in bulk seed collections from southern British Columbia, which can approach hot desert-type environments.

Table 4. Among- and within-population variance components for interior spruce and lodgepole pine. The effects of environment, genotype × environment interaction and experimental design were removed, to express the genotype main effect as proportion of the genotype plus the within-population residual component. Standard errors are given in brackets.

	Variance components (%)				
Source of Variance	Height	Diameter	Budbreak	Budset	Cold injury
Interior spruce					
Among populations	16.6 (2.4)	15.2 (2.4)	7.4 (1.7)	19.3 (2.7)	41.1 (4.6)
Within populations	83.4 (2.8)	84.8 (3.1)	92.6 (3.1)	80.7 (3.1)	58.9 (2.6)
Lodgepole pine					
Among populations	19.0 (2.5)	5.4 (1.3)	10.9 (2.0)	21.8 (2.7)	15.0 (2.4)
Within populations	81.0 (3.0)	94.6 (2.7)	89.1 (3.1)	78.2 (2.9)	85.0 (2.9)

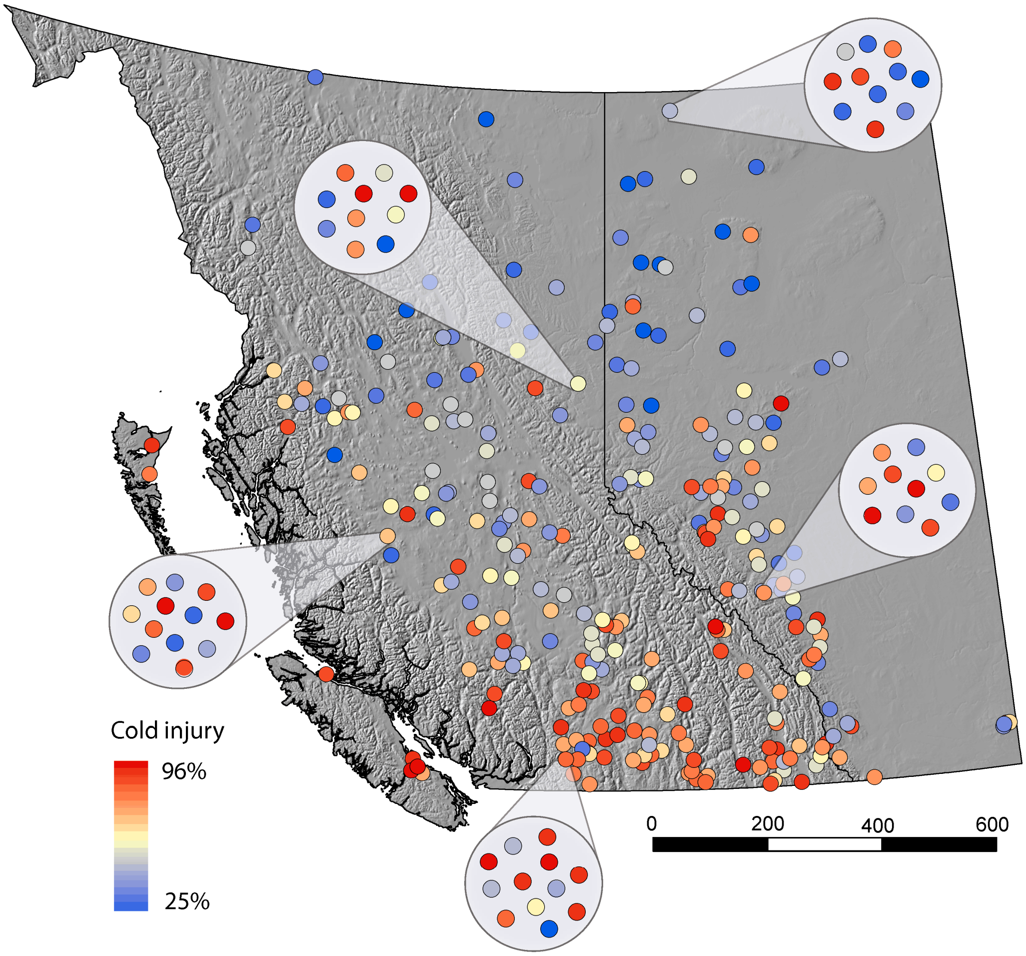

Figure 2. Cold injury of lodgepole pine populations. Each point on the landscape represents the average expression of all individuals from a given seedlot across all growth chamber environments. Five inserts show the makeup of that average, revealing high within population variation.

4.2. Variance partitioning by climate of origin

Among-population variation was further partitioned with a nonlinear approach, the multivariate regression tree analysis. Using climate variables as partitioning criteria in the MRT analysis, populations of interior spruce are split into six groups (Fig. 3a). Overall the tree explains 22% of the variance in the dataset, compared to an average of 20% in Table 2. The first split separates sources using the partitioning criterion mean coldest month temperatures (MCMT), approximately describing a separation by the Rocky Mountains. The leaf charts at the nodes of the dendrogram describe means for groups of similarly adapted seedlots in the five traits height, diameter, budbreak, budset and cold injury. All trait values are expressed as standard deviation from an overall mean of zero, and therefore upward bars are interpreted as above-average height, diameter and frost injury, as well as later budbreak and later budset than average.

In spruce, the first node to the left represents 95 provenances from low minimum temperature origins, which show average height growth, slightly below-average diameter, early budbreak, approximately average budset, and low cold injury. The subsequent split to the right singles out a subset of ten provenances from this group with very poor growth, and very early budset that are characterized by low winter minimum temperatures but in addition also by a less continental climate (driven by cool summer temperatures – these are high elevation provenances from Alberta). The remaining 85 sources come from the boreal plains. Following all splits toward the right, we arrive at a provenance group from environments with

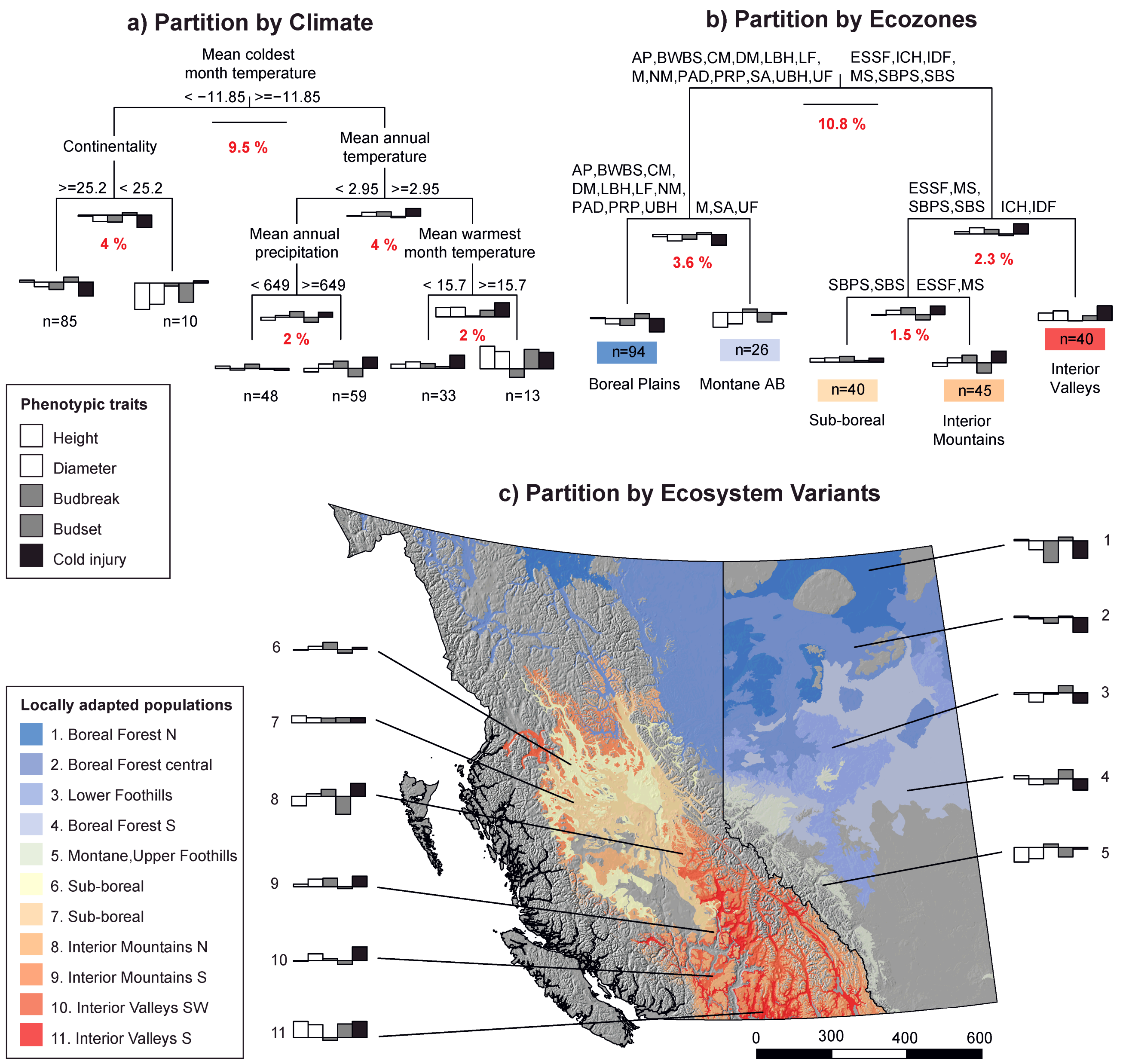

Figure 3. Geographic patterns of genetic adaptation to climate in interior spruce. Multivariate regression tree analysis was used to partition the genetic dataset by climate (a), and by ecozone (b). The spatial extent of the groups, resulting from the partition by ecosystem variant (c), is displayed across British Columbia (BC) and Alberta (AB). In gray scale colored bars represent group means expressed in deviation from an overall mean of zero (horizontal line). Abbreviations in the ecozone partitioning (b) represent the second level of Alberta's Natural Regions and Subregions classification (A, Alpine; SA, Subalpine; M, Montane; CM, Central Mixedwood; DM, Dry Mixedwood; NM, Northern Mixedwood; BSA, Boreal Subarctic; PAD, Peace-Athabasca Delta; LBH, Lower Boreal Highlands; UBH, Upper Boreal Highlands; AP, Athabasca Plain; LF, Lower Foothills; UF, Upper Foothills; FP, Foothills Parkland; PRP, Peace River Parkland) and the ecological zones of British Columbia's Bioclimatic Ecosystem Classification (BWBS, Boreal White and Black Spruce; SBPS, Sub-Boreal Pine-Spruce; SBS, Sub-Boreal Spruce; ESSF, Engelmann Spruce –Subalpine Fir; MS, Montane Spruce; IDF, Interior Douglas-fir; CDF, Coastal Douglas-fir; ICH, Interior Cedar-Hemlock; CWH, Coastal Western Hemlock).

warm winter, annual, and summer temperatures. Those provenances originate from the interior valleys of British Columbia, and they are characterized by very high growth, long growing season utilization, but also high cold injury. The remaining groups are 33 provenances from the interior plateau of British Columbia with cooler summers, 59 provenances from higher elevations with higher precipitation, and a group of 48 provenances from interior British Columbia from overall cooler and drier locations.

Using ecozones as partitioning criteria (Fig. 3b), we obtain similar results as in Fig. 3a. The interior spruce provenances are split into five groups, explaining 18.2% of the variance. The two groups at the internodes after the first split have the same characteristics as in the partitioning by climate. They separate further into groups that represent five major geographic regions: the boreal plains, montane Alberta, the subboreal, the interior mountains and the interior valleys (Fig. 3b). Further subdivision of the groups, using 115 ecosystem variants as partitioning criteria, results in eleven groups for spruce. Notable subgroups are provenances from the boreal subarctic with very low cold injuries and a very early budbreak in common gardens (Fig 3c, group 1), montane populations from Alberta and British Columbia, which are characterized by a short growing season with late budbreak and early budset (groups 5, 8 and 9). On both sides of the Rocky Mountains there are gradients in cold injury increasing from the north toward the south (groups 1–5 and groups 6–11).

In lodgepole pine, either climate or ecological zones as partitioning criteria identify five groups that explain 14% of the variance. Similar to spruce, genetic differentiation is mainly driven by temperature variables, and high elevation sources are partitioned out by a high value for precipitation (far left group in Fig 4a and 4b). Another consistent group at the zone level are sources from coastal BC with late budbreak, late budset and high cold injury (far right groups in Fig 4a and 4b). For other regions, climate constraints and geographical constraints produce somewhat different main groups, although there is some correspondence between the second climate group from the left (n=21) with the dry mixedwood region in Alberta. The two remaining climate groups, n=83 and n=53, represent a continuum from higher to lower elevation located across interior British Columbia, while the ecological zone criteria partition out higher elevation sources from both British Columbia and Alberta into one group (second from left). Further subdivisions by ecological variants produce a few notable groups, such as the group from the dry mixedwood region of Alberta with good growth and very low cold injury that corresponds to the hybrid zone with jack pine. The large sub-boreal group (n=125) splits into three groups that correspond to the same continuum from low to high elevation across the interior plateau, which is represented by the two climate groups 3 and 4 (n=83 and n=53) in Fig 4a.

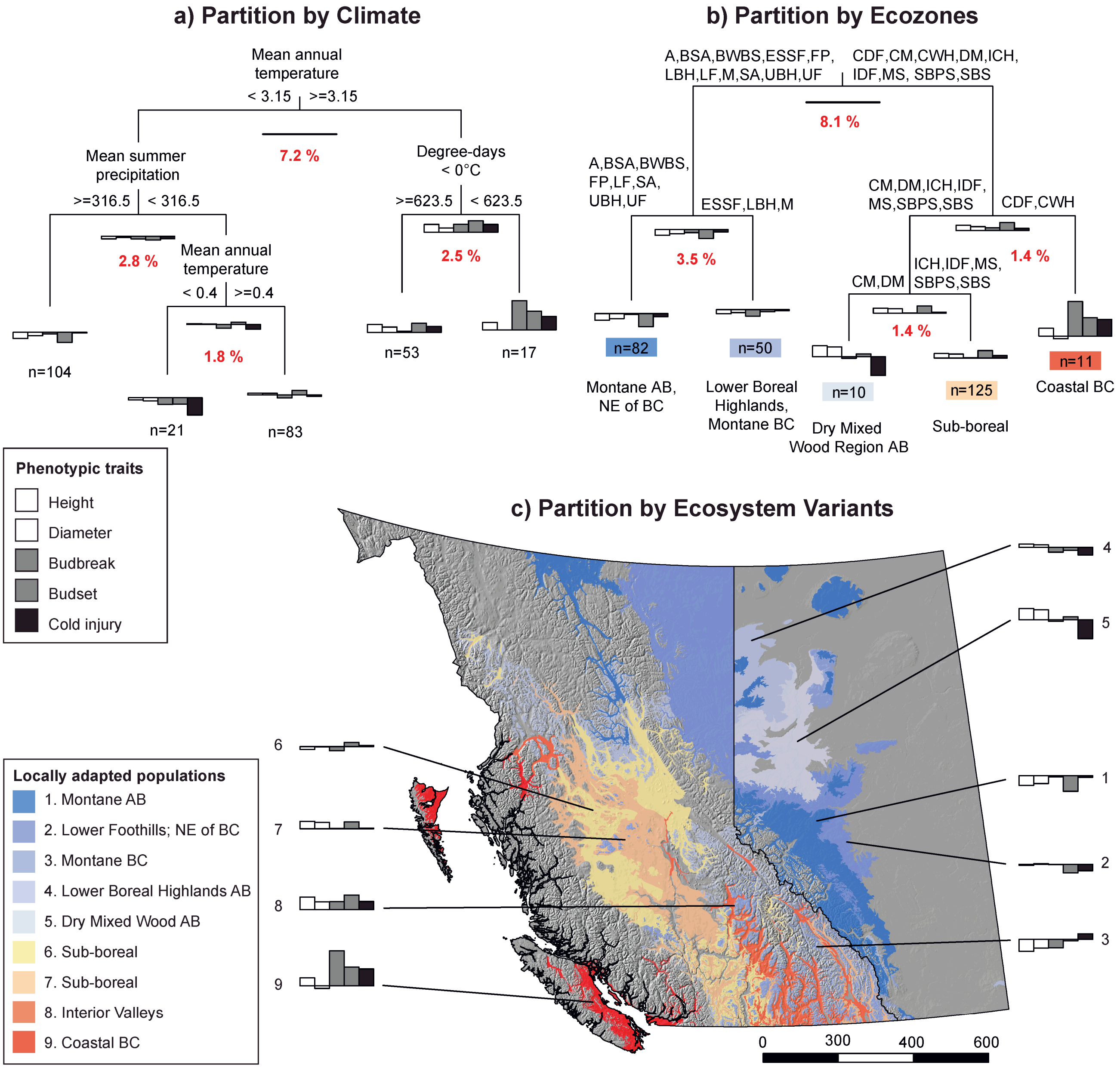

Figure 4. Geographic patterns of genetic adaptation to climate in lodgepole. Multivariate regression tree analysis was used to partition the genetic dataset by climate (a), and by ecozone (b). The spatial extent of the groups, resulting from the partition by ecosystem variant (c), is displayed across British Columbia (BC) and Alberta (AB). Red numbers indicate the variance explained by a particular split. In gray scale colored bars represent group means expressed in deviation from an overall mean of zero (horizontal line). Explanations for the abbreviations in the partitioning by ecozone are given in Fig. 3.

4.3. Simple linear correlations between traits and climate

In addition to these multivariate regression tree analyses, we also conducted some straightforward checks by means of simple correlation coefficients between all measured traits and climate variables used in the analysis, as well as latitude and elevation of the source locations. In general, the variance explained by linear correlations are low ($r^2 < 0.2$), but not inconsistent with the values of variance explained by the regression tree analysis (Fig. 5 and 6). The average variance explained across all traits and chambers is highest for the same climate variables that drive the first splits in the climate regression trees. For interior spruce mean coldest month temperature explains with on average 10.8% the most variance, which closely agrees with the variance explained in the first split of the climate regression tree (Fig. 3a). The same is the case for lodgepole pine; mean annual temperature explained half the variance in the climate partitioning (Fig. 4a), compared to a value of 8.9% across all traits in the correlation analysis.

For the growth traits height and diameter, both species show the strongest correlations with climate variables that are associated with warm and long summers (mean warmest month temperature and degree-days above 5°C) and elevation (Fig. 5 and 6), although diameter in spruce does not conform. Cold and long winters (mean coldest month temperature, degree-days below 0°C) and latitude, are strongly correlated with cold injury in both species, with the highest values being observed for interior spruce (Fig. 5), which conforms to the previous

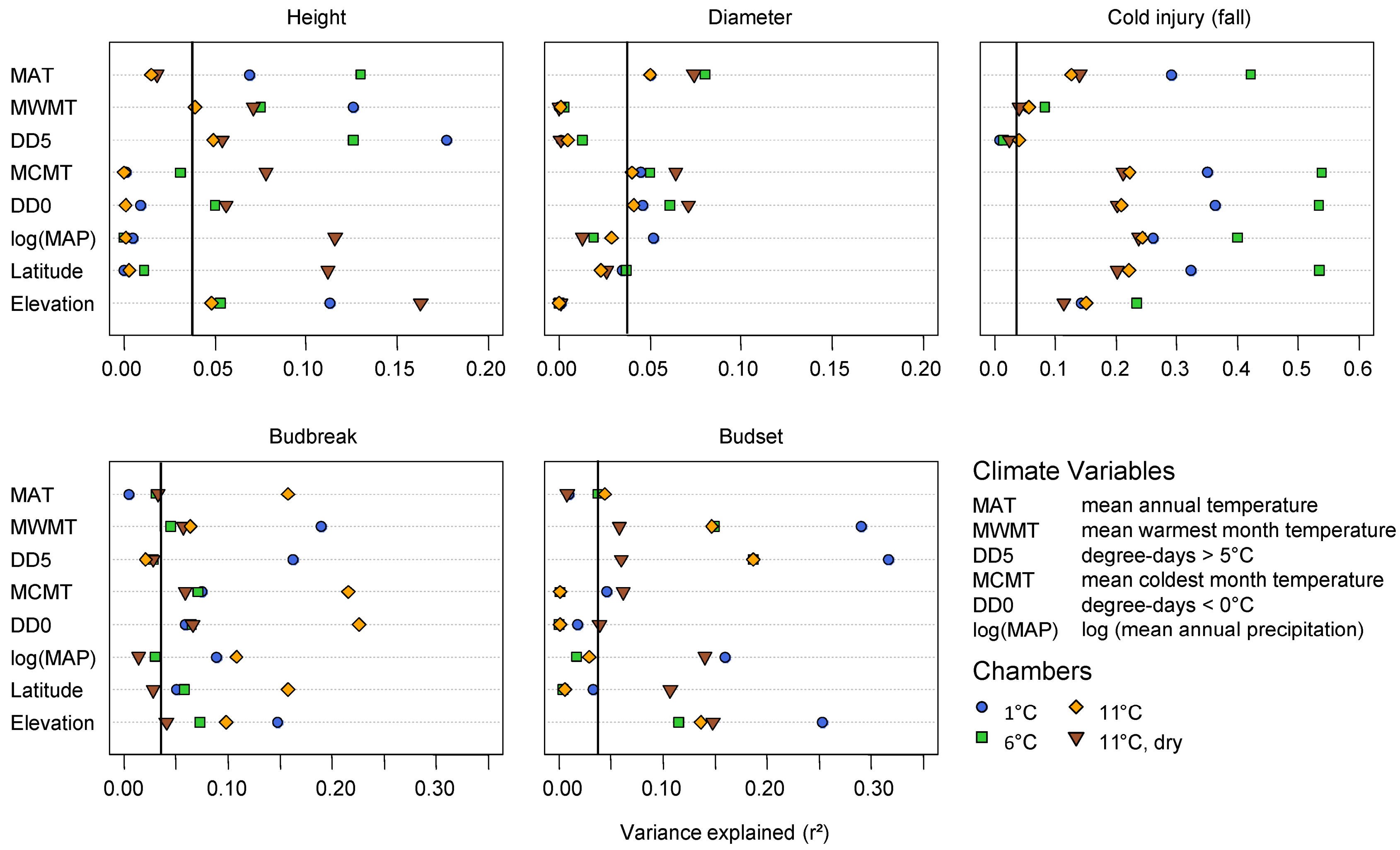

Figure 5. Interior spruce variance explained by source climate and geography. The dot charts display the variance explained (r^2), i.e. the strength of the Pearson's correlation coefficients between measured phenotypic variation and the climatic conditions present at the source locations, as well as latitude and elevation. The vertical line in each chart represents the critical value of $r^2=0.029$ for df=252 and $\alpha=0.0063$ after the adjustment (Bonferroni) for eight multiple inferences.

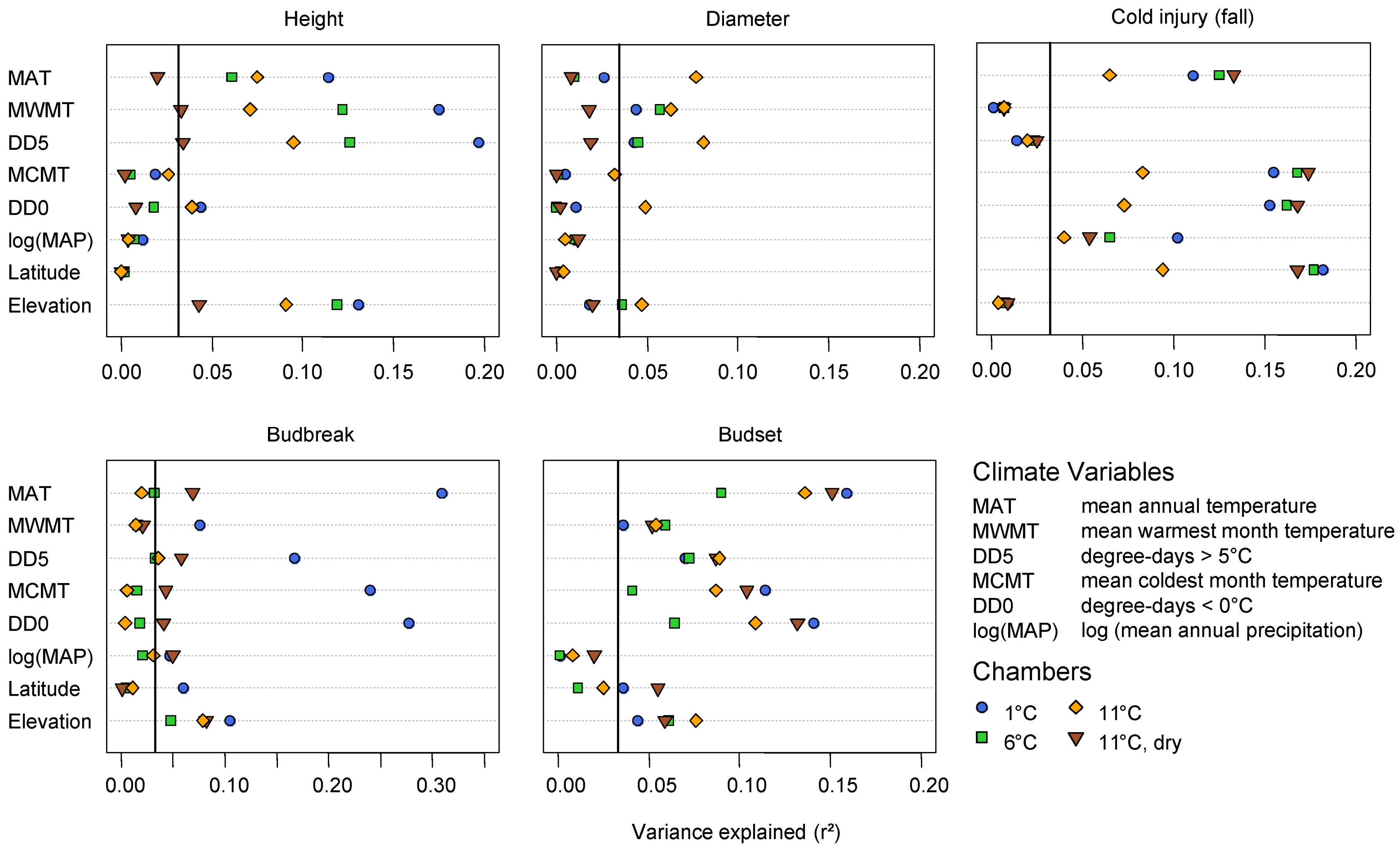

Figure 6. Lodgepole pine variance explained by source climate and geography. The dot charts display the variance explained (r^2), i.e. the strength of the Pearson‘s correlation coefficients between measured phenotypic variation and the climatic conditions present at the source locations, as well as latitude and elevation. The vertical line in each chart represents the critical value of r^2=0.026 for df=279 and α=0.0063 after the adjustment (Bonferroni method) for eight multiple inferences.

variance component analysis (Table 4). Regarding the phenology traits budbreak and budset, linear correlations with climate variables appear idiosyncratic. The most consistent response can be seen in budset for pine (Fig 6), where mean annual temperature and degree-days below zero explain the most variance across all chambers. But this result is opposite to spruce, where mean warmest temperature and degree days above five show the strongest correlations.

5. Discussion

5.1. High within-population variation in adaptive traits

Although not unusual for forest trees, this study documented a strikingly high level of within-population diversity in growth and adaptive traits. With the exception of one trait in one species, genetic population structure over a wide range of environments accounted only for around 15% (Table 4), and a corresponding visual example (Fig. 2) showed that genotypes adapted to extreme cold environments could be found in near-desert conditions in southwestern British Columbia, while genotypes that apparently lack any degree of hardiness were present in a sample from subartic climate in northeastern Alberta. High within-population genetic diversity is likely to be maintained across the heterogeneous forest landscape by gene flow (Campbell *et al.*, 1999, Yeaman & Jarvis, 2006).

However, it is important to note that not all of the within-population diversity that we observed in this study implies an evolutionary capacity to adapt to new climate conditions. Some of the residual variance includes measurement errors and developmental noise. Also, epistatic and dominance genetic variation do not contribute to genetic gain following natural selection. Only additive within-population genetic variation reflects adaptive potential under directional selection. Our study could not quantify the proportion of additive genetic variation that contributes to the observed within-population variance for lack of family structure. However, based on other studies, heritabilities for the adaptive traits that we measured are generally high. For example, Nienstaedt (1985) estimated a narrow sense heritability (h^2) of 0.70 for bud burst of white spruce in a field trial with 92 families. Other forest trees with similar life histories and ranges have equally high budbreak heritabilities. Norway spruce (*Picea abies*) showed narrow sense heritabilities of 0.49–0.65 (Sonesson & Eriksson, 2003), and Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*) had a heritability of 0.69 in a similar seedling experiment (El-Kassaby & Park, 1993). Budset shows a broader range of heritabilities, with 0.51–0.83 for Norway spruce, (Sonesson & Eriksson, 2003), and 0.16–0.81 for Douglas-fir (Aitken & Adams, 1995a, Aitken & Adams, 1995b, O'Neill *et al.*, 2001). Growth traits generally have low heritabilities in field trials (typically between 0.10 and 0.35 in forest trees), but they tend to be high in growth chamber experiments, such as ours, with heritabilites of 0.25–0.8 (Jonsson *et al.*, 2000, Sonesson & Eriksson, 2003, Sonesson *et al.*, 2002).

We therefore conclude that much of the within-population variation that we documented in this provenance experiment is likely to be additive genetic variation, implying a substantial amount of evolutionary capacity of local populations to adapt to new environmental conditions.

5.2. Geographic patterns of adaptive variation

Around 15-20% of among-population genetic structure could be explained by climate or geographic variables by either multivariate regression tree analysis (Fig. 3 and 4) or linear correlations (Fig. 5 and 6). Again, this indicates a high level of genetic variation that cannot clearly be linked to adaptation to specific environments, but that likely reflects high levels of gene flow introducing non-optimal genotypes to all populations. If we consider that about 85% of the phenotypic variation resides within populations, and only around 15-20% of the among-population variation can be linked to climate, then only 2-3% of the total phenotypic variation is explained by climate. Even if we assume that half of the phenotypic variation is in fact additive genetic variation, still only around 4-5% of the genetic variation could be attributed to macroclimatic conditions in this study. Despite this high level of unexplained variation in growth and adaptive traits, there were clear patterns of interpretable local adaptation in multitrait combinations that were consistent, regardless of whether climate or geographic delineations were used as partitioning criteria.

Multitrait combinations in interior spruce that have apparent adaptive value include adaptations to continental climate with harsh winters across the boreal plains: high cold hardiness in combination with early budbreak and late budset reflects rapid transitions from cold winter temperatures to suitable growing conditions in early spring with relatively low risk of frost once a certain heatsum in spring is reached. Under the most northern boreal conditions (group 1 in Fig. 3c), this trait combination is most obvious with an extremely early budbreak for a given heatsum in a controlled environment. These genotypes are adapted to immediately respond to warming in spring to make the most of a very limited growing season. Lodgepole pine's range is restricted to boreal highlands and foothills that do not have an extremely continental climate. The populations closest to boreal conditions (groups 4 and 5, Fig 4c), however, show similar tendencies in frost hardiness and phenology to spruce.

Montane populations of spruce (groups 5, 8 and 9 in Fig 3c), show a different combination of growth and adaptive traits in a common garden environment. Relative to other provenances, all high elevation sources from Alberta and British Columbia are the opposite in phenology and hardiness to boreal populations. They break bud late, set bud early, do not have strong tolerance to frost, and tend to be poor growers. We interpret this trait combination as an adaptation to a long-lasting snow cover that serves as a protective layer against frost. Once the snowpack has melted, there is no need for cold protection and also no need for a particularly low or carefully fine-tuned heatsum requirement. By the time snow has melted, very warm temperatures will rapidly force dormancy release. Regarding budset, an early cessation for a given day length makes sense as well for high elevation conditions, where the growing season ends earlier than in valleys. In a common garden setting, the limited utilization of the available growing season puts high elevation sources at a disadvantage and we see reduced growth in both species.

Sources from the sub-boreal interior plateau of British Columbia seem to represent average genotypes in our study, which is not surprising because they come from intermediate climate conditions and a large number of our samples originate from this region in both species. Genotypes start to divert from this average toward the southern interior valleys in spruce and pine, and towards the coastal range of pine where the species experiences the warmest and most maritime climate conditions. In both species, populations from the interior valleys grow best (the pine group from Alberta's dry mixedwood being the only exception), which can be interpreted as an investment of resources to compete for light in more favorable growing environments with higher interspecies competition. Investments in frost hardiness are low for both species in these regions.

Lodgepole pine populations in the coastal environment stand out by having an exceptionally late budbreak, likely caused by an additional chilling requirement that needs to be fulfilled before heatsum accumulation in spring. Such a chilling requirement is common for species or provenances from maritime climates, and have been observed for Sitka spruce (Cannell & Smith, 1983, Hannerz *et al.*, 2003) as well as maritime provenances of Scots pine (*Pinus sylvestris*) and silver birch (*Betula pendula*) (Leinonen, 1996). They prevent trees from flushing in midwinter due to regular occurrence of forcing temperatures above 5°C under coastal climate. It should also be noted that these populations belong to the coastal subspecies *Pinus contorta* ssp. *contorta* as opposed to the interior subspecies *P. contorta* ssp. *latifolia*.

5.3. The role of hybrid zones in adaptation

Our study area comprises two closely related spruce species, white and Engelmann spruce, and their hybrids. The boreal plains are pure white spruce, while the complex terrain throughout the interior of British Columbia results in extensive hybridization and introgression (Horton, 1959, Roche, 1969). Pure Engelmann spruce can be found at high elevation. We find that the trait that most closely aligns with the hybrid zones is frost hardiness, with pure Engelmann spruce and hybrids having distinctly low hardiness compared to white spruce. De La Torre *et al.* (2014) found precipitation as snow being the main limiting factor of white spruce in Engelmann spruce habitat, while Engelmann spruce is limited in growth potential by its shorter growing season and by low temperatures, when the protective snow layer is missing.

A similar pattern was apparent for lodgepole pine populations from Alberta's dry mixedwood (groups 4 and 5 in Fig. 4c), which share phenology and cold injury characteristics with the spruce populations from the plains, but show very good growth. According to Cullingham *et al.* (2012) lodgepole pine hybridizes exactly in this area with jack pine (*Pinus banksiana*), a species inhabiting the harsh winter conditions present across the boreal plains, and therefore having a high cold hardiness. The contribution of jack pine may also cause the good growth, as its juvenile growth is faster (on average 4 cm/year), with hybrid populations being intermediate (Rweyongeza *et al.*, 2007).

5.4. Conclusions for seed transfer

To manage seed transfer in forestry operations, British Columbia originally established 67 seed zones that were later consolidated to 21 seedzones, which are now used to govern lodgepole pine and interior spruce reforestation (Ying & Yanchuk, 2006). In Alberta, 44 seed zones are in use for interior spruce and 34 for lodgepole pine (ESRD, 2009). Seeds from natural stands may be collected anywhere within a seed zone for planting elsewhere within the same seed zone. In addition, altitudinal (e.g., +600/-200m), or latitudinal (e.g., 2°N/1°S) transfer limits may apply (Snetsinger, 2005). Deployment zones for improved planting stock tend to be larger, because the environmental tolerances of these genotypes have been well studied in progeny trials. British Columbia has 16 and eleven zones for lodgepole pine and interior spruce (Snetsinger, 2005), and Alberta six and nine zones for lodgepole pine and interior spruce in Alberta. (ESRD, 2009). For natural seedlots, a precautionary principle is applied that prescribes a large number of seedzones to avoid maladaptation in the absence of genetic data.

Our data suggests that seed zone delineations for collections from natural stands can be substantially consolidated in both British Columbia and Alberta. Given our findings of high within-population genetic diversity (85%), and a limited amount of among-population diversity that can be attributed to climate (15-20%), our data suggest that rather broad seed zone delineations appear justifiable. In fact, the seed zone delineations for improved planting stock from breeding programs appear appropriate to use with seed from natural stands as well. The assemblages of ecosystem variants according to multivariate regression tree analysis (Table 5 and 6) quite closely align with existing seed zone delineations for improved planting stock. Further, current delineations for improved seed explain almost exactly the same amount of variation in adaptive traits in bulk seedlots as in our partitioning approach: 20% in interior spruce and 13% in lodgepole pine (analysis not shown).

The Tables 5 and 6 represent groups of provenances for which we could not find genetic differentiation in this study regarding adaptation to climate. Although this suggests that only four to six seedzones are needed for each province and species, we should note that our study has the same limitations as any common garden experiment: not all relevant traits can be assessed, and not all genetic structure can

Table 5. Groups of similarly adapted seedlots of interior spruce, derived by multivariate regression tree analysis based on ecosystem variants.

		Ecovariants by province‡							
Group*	Group name*	Alberta				British Columbia			
1	Boreal Forest N	CM11	LBH11	LBH14	LBH16	BWBSdk2			
		NM11							
2	Boreal Forest Central	AP11	CM12	CM13	DM11	BWBSdk1	BWBSmw1	BWBSmw2	BWBSwk2
		DM12	DM13	LBH13	LBH15				
		PAD11	UBH13						
3	Lower Foothills	CM21	CM32	CM33	CM34				
		DM23	LF12	LF13	LF15				
		LF22							
4	Boreal Forest S	CM22	CM23	CM24	CM31				
		DM21	DM22	LF11	LF14				
		LF21	PRP11						
5	Montane, Upper Foothills	M11	M22	M44	M54				
		M55	M56	SA11	SA22				
		SA31	SA32	UF11	UF13				
		UF24	UF25						
6	Sub-boreal					SBPSxc	SBSmc2	SBSmk1	SBSmm
						SBSwk2	SBSwk3		
7	Sub-boreal					SBPSmk	SBSdk	SBSdw1	SBSdw2
						SBSdw3	SBSmc3	SBSmk2	SBSmw
						SBSvk	SBSwk1		
8	Interior Mountains N					ESSFdc2	ESSFdk	ESSFmv4	ESSFmw
						ESSFwc3	ESSFwc4	ESSFwm	ESSFxc
						MSdm2	MSxk	MSxv	
9	Interior Mountains S					ESSFdc1	ESSFdv	ESSFmc	ESSFmv3
						ESSFwc1	ESSFwc2	ESSFwk1	MSdc2
						MSdk	MSdm1	MSun	
10	Interior Valleys SW					ICHdk	ICHmc2	ICHmk3	ICHmm
						ICHmw2	ICHvk1	ICHwk1	ICHwk2
						ICHwk4	IDFdk1		
11	Interior Valleys S					ICHdw	ICHmk1	ICHmw1	ICHmw3
						IDFdk2	IDFdm1	IDFdm2	IDFmw2

*The numbers and names of the groups correspond to Fig. 3c.

‡Capital letters in the variant abbreviations represent the second level of Alberta's Natural Regions classification and the ecological zones of British Columbia's Biogeoclimatic Ecosystem Classification, while small letters and numbers specify the further subdivision down to level four of the Alberta classification and the approximately equivalent variants for British Columbia. Natural Subregions Alberta: A, Alpine; SA, Subalpine; M Montane; CM, Central Mixedwood; DM, Dry Mixedwood; NM, Northern Mixedwood; BSA, Boreal Subarctic; PAD, Peace-Athabasca Delta; LBH, Lower Boreal Highlands; UBH, Upper Boreal Highlands; AP, Athabasca Plain; LF, Lower Foothills; UF, Upper Foothills; FP, Foothills Parkland; PRP, Peace River Parkland. Ecological zones British Columbia: BWBS, Boreal White and Black Spruce; SBPS, Sub-Boreal Pine–Spruce; SBS, Sub-Boreal Spruce; ESSF, Engelmann Spruce–Subalpine Fir; MS, Montane Spruce; IDF, Interior Douglas-fir; CDF, Coastal Douglas-fir; ICH, Interior Cedar-Hemlock; CWH, Coastal Western Hemlock.

Table 6. Groups of similarly adapted seedlots of interior spruce, derived by the multivariate regression tree analysis based on ecosystem variants.

		Ecovariants by province‡							
Group*	Group name*	Alberta				British Columbia			
1	Montane AB	A13	BSA11	BSA12	FP11	BWBSdk1	BWBSdk2		
		FP12	LF21	LF22	LF23				
		SA11	SA12	SA22	SA31				
		SA32	SA41	SA42	UBH12				
		UBH13	UF11	UF12	UF13				
		UF14	UF15						
2	Lower Foothills, NE of BC	LF11	LF12	LF13	LF14	BWBSmw1	BWBSmw2	BWBSwk2	
		LF15	UF24	UF25					
3	Montane BC	LBH14	M55	M56		ESSFdc1	ESSFdk	ESSFmv1	ESSFwc2
						ESSFwc4	ESSFwm	ESSFxc	ESSFxv2
4	Lower Boreal Highlands AB	LBH11	LBH16	M11	M21	ESSFdc2	ESSFdv	ESSFmm1	ESSFmv3
		M54				ESSFmv4	ESSFwk1	ESSFwv	
5	Dry Mixedwood AB	CM33	CM34	DM12	DM13				
6	Sub-boreal					ICHvk1	ICHwc	ICHwk4	IDFxh1
						IDFxh2	MSdc1	MSdm1	MSdm2
						MSun	MSxk	MSxv	SBPSmc
						SBPSxc	SBSdk	SBSmk1	SBSmk2
						SBSmm	SBSun	SBSwk1	SBSwk2
						SBSwk3			
7	Sub-boreal					ICHmk1	IDFdk1	IDFdk2	IDFdk3
						IDFdk4	MSdk	SBPSdc	SBPSmk
						SBSdw1/mw	SBSdw2	SBSdw3	SBSmc1
						SBSmc2	SBSmc3		
8	Interior Valleys					ICHdw	ICHmc2	ICHmw1	ICHmw2
						ICHmw3	IDFdm1	IDFdm2	IDFmw1
						IDFmw2	SBSdh1	SBSmh	
9	Coastal BC					CDFmm	CWHds1	CWHmm2	CWHvm1
						CWHwh1	CWHws1	CWHxm1	CWHxm2

*The numbers and names of the groups correspond to Fig. 4c.

‡Explanations for the abbreviations of the ecosystem variants are given in Table 5.

be detected with a limited set of environments and a given sample size. Nevertheless, this research in combination with data from long-term field experiments (Rweyongeza *et al.*, 2010, Rweyongeza *et al.*, 2007) suggests that more than 30 current seedzones for lodgepole pine and interior spruce used in Alberta are not necessary. Instead, we recommend that six pine zones and nine spruce zones used for improved planting stock are appropriate for bulk seedlot collections from natural stands as well.

Also for British Columbia, our groupings (Table 5 and 6) match the established species-specific seed zones for genetically improved material well. Groups of ecosystem delineations from the regression tree analysis track similar altitudinal boundaries as those implemented in the separation in high and low units within the official seed zones for British Columbia, but our delineations are less conservative with respect to spatial differentiation, spanning larger latitudinal and longitudinal ranges than the existing seed zones.

5.5. Implications for climate change

This study was conducted with open-pollinated, bulk seedlots used in commercial reforestation programs on a large scale. In British Columbia 40% of the reforestation activities on public lands rely on such planting stock, representing about 60 million seedlings of 150 million planted seedlings in total (BC Ministry of Forests, 2014). In Alberta virtually all reforestation is based on bulk seedlots, comprising 70 million seedlings of spruce and pine planted annually (ESRD, 2013). Our findings suggest that reforestation activities with bulk seedlots should introduce a remarkable amount of genetic diversity into the landscape and it appears that the degree of genetic diversity in climate-related adaptive traits in these seedlots should provide an adequate evolutionary capacity of planted forests to adapt to environmental change.

If only 15–20% of among-population genetic variation in adaptive traits could be linked to climate, one may ask whether assisted migration prescriptions to address climate change are necessary at all. However, a reduction of growth due to maladaptation to climate by as little as 5% would still have considerable economic impacts. For perspective, large investments in tree breeding programs are justified by small incremental gains in productivity, e.g. 5–7% improvement in height or 10–12% in stem volume per generation (McKeand & Svensson, 1997, Rehfeldt *et al.*, 1991, Talbert *et al.*, 1985). It therefore remains important to match genotypes to environments to which they are best adapted.

Even though climate could not explain large amounts of among-population variance, multitrait combinations representing regional genetic differentiation could clearly be interpreted as adaptation to climate. We therefore propose that the seed zones that we derived in this study should also serve well to guide assisted migration under climate change. To develop such assisted migration prescription, the climate envelopes of seed zone delineations could be projected under climate change as, for example, in Gray *et al.* (2011). In addition, genetic information on long-term survival and growth from provenance trials should be incorporated in assisted migration prescriptions as well.

6. Bibliography

AFGRC, Alberta Forest Genetics Research Council (2007) Research Priorities. Retrieved Sept. 21, 2013, from http://www.abtreegene.com/images/Priorities1.pdf

Ainsworth EA, Long SP (2005) What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy. *New Phytologist,* **165**, 351-371.

Aitken SN, Adams WT (1995a) Impacts of genetic selection for height growth on annual developmental cycle traits in coastal Douglas-fir. In: Evolution of breeding strategies for conifers from the Pacific Northwest. Joint meeting of the IUFRO Working Parties S2.02.05 (Douglas-fir), S2.02.06 (*Pinus contorta*), S2.02.12 (Sitka spruce) and S2.02.14 (*Abies*), August 1-4, 1995, Limoges, France. INRA, Station d'Amelioration des Arbres Forestiers, Ardon, France. AD1: 1–8.

Aitken SN, Adams WT (1995b) Screening for cold hardiness in coastal Douglas-fir. In: Eucalypt plantations: improving fibre yield and quality. Proceedings of the CRC/IUFRO Conference, February 19-24, 1994, Hobart, Australia. (eds Potts BM, Borralho NMG, Reid JB, Cromer RN, Tibbits WN, Raymond CA) pp 321-324.

Aitken SN, Hannerz M (2001) Genecology and Gene Resource Management Strategies for Conifer Cold Hardiness. In: *Conifer cold hardiness.* (eds Bigras FJ, Colombo SJ) pp 23-53. Dordrecht, Netherlands, Kluwer Academic Publishers.

Aitken SN, Yeaman S, Holliday JA, Wang T, Curtis-McLane S (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications,* **1**, 95-111.

Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* **259**, 660-684.

Andalo C, Beaulieu J, Bousquet J (2005) The impact of climate change on growth of local white spruce populations in Quebec, Canada. *Forest Ecology and Management,* **205**, 169-182.

ATISC, Alberta Tree Improvement and Seed Centre (2007a) Controlled parentage program plan for the region G2 white spruce tree improvement project in the northwest boreal region of Alberta. Technical Report 07-09. Smoky Lake, Alberta, Canada. pp 34.

ATISC, Alberta Tree Improvement and Seed Centre (2007b) Controlled parentage program plan for the region J lodgepole pine tree improvement project in the northwest boreal region of Alberta. Technical Report 07-11. Smoky Lake, Alberta, Canada. pp 38.

Aubin I, Garbe CM, Colombo S *et al.* (2011) Why we disagree about assisted migration: Ethical implications of a key debate regarding the future of Canada's forests. *Forestry Chronicle,* **87**, 755-765.

Barrow E, Yu G (2005) Climate scenarios for Alberta. Prairie Adaptation Research Collaborative (PARC), University of Regina, Regina, Saskatchewan, Canada.

BC Ministry of Forests, B.C. Ministry of Forests Lands and Natural Research Operations (2013) Beetle facts. National Forestry Database. Retrieved Jan. 20, 2014, from http://www.for.gov.bc.ca/hfp/mountain_pine_beetle/

BC Ministry of Forests, B.C. Ministry of Forests Lands and Natural Research Operations (2014) Seed production, Historical seedling request graph. Tree Improvement Branch. Retrieved Jan. 12, 2014, from http://www.for.gov.bc.ca/hti/seedproduction/seedorchards.htm

Benowicz A, El-Kassaby YA (1999) Genetic variation in mountain hemlock (*Tsuga mertensiana* Bong.): quantitative and adaptive attributes. *Forest Ecology and Management,* **123**, 205-215.

Berg EE, Henry JD, Fastie CL, De Volder AD, Matsuoka SM (2006) Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: Relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management,* **227**, 219-232.

Bigras FJ, Ryyppö A, Lindström A, Stattin E (2001) Cold Acclimation and Deacclimation of Shoots and Roots of Conifer Seedlings. In: *Conifer cold hardiness.* (eds Bigras FJ, Colombo SJ) pp 57-88. Dordrecht, Netherlands, Kluwer Academic Publishers.

Botkin DB, Saxe H, Araujo MB *et al.* (2007) Forecasting the effects of global warming on biodiversity. *BioScience,* **57**, 227-236.

Bryson RA, Barerreis DA, Wendland WM (1970) The character of late-glacial and post-glacial climate change. In: *Pleistocene and Recent Envionments of the Central Great Plains.* (eds Dort W, Jones JK) pp 53-74. Lawrence, Kansas, USA, University of Kansas Press.

Burger R, Lynch M (1995) Evolution and extinction in a changing environment: a quantitative-genetic analysis. *Evolution,* **49**, 151-163.

Campbell ID, McDonald K, Flannigan MD, Kringayark J (1999) Long-distance transport of pollen into the Arctic. *Nature,* **399**, 29-30.

Campbell RK (1979) Genecology of Douglas-Fir in a Watershed in the Oregon Cascades. *Ecology,* **60**, 1036-1050.

Campbell RK, Sugano AI (1979) Genecology of bud-burst phenology in douglas-fir - response to flushing temperature and chilling. *Botanical Gazette,* **140**, 223-231.

Canadian Forest Service (2013) National Forestry Database. Retrieved Oct. 20, 2013, from http://nfdp.ccfm.org/index_e.php

Cannell MGR, Smith RI (1983) Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of Applied Ecology,* **20**, 951-963.

Carroll AL, Regniere J, Logan JA, Taylor SW, Bentz BJ, Powell JA (2006) Impacts of climate change on range expansion by the mountain pine beetle. Mountain Pine Beetle Initiative working paper 2006-14. Pacific Forestry Centre, Canadian Forest Service, Victoria, British Columbia, Canada.

Carroll AL, Taylor SW, Regniere J, Safranyik L (2004) Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Mountain Pine Beetle Symposium: Challenges and Solutions. Information Report BC-X-399. (eds Shore TL, Brooks JE, Stone JE) Natural Resources Canada, Canadian Forest Service, Victoria, British Columbia, Canada. pp 223-232.

Carter KK (1996) Provenance tests as indicators of growth response to climate change in 10 north temperate tree species. *Canadian Journal of Forest Research,* **26**, 1089-1095.

Christensen JH, Hewitson B, Busuioc A *et al.* (2007) Regional Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report by the Intergovernmental Panel on Climate Change.* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp 847-940. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Critchfield WB, Little EL (1966) *Geographic distribution of the pines of the world,* Washington (DC), USA, U.S. Department of Agriculture

Crowe KA, Parker WH (2005) Provisional breeding zone determination modeled as a maximal covering location problem. *Canadian Journal of Forest Research,* **35**, 1173-1182.

Cullingham CI, James PMA, Cooke JEK, Coltman DW (2012) Characterizing the physical and genetic structure of the lodgepole pine jack pine hybrid zone: mosaic structure and differential introgression. *Evolutionary Applications,* **5**, 879-891.

Daly C, Gibson WP, Taylor GH, Johnson GL, Pasteris P (2002) A knowledge-based approach to the statistical mapping of climate. *Climate Research,* **22**, 99-113.

Davis MB (1981) Quaternary History and the Stability of Forest Communities. In: *Forest Succession.* (eds West DC, Shugart HH, Botkin DB) pp 132-153. New York, USA, Springer.

Davis MB, Shaw RG (2001) Range shifts and adaptive responses to Quaternary climate change. *Science,* **292**, 673-679.

Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. *Ecology,* **86**, 1704-1714.

De'Ath G (2002) Multivariate regression trees: a new technique for modeling species-environment relationships. *Ecology,* **83**, 1105-1117.

De La Torre A, Wang T, Jaquish B, Aitken SN (2014) Adaptation and exogenous selection in a *Picea glauca* x *Picea engelmannii* hybrid zone: implications for forest management under climate change. *New Phytologist,* **201**, 687-699.

Ekberg I, Eriksson G, Dormling I (1979) Photoperiodic reactions in conifer species. *Ecography,* **2**, 255-263.

El-Kassaby YA, Park YS (1993) Genetic-variation and correlation in growth, biomass, and phenology of Douglas-fir diallel progeny at different spacings. *Silvae Genetica,* **42**, 289-297.

Eriksson G, Ekberg I, Clapham D (2006) *An introduction to forest genetics,* Uppsala, Sweden.

ESRD, Alberta Environment and Sustainable Resource Development (2009) Alberta Forest Genetic Resource Management and Conservation Standards. Pub. No. Ref. T/213. Forestry Division, Edmonton, Alberta, Canada. pp 121.

ESRD, Alberta Environment and Sustainable Resource Development (2013) Sustainable Forest Management, 2012 Facts & Statistics, Reforesting Harvested Areas. Retrieved Jan. 7, 2014, from http://esrd.alberta.ca/lands-forests/forest-management/forest-management-facts-statistics/default.aspx

Etterson JR, Shaw RG (2001) Constraint to adaptive evolution in response to global warming. *Science,* **294**, 151-154.

Flint HL, Boyce BR, Beattie DJ (1967) Index of injury - a useful expression of freezing injury to plant tissues as determined by electrolytic method. *Canadian Journal of Plant Science,* **47**, 229-230.

Forest Genetics Council of British Columbia (2012) Annual Report 2012/2013. (ed Woods JH) Forest Genetics Council of British Columbia, British Columbia, Canada. pp 20.

Franks SJ, Weber JJ, Aitken SN (2013) Evolutionary and plastic responses to climate change in terrestrial plant populations. *Evolutionary Applications*.

Gray LK, Gylander T, Mbogga MS, Chen PY, Hamann A (2011) Assisted migration to address climate change: recommendations for aspen reforestation in western Canada. *Ecological Applications,* **21**, 1591-1603.

Guo W, Li B, Zhang X, Wang R (2007) Architectural plasticity and growth responses of *Hippophae rhamnoides* and *Caragana intermedia* seedlings to simulated water stress. *Journal of Arid Environments,* **69**, 385-399.

Hamann A, Gylander T, Chen P (2010) Developing seed zones and transfer guidelines with multivariate regression trees. *Tree Genetics & Genomes,* **7**, 399-408.

Hamann A, Koshy MP, Namkoong G, Ying CC (2000) Genotype x environment interactions in *Alnus rubra*: developing seed zones and seed-transfer guidelines with spatial statistics and GIS. *Forest Ecology and Management,* **136**, 107-119.

Hamann A, Wang TL (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology,* **87**, 2773-2786.

Hamann A, Wang TL, Spittlehouse DL, Murdock TQ (2013) A comprehensive, high-resolution database of historical and projected climate surfaces for Western North America. *Bulletin of the American Meteorological Society,* **94**, 1307-1309.

Hamrick JL, Godt MJW, Sherman-Broyles SL (1992) Factors influencing levels of genetic diversity in woody plant species. *New Forests,* **6**, 95-124.

Hamrick JL, Nason D (2000) Gene flow in forest trees In: *Forest genetics and Conservation: principles and practice.* (eds Young A, Boshier D, Boyle T) pp 81-90. Collingwood, Australia, CSIRO Publishing.

Hannerz M (1999) Evaluation of temperature models for predicting bud burst in Norway spruce. *Canadian Journal of Forest Research,* **29**, 9-19.

Hannerz M, Aitken SN, King JN, Budge S (1999) Effects of genetic selection for growth on frost hardiness in western hemlock. *Canadian Journal of Forest Research,* **29**, 509-516.

Hannerz M, Ekberg I, Norell L (2003) Variation in chilling requirements for completing bud rest between provenances of Norway spruce. *Silvae Genetica,* **52**, 161-168.

Hogg EH, Brandt JP, Michaelian M (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research,* **38**, 1373-1384.

Horton K (1959) Characteristics of subalpine spruce in Alberta. Technical Note No. 76. Forest Research Division, Ottawa, Canada. pp 20.

Howe GT, Aitken SN, Neale DB, Jermstad KD, Wheeler NC, Chen THH (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany,* **81**, 1247-1266.

IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report by the Intergovernmental Panel on Climate Change. (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp 996, Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Jonsson A, Eriksson G, Ye ZH, Yeh FC (2000) A retrospective early test of *Pinus sylvestris* seedlings grown at wide and dense spacing. *Canadian Journal of Forest Research,* **30**, 1443-1452.

Jump AS, Penuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters,* **8**, 1010-1020.

Kramer K (1995) Phenotypic plasticity of the phenology of 7 european tree species in relation to climatic warming. *Plant Cell and Environment,* **18**, 93-104.

Kremer A, Ronce O, Robledo-Arnuncio JJ *et al.* (2012) Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*.

Lanner RM (1976) Patterns of shoot development in *Pinus* and their relationship to growth potential. In: *Tree physiology and yield improvement.* (eds Cannell MGR, Last FT). London, England, Academic Press Limited.

Leinonen I (1996) Dependence of dormancy release on temperature in different origins of Pinus sylvestris and Betula pendula seedlings. *Scandinavian Journal of Forest Research,* **11**, 122-128.

Leinonen I, Hanninen H (2002) Adaptation of the timing of bud burst of Norway spruce to temperate and boreal climates. *Silva Fennica,* **36**, 695-701.

Little EL (1971) *Atlas of United States trees: volume 1. Conifers and important hardwoods,* Washington (DC), USA, U.S. Department of Agriculture, Forest Service.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD (2009) The velocity of climate change. *Nature,* **462**, 1052-1057.

Loehle C (1998) Height growth rate tradeoffs determine northern and southern range limits for trees. *Journal of Biogeography,* **25**, 735-742.

Lynch M, Lande R (1993) Evolution and extinction in response to environmental change. In: *Biotic Interactions and Global Change.* (eds Kareiva PM, Kingsolver JG, Huey RB) pp 234-250. Sunderland, Massachusetts, USA, Sinauer Associates Incorporated.

Macdougall D (2006) *Frozen Earth: The Once and Future Story of Ice Ages,* Berkeley, California, USA, University of California Press.

Malcolm JR, Markham A, Neilson RP, Garaci M (2002) Estimated migration rates under scenarios of global climate change. *Journal of Biogeography,* **29**, 835-849.

Marris E (2009) Planting the forest of the future. *Nature,* **459**, 906-908.

Martinez-Meier A, Sanchez L, Dalla-Salda G, Gallo L, Pastorino M, Rozenberg P (2009) Ring density record of phenotypic plasticity and adaptation to drought in Douglas-fir. *Forest Ecology and Management,* **258**, 860-867.

Matyas C (1994) Modeling climate change effects with provenance test data. *Tree Physiology,* **14**, 797-804.

Mbogga MS, Hamann A, Wang TL (2009) Historical and projected climate data for natural resource management in western Canada. *Agricultural and Forest Meteorology,* **149**, 881-890.

McKay JK, Latta RG (2002) Adaptive population divergence: markers, QTL and traits. *Trends in Ecology & Evolution,* **17**, 285-291.

McKeand S, Svensson J (1997) Sustainable management of genetic resources. *Journal of Forestry,* **95**, 4-9.

McKenney D, Pedlar J, O'Neill G (2009) Climate change and forest seed zones: Past trends, future prospects and challenges to ponder. *Forestry Chronicle,* **85**, 258-266.

McLachlan JS, Clark JS, Manos PS (2005) Molecular indicators of tree migration capacity under rapid climate change. *Ecology,* **86**, 2088-2098.

McLachlan JS, Hellmann JJ, Schwartz MW (2007) A framework for debate of assisted migration in an era of climate change. *Conservation Biology,* **21**, 297-302.

McLane SC, Daniels LD, Aitken SN (2011) Climate impacts on lodgepole pine (*Pinus contorta*) radial growth in a provenance experiment. *Forest Ecology and Management,* **262**, 115-123.

Meehl GA, Stocker TF, Collins WD *et al.* (2007) Global Climate Projections. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report by the Intergovernmental Panel on Climate Change.* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp 747-846. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Meidinger D, Pojar J (1991) Ecosystems of British Columbia. Special Report Series No. 6. Ministry of Forests, Victoria, British Columbia, Canada. pp 330.

Merilä J, Crnokrak P (2001) Comparison of genetic differentiation at marker loci and quantitative traits. *Journal of Evolutionary Biology,* **14**, 892-903.

Michaelian M, Hogg EH, Hall RJ, Arsenault E (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology,* **17**, 2084-2094.

Millar CI, Stephenson NL, Stephens SL (2007) Climate change and forests of the future: Managing in the face of uncertainty. *Ecological Applications,* **17**, 2145-2151.

Millard P, Sommerkorn M, Grelet GA (2007) Environmental change and carbon limitation in trees: a biochemical, ecophysiological and ecosystem appraisal. *New Phytologist,* **175**, 11-28.

Morgenstern EK (1996) *Geographic Variation in Forest Trees: Genetic Basis and Application of Knowledge in Silviculture,* Vancouver, British Columbia, Canada, University of British Columbia Press.

Mote PW, Salathé EP (2010) Future climate in the Pacific Northwest. *Climatic Change,* **102**, 29-50.

Namkong G, Koshy MP, Aitken SN (2000) Selection. In: *Forest genetics and Conservation: principles and practice.* (eds Young A, Boshier D, Boyle T) pp 101-113. Collingwood, Australia, CSIRO Publishing.

Natural Regions Committee (2006) Natural regions and subregions of Alberta. Pub. No. T/852. Compiled by DJ Downing and WW Pettapiece. Government of Alberta., Edmonton, Alberta, Canada. pp 254.

Nicotra AB, Atkin OK, Bonser SP *et al.* (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science,* **15**, 684-692.

Nienstaedt H (1985) Inheritance and correlations of frost injury, growth, flowering, and cone characteristics in white spruce, *Picea glauca* (Moench) Voss. *Canadian Journal of Forest Research,* **15**, 498-504.

Norgren O, Little CHA, Sundblad LG (1996) Seedling shoot, needle and bud development in three provenances of *Pinus sylvestris* and *Pinus contorta* cultivated in northern Sweden. *Scandinavian Journal of Forest Research,* **11**, 356-363.

O'Neill G, Carlson M, Berger V, Yanchuk A (2007) Responding to Climate Change: Assisting seedlot migration to maximize adaptation of future forest plantations. *Forest Genetics Council of British Columbia, Tick Talk 8*, 9-12.

O'Neill GA, Adams WT, Aitken SN (2001) Quantitative genetics of spring and fall cold hardiness in seedlings from two Oregon populations of coastal Douglas-fir. *Forest Ecology and Management,* **149**, 305-318.

O'Neill GA, Aitken SN (2004) Area-based breeding zones to minimize maladaptation. *Canadian Journal of Forest Research,* **34**, 695-704.

O'Neill GA, Berger V, Carlson M, Ukrainetz NK (2011) Assited Migration Adaptation Trial (AMAT). Assited Migration Bulletin 01. British Columbia Ministry of Forests, Lands and Natural Resource Operations, Tree Improvement Branch, Vernon, British Columbia, Canada.

O'Neill GA, Hamann A, Wang TL (2008a) Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *Journal of Applied Ecology,* **45**, 1040-1049.

O'Neill GA, Ukrainetz NK, Carlson M *et al.* (2008b) Assisted migration to address climate change in British Columbia: recommendations for interim seed transfer standards. Technical Report 048. B.C. Ministry of Forests and Range, Research Branch Victoria, British Columbia, Canada.

Parker WH (1992) Focal point seed zones: site-specific seed zone delineation using geographic information-systems. *Canadian Journal of Forest Research,* **22**, 267-271.

Patterson H, Williams E (1976) A new class of resolvable incomplete block designs. *Biometrika,* **63**, 83-92.

Pedlar JH, McKenney DW, Aubin I *et al.* (2012) Placing Forestry in the Assisted Migration Debate. *BioScience,* **62**, 835-842.

Peng C, Ma Z, Lei X *et al.* (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change,* **1**, 467-471.

R Development Core Team (2013) *R: A Language and Environment for Statistical Computing,* Vienna, Austria, R Foundation for Statistical Computing.

Rehfeldt GE (1983) Seed transfer in the Northern Rocky Mountains. In: Proceedings for the USDA Forest Service Forest Genetic Workshop. pp 1-26. Charlottetown, South Carolina.

Rehfeldt GE (1990) Adaptability versus zone size: continuous zones for the Rocky Mountains (USA). In: Joint Meeting of Western Forest Genetics Association and IUFRO Working Parties. pp S 2.02-05.

Rehfeldt GE, Tchebakova NM, Parfenova YI, Wykoff WR, Kuzmina NA, Milyutin LI (2002) Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology,* **8**, 912-929.

Rehfeldt GE, Wykoff WR, Hoff RJ, Steinhoff RJ (1991) Genetic gains in growth and simulated yield of Pinus monticola. *Forest Science,* **37**, 326-342.

Rehfeldt GE, Wykoff WR, Ying CC (2001) Physiologic plasticity, evolution, and impacts of a changing climate on *Pinus contorta*. *Climatic Change,* **50**, 355-376.

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton DA (1999) Genetic responses to climate in *Pinus contorta*: Niche breadth, climate change, and reforestation. *Ecological Monographs,* **69**, 375-407.

Repo T, Nilsson J-E, Rikala R, Ryyppö A, Sutinen M-L (2001) Cold Hardiness of Scots Pine (*Pinus sylvestris* L.). In: *Conifer cold hardiness.* (eds Bigras FJ, Colombo SJ) pp 463-494. Dordrecht, Netherlands, Kluwer Academic Publishers.

Roche L (1969) A Genecological Study of Genus Picea in British Columbia. *New Phytologist,* **68**, 505-554.

Rweyongeza DM, Dhir NK, Barnhardt LK, Hansen C, Yang R-C (2007) Population differentiation of the lodgepole pine (*Pinus contorta*) and jack pine (*Pinus banksiana*) complex in Alberta: growth, survival, and responses to climate. *Canadian Journal of Botany,* **85**, 545-556.

SAS Institue Inc. (2008) *SAS/STAT® 9.2 user's guide,* Cary, NC, USA, SAS Institute Inc.

Sauchyn D, Kulshreshtha S (2008) Prairies. In: *From Impacts to Adaptation: Canada in a Changing Climate 2007.* pp 275-328. Ottawa, Ontario, Canada, Government of Canada.

Savolainen O, Pyhäjärvi T, Knürr T (2007) Gene Flow and Local Adaptation in Trees. *Annual Review of Ecology, Evolution, and Systematics,* **38**, 595-619.

Saxe H, Cannell MGR, Johnsen B, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist,* **149**, 369-399.

Schmitt J, Stinchcombe JR, Heschel MS, Huber H (2003) The adaptive evolution of plasticity: Phytochrome-mediated shade avoidance responses. *Integrative and Comparative Biology,* **43**, 459-469.

Schnabel A, Hamrick JL (1990) Comparative-analysis of population genetic-structure in *Quercus macrocarpa* and *Quercus gambelii* (*Fagaceae*). *Systematic Botany,* **15**, 240-251.

Schreiber SG, Hamann A, Hacke UG, Thomas BR (2013) Sixteen years of winter stress: an assessment of cold hardiness, growth performance and survival of hybrid poplar clones at a boreal planting site. *Plant Cell and Environment,* **36**, 419-428.

Snetsinger J (2005) *Chief Forester's Standards for Seed Use,* Victoria, British Columbia, Canada, Ministry of Forests.

Snetsinger J (2009) Amendments to the Standards - November 2008, Climate Based Upward Elevation Changes. Retrieved Sept. 14, 2013, from http://www.for.gov.bc.ca/code/cfstandards/amendmentNov08.htm

Solomon S, Qin D, Manning M *et al.* (2007) 2007: Technical Summary. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report by the Intergovernmental Panel on Climate Change.* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp 19-91. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Sonesson J, Eriksson G (2003) Genetic variation in drought tolerance in *Picea abies* seedlings and its relationship to growth in controlled and field environments. *Scandinavian Journal of Forest Research,* **18**, 7-18.

Sonesson J, Jansson G, Eriksson G (2002) Retrospective genetic testing of *Picea abies* under controlled temperature and moisture regimes. *Canadian Journal of Forest Research,* **32**, 81-91.

Spittlehouse DL (2008) Climate change, impacts, and adaptation scenarios: climate change and forest and range management in British Columbia. Technical Report 045. B.C. Ministry of Forests and Range, Research Branch, Victoria, British Columbia, Canada.

Talbert JT, Weir RJ, Arnold RD (1985) Costs and benefits of a mature 1st-generation loblolly pine tree improvement program. *Journal of Forestry,* **83**, 162-166.

Trenberth KE, Jones PD, Ambenje P *et al.* (2007) Observations: Surface and Atmospheric Climate Change. In: *Climate Change 2007: The Physical*

Science Basis. Contribution of Working Group I to the Fourth Assessment Report by the Intergovernmental Panel on Climate Change. (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL) pp 235-336. Cambridge, United Kingdom and New York, NY, USA, Cambridge University Press.

Valladares F, Chico JM, Aranda I, Balaguer L, Dizengremel P, Manrique E, Dreyer E (2002) The greater seedling high-light tolerance of *Quercus robur* over *Fagus sylvatica* is linked to a greater physiological plasticity. *Trees-Structure and Function,* **16**, 395-403.

Van Den Berg DA, Lanner RM (1971) Bud development in lodgepole pine. *Forest Science,* **17**, 479-486.

Walker JI, Sydneysmith R (2008) British Columbia. In: *From Impacts to Adaptation: Canada in a Changing Climate 2007.* pp 329-386. Ottawa, Ontario, Canada, Government of Canada

Walther GR, Post E, Convey P *et al.* (2002) Ecological responses to recent climate change. *Nature,* **416**, 389-395.

Wang T, Hamann A, Spittlehouse DL, Murdock TQ (2012) ClimateWNA—High-Resolution Spatial Climate Data for Western North America. *Journal of Applied Meteorology and Climatology,* **51**, 16-29.

Wang T, Hamann A, Yanchuk A, O'Neill GA, Aitken SN (2006) Use of response functions in selecting lodgepole pine populations for future climates. *Global Change Biology,* **12**, 2404-2416.

Wang TL, O'Neill GA, Aitken SN (2010) Integrating environmental and genetic effects to predict responses of tree populations to climate. *Ecological Applications,* **20**, 153-163.

Weiser CJ (1970) Cold resistance and injury in woody plants. *Science,* **169**, 1269-1278.

Welsh C, Lewis K, Woods A (2009) The outbreak history of Dothistroma needle blight: an emerging forest disease in northwestern British Columbia, Canada. *Canadian Journal of Forest Research,* **39**, 2505-2519.

Westfall J (2001) 2001 Summary of Forest Health Conditions in British Columbia. Pest management report series. Ministry of Forests, Forest Practices Branch, British Columbia, Canada. pp 24.

Westfall J, Ebata T (2012) 2012 Summary of Forest Health Conditions in British Columbia. Pest Management Report Number 15. Pest management report series. Ministry of Forests, Lands and Natural Resource Operations, British Columbia, Canada. pp 92.

Williams ER, Matheson AC, Harwood CE (2002) *Experimental design and analysis for tree improvement,* Australia, CSIRO Publishing.

Williams ER, Talbot M (1993) *ALPHA+: Experimental design for variety trials. Design User Manual*, CSIRO, Canberra and SASS, Edinburgh.

Woods A (2011) Is the health of British Columbia's forests being influenced by climate change? If so, was this predictable? *Canadian Journal of Plant Pathology,* **33**, 117-126.

Woods A, Coates KD, Hamann A (2005) Is an unprecedented dothistroma needle blight epidemic related to climate change? *BioScience,* **55**, 761-769.

Worrall JJ, Rehfeldt GE, Hamann A, Hogg EH, Marchetti SB, Michaelian M, Gray LK (2013) Recent declines of *Populus tremuloides* in North America linked to climate. *Forest Ecology and Management,* **299**, 35-51.

Wu HX, Ying CC (2004) Geographic pattern of local optimality in natural populations of lodgepole pine. *Forest Ecology and Management,* **194**, 177-198.

Yeaman S, Jarvis A (2006) Regional heterogeneity and gene flow maintain variance in a quantitative trait within populations of lodgepole pine. *Proceedings of the Royal Society B-Biological Sciences,* **273**, 1587-1593.

Ying CC, Yanchuk AD (2006) The development of British Columbia's tree seed transfer guidelines: Purpose, concept, methodology, and implementation. *Forest Ecology and Management,* **227**, 1-13.