Selection on *Picea mariana* shifts with climate and evolutionary response to climate change is largely unconstrained by phenotypic integration

Authors

Sabina Henry[1], Julie Messier[1]

Affiliations

1 Department of Biology, University of Waterloo, Waterloo, Ontario, Canada

Corresponding author:

Email address: sihenry@uwaterloo.ca

ABSTRACT

The local persistence of long-lived organisms is at risk as climate change drives a rapid shift in selection regimes world-wide. Although adaptive evolution is one of the main mechanisms by which populations persist in changing environments, we have little information regarding how selection regimes will shift in response to continued climate change, nor on the potential for trees to evolve adaptively under novel selection pressures. To address these gaps, here we assessed the changes in selection in three sites along a spatial climate gradient which mimics expected temporal changes in climate and determined whether trait covariance might accelerate or impede the rate of adaptive evolution of seven *Picea mariana* populations in the warmer and drier environment. In three common garden sites established 50 years ago, we measured an array of traits which represent water use, response to temperature, structural investment, and metabolic efficiency. Our findings reveal that all 10 traits measured in this study were under selection in at least one site. We also find different traits are under selection in each site, with four instances where the shift in selection gradient is consistent with shifts in climate: water use efficiency (WUE); needle carbon to nitrogen ratio (CN); the interaction between WUE and CN; and the interaction between CN and huber value. In the warm and dry site, traits under selection were largely uncorrelated, with only four of the 49 trait combinations under selection exhibiting intra population trait covariances. The shifts in selection gradient suggest that climate change may select for needles with higher WUE, higher structural carbon and higher hydraulic supply to the needles. The few trait-trait correlations indicate that phenotypic integration should neither impede nor facilitate adaptive evolution, leaving *P. mariana* provenances with the evolutionary flexibility to respond to climate change regardless of the direction to selection.

INTRODUCTION

As climates shift under global climate change, the growth, productivity and persistence of tree species globally are at risk (Allen *et al*., 2010; Choat *et al*., 2012). This is especially true for the boreal forest which is experiencing climate change at a rapid rate compared to regions at lower latitudes (Aubin *et al*., 2018; Chagnon *et al*., 2022). These rapid shifts in environmental conditions expose local populations to new selection pressures with little time for evolution by natural selection to occur, leaving long-lived sessile organisms at particular risk of becoming mismatched with new environmental conditions (Barrett & Schluter, 2008; de Lafontaine *et al*., 2018). Studies worldwide have reported widespread forest tree mortality driven by this mismatch, leaving adaptation and migration as possible outcomes which may preserve population persistence (Shaw *et al*., 2005; McDowell *et al.*, 2020; Münchinger *et al.*, 2023). However, migration rates are likely too slow to match the pace of climate change (Malcolm *et al*., 2002; Iverson *et al*., 2004; Brecka *et al*., 2018). As a result, research has focused on identifying adaptations which would allow for the persistence of populations in the face of climate change. Adaptations are phenotypic characteristics associated with higher fitness within a population in a given environment. These can occur through adaptive plasticity, whereby an individual's plastic response increases fitness or through adaptive evolution whereby traits which confer high fitness are preferentially passed on from one generation to the next. Although both adaptive plasticity and adaptive evolution can contribute to population persistence most work to date focuses on adaptive plasticity and we know little about the potential for adaptive evolution in trees (henceforth, adaptive potential). Indeed, in recent years many studies have aimed to assess adaptive capacity in the face of climate change by solely quantifying adaptive plasticity of phenotypic traits using locally adapted populations from warm and dry environments (Andrés-Hernández *et al*., 2023; Blasini *et al*., 2021; Challis *et al*., 2022; Robert *et al*., 2024). However, recent meta-analyses on adaptive capacity have highlighted the need to also examine the role of adaptive evolution to provide a more comprehensive assessment of population adaptive capacity in the face of climate change (Lindner *et al.*, 2010; Royer-Tardif *et al.*, 2021). As a result, research on the adaptive potential of important tree species is required to determine whether populations will be able to persist in their current environments. However, a missing piece of the puzzle remains; in order to assess the adaptive potential of a population we need to understand how selection on populations might shift with climate change. Once we understand how selection is likely to shift, we can then identify populations which may have a higher adaptive potential than others in the face of climate change. Here I first ask how selection on *Picea mariana* shifts with climate in the Canadian boreal forest and then ask whether different *P. mariana* provenances have different adaptive potentials to warmer and drier environments.

Over the next 100 years, the climate of the boreal forest is expected to get warmer and drier (Figure 1). Current emission trends suggest that continued increase in greenhouse gas emission over time is likely. Trends modelled using this climate scenario (CanESM2 RCP 8.5 model) show warming temperatures across the boreal forest, with most regions experiencing a ~ 4 ºC increase in mean annual temperature (Boucher *et al.*, 2020). In addition to warming, water availability in environments is predicted to decrease. Water availability in environments depends on the interplay between evaporation, due to temperature and irradiation, and levels of precipitation. Water availability is reflected by the climate moisture index (CMI), which is the difference between annual precipitation and potential evapotranspiration. While a decrease in CMI is predicted across most of the boreal forest (with the exception of the most eastern regions), in the western regions CMI is expected to reach negative values, which indicate that a closed canopy forest would not be maintained in this region. Yet exactly how these shifts in environmental conditions will affect boreal tree species remains unclear.

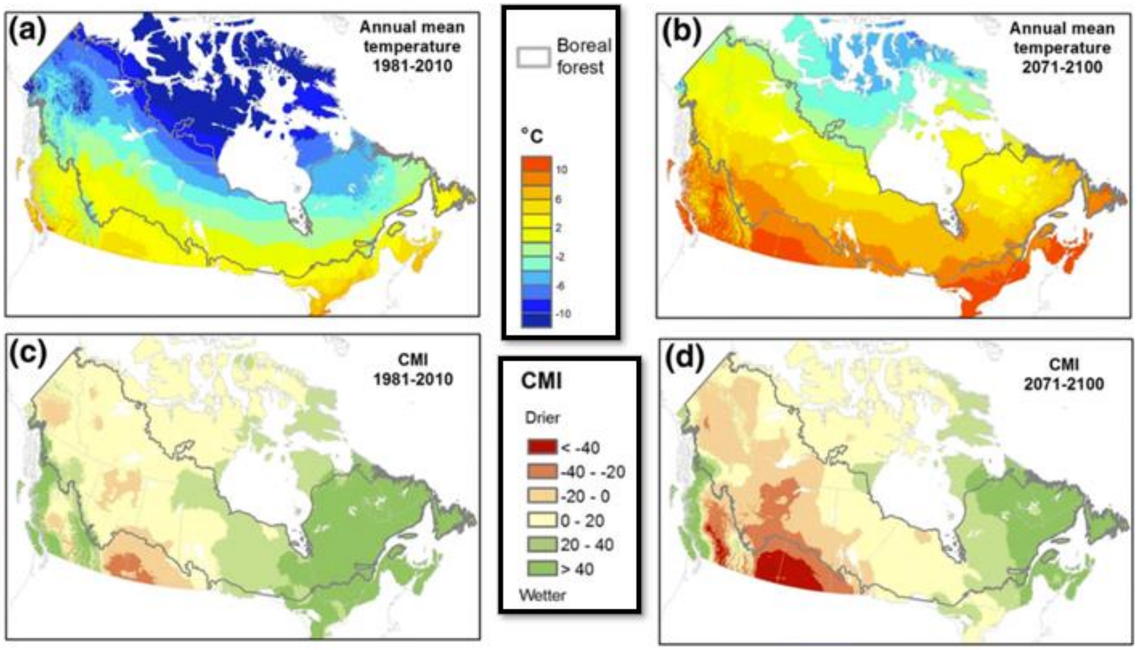


Figure 1. Projections of annual mean temperature (ºC) and Climate Moisture Index (CMI) for the 1981 – 2010 and 2071 – 2100 periods based on the CanESM2 RCP 8.5 model. Grey line represents the range of the Canadian boreal forest. Figure adapted from Boucher *et al.* (2020).

In the boreal forest the response of *P. mariana* to warming has not been uniform, with warming expected to increase the growth rates of trees in the northern boreal forest where water is not limiting, and southern regions expected to face increased drought stress and thus lower growth rates and higher mortality (Sniderhan *et al*., 2021). Indeed, many studies have found productivity to increase in response to warming (Gamache & Payette, 2004) and many others have found it to decrease (Hogg *et al.*, 2005; Girardin *et al*., 2016; Robert *et al*., 2024). An advance of the timing of spring since 1950 has been documented for most of North America (Cayan *et al.*, 2001; Sniderhan *et al*., 2021) however for southern latitudes, productivity is more water limited (Chagnon *et al*., 2022). Changes in temperature can change the length of the growing season, an important determinant of forest productivity in temperate and boreal forests (Kimball *et al*., 2004). Water limitation in the southern regions of the boreal forest can be further exacerbated by increases in temperature increasing water loss from the environment which negatively impacts growth and increases mortality from the leaves in dryer sites, unless stomata close (Shaw *et al*., 2005; Peng *et al*., 2011; Choat *et al.*, 2018; Chagnon *et al*., 2022; Münchinger *et al*., 2023). Research on the impact of climate change on *P. mariana* focuses mainly on changes in growth. Looking at growth integrates the response of the entire phenotype and is thus informative of the overall impacts of climate change on individual- and population-level performance, but we do not know which traits are driving this response. Here, I address this by measuring which traits are under selection in a natural population and are thus driving this change in growth response.

I expect selection from warmer and dryer climates to act on traits related to water use, photosynthesis, structural support and temperature regulation (Aubin *et al.*, 2016; Boisvert-Marsh *et al*., 2020; Sniderhan *et al*., 2021). Water is required in the photosynthetic pathway and is the main chemical component of live plant cells. It is also required to maintain turgor and therefore support the softer tissues, as well as to transport the nutrients across the plant tissues. Low water availability in environments has been shown to decrease forest productivity, as such, trees have shown adaptations to cope with this environmental stress. Therefore, in environments with low water availability traits representing water conservation strategies are likely to confer higher performance and be the targets of selection. Trees must balance resource allocation between growth, reproduction, and structural support. A portion of the tree’s energy is invested in building strong wood and bark to support height and canopy spread. Temperature limited trees exposed to warming temperatures may develop weaker wood. This is because elevated temperatures accelerate growth and as a consequence reduces investment in structural support leading to lower wood and branch density. This makes them more vulnerable to break under mechanical stress, such as during storms (Ahrens *et al*., 2020). Temperature (heat) controls the rate of plant metabolism, which in turn determines the rate of photosynthesis. Most biological metabolic activity takes place within the range of 0–50° C (Hopkins & Hüner, 2004). The optimal tree productivity coincides with 15–25 °C, which is the optimal range of photosynthesis (Hopkins & Hüner, 2004). Temperatures become lethal over 44°C (Schulze *et al.*, 2002). However, it is important to note that plants have been shown to thermoregulate, whether it is to maintain stable tissue temperatures or to produce heat to attract pollinators, there is evidence that plant temperatures are not just passively tracking ambient temperatures. The “leaf homeothermy hypothesis” states that specific suites of leaf traits have evolved to buffer variation in temperature and maintain leaf temperatures within a narrower range of variation around the metabolic optima for photosynthesis (Michaletz *et al*., 2015). In theory, the warmer an environment is, the more cooling the leaves will need to maintain this metabolic optimum. As such, in the range of temperatures that decrease plant metabolic activity, I expect enhanced leaf cooling to confer higher performance and thus be a target of selection in such an environment.

In addition to the adaptive value of individual traits, phenotypic integration may affect population response to selection. Specifically, when the phenotype is highly integrated, (i.e. trait covariance is strong) then the response to selection of one trait will be affected by selection on the other trait. A population’s response to climate change can either facilitate or impede the adaptive evolution of the population depending on the magnitude and direction of trait covariance. Adaptive evolution is constrained when trait covariances are strong such that the response to selection is determined largely by the direction of maximum trait covariation rather than the direction of selection (Figure 2A) (Björklund, 1996; Schluter, 1996). When integration is strong and the direction of maximum trait covariation conflicts with the direction of selection, then the response to selection is weak. However, when phenotypic integration is strong and selection is aligned with the direction of maximum trait covariation, then the response to selection can be greater than in a population with no integration present (Figure 2B) (Björklund, 1996). Last, when there is no covariance between traits under selection, the trait values of the populations can evolve independently (Figure 2C). Provided that adequate heritable trait variation is present in the population, this can benefit populations as their response to climate change can proceed unconstrained by trait covariation (Via & Lande, 1985).

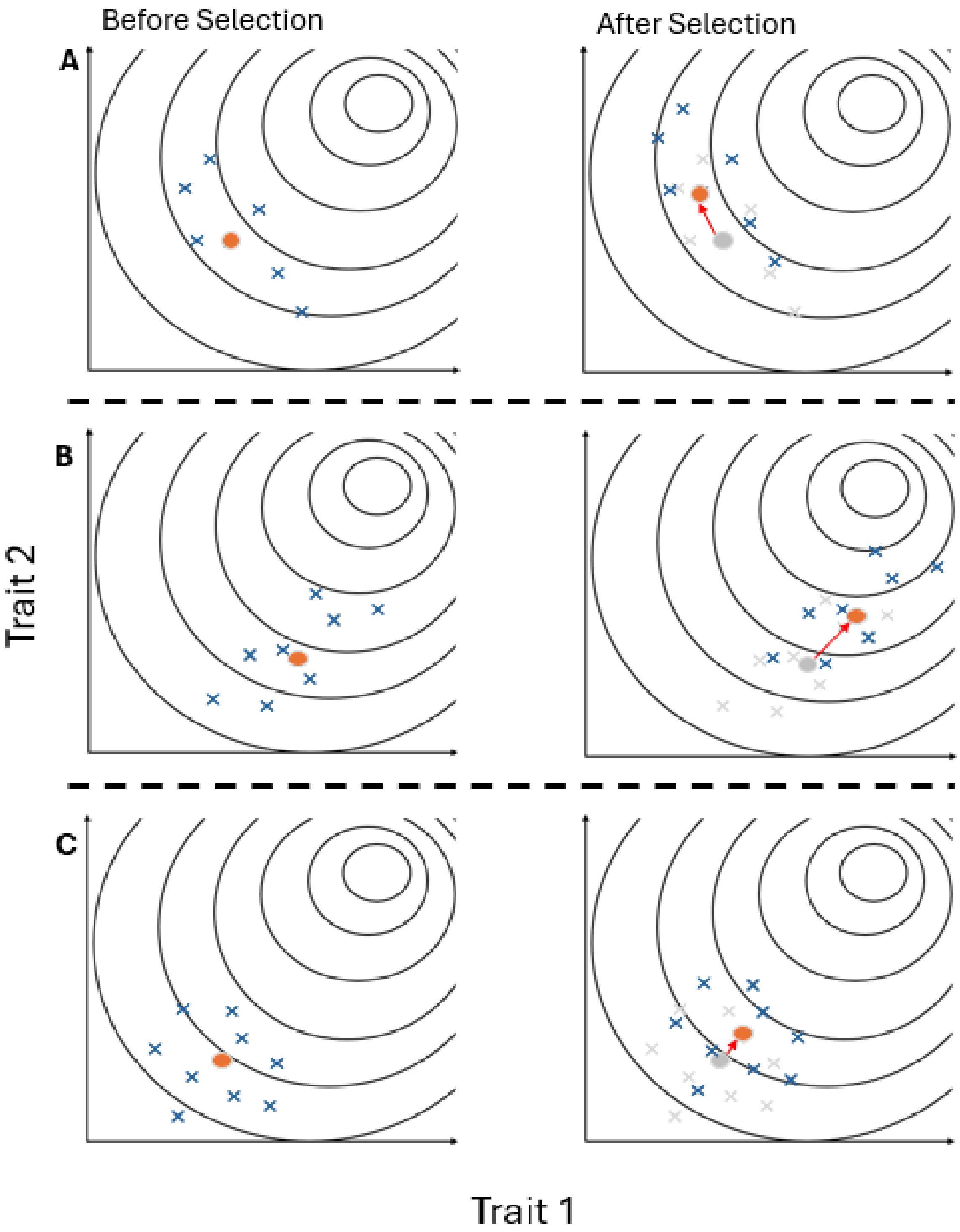


Figure 2. Hypothetical fitness landscapes for trait covariance that impedes (A) facilitates (B) or leaves response to selection unconstrained (C). Contour lines represent the topography of the fitness landscape with the top right corner representing the adaptive peak.

P. mariana is well adapted to tolerate cold environments, it is one of the species which marks the northern tree line of Canada and is particularly well adapted to waterlogged, poorly drained and rich organic soils (Burns, 1990), which contrast with the warming and drying climate. However, this generalist species grows on a wide range of soil conditions and is present along the entire range of the boreal forest (Burns, 1990). It is thus unclear how this cold- and wet-adapted species will persist in warmer and drier conditions that are expected to accompany climate change (Robert *et al*., 2024).

Here I ask, how does selection on *P. mariana* change along a spatial climate gradient, and do different *P. mariana* populations have trait covariances that accelerate or impede response to selection in a warm and dry environment? In each of three common garden sites which span a spatial temperature and water availability gradient, I studied seven provenances from across *P. mariana*'s range. I first assess for each site the strength and direction of selection on a set of traits associated with plant response to temperature and drought and then I assess which of the seven provenances, if any, have higher potential for adaptive evolution in the warmest and driest site.

METHODS

STUDY SITES

This research makes use of three sites from a range wide *P. mariana* provenance trial started in 1967 (Morgenstern and Kokocinski, 1976). Sites included in my research were selected based on the following criteria: sites containing the same planted provenances, sites including provenances that span as much of *P. mariana*'s range as possible, and sites which fall along a spatial temperature and water availability gradient.

The three sites selected are located near Petawawa, Ontario (PET); Chapleau, Ontario (LAU); and Chibougamau, Quebec (CHI). Five provenances are common to all three sites and two provenances, (6856 and 6979) are common to PET and CHI only. The provenances included in this research span the southern latitudes of the boreal forest, from Newfoundland to Alberta (Figure 3). The sites selected fall along a spatial temperature and water availability gradient (Figure 4). Site climates were defined with BioSIM data using the yearly averages from 1980-2020 (Fortin, 2022).

The warmest and driest of the three sites, PET, is characterized by a mean annual temperature (MAT) of 4.7 ºC and a climate moisture index (CMI) of -1 (Table 1). The intermediate site, LAU, has moderate MAT (1.5 ºC) and CMI (9). The coldest and dampest site, CHI, is characterized by a MAT of -0.4 ºC and a CMI of 27. In addition to temperature and water availability, sites were characterized by soil water holding capacity (WHC), total annual precipitation (TAP), spacing between trees, and survival of provenances (Table 1).

Each provenance trial was set up with at least three blocks. Within a block, 16 trees per provenance were planted in a 4x4 grid forming small plots with consistent spacing between the trees (Morgenstern and Kokocinski, 1976) (Figure 5). Spacing between trees differed among sites (Table 1).

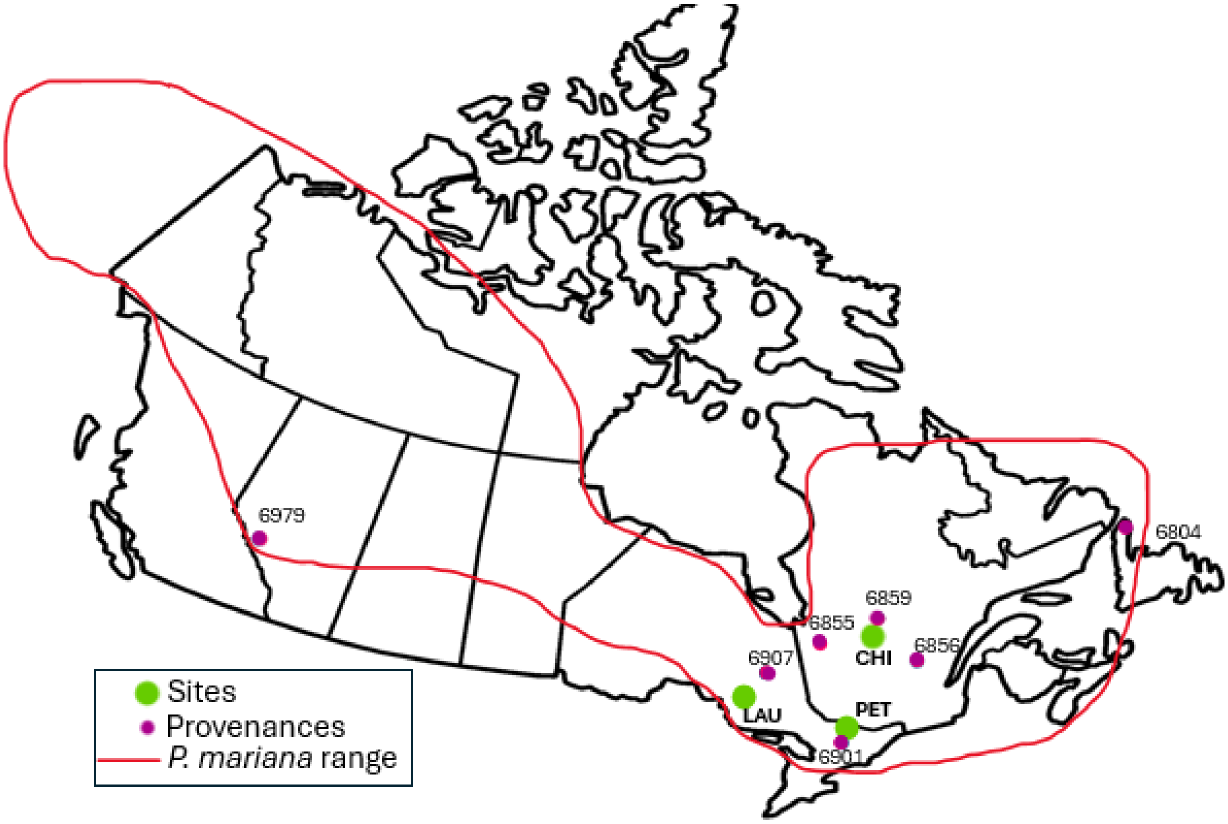


Figure 3. Location of each site (green) and provenance (purple) used in this study. Approximate range of the boreal forest shown in red.

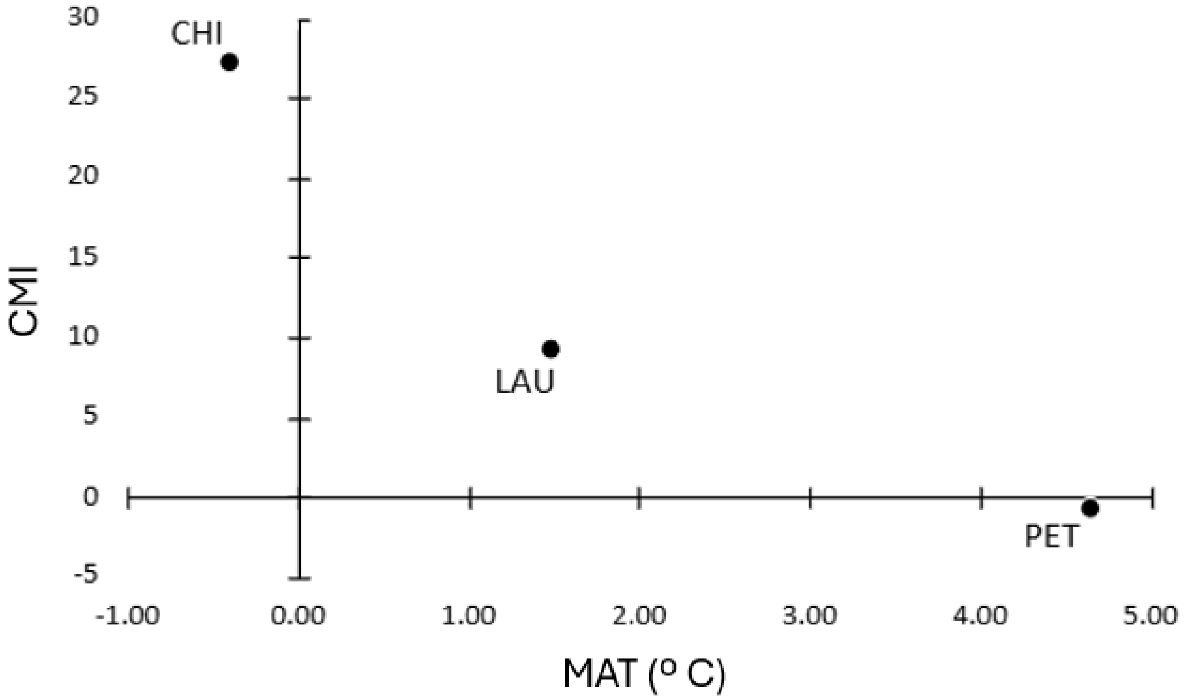
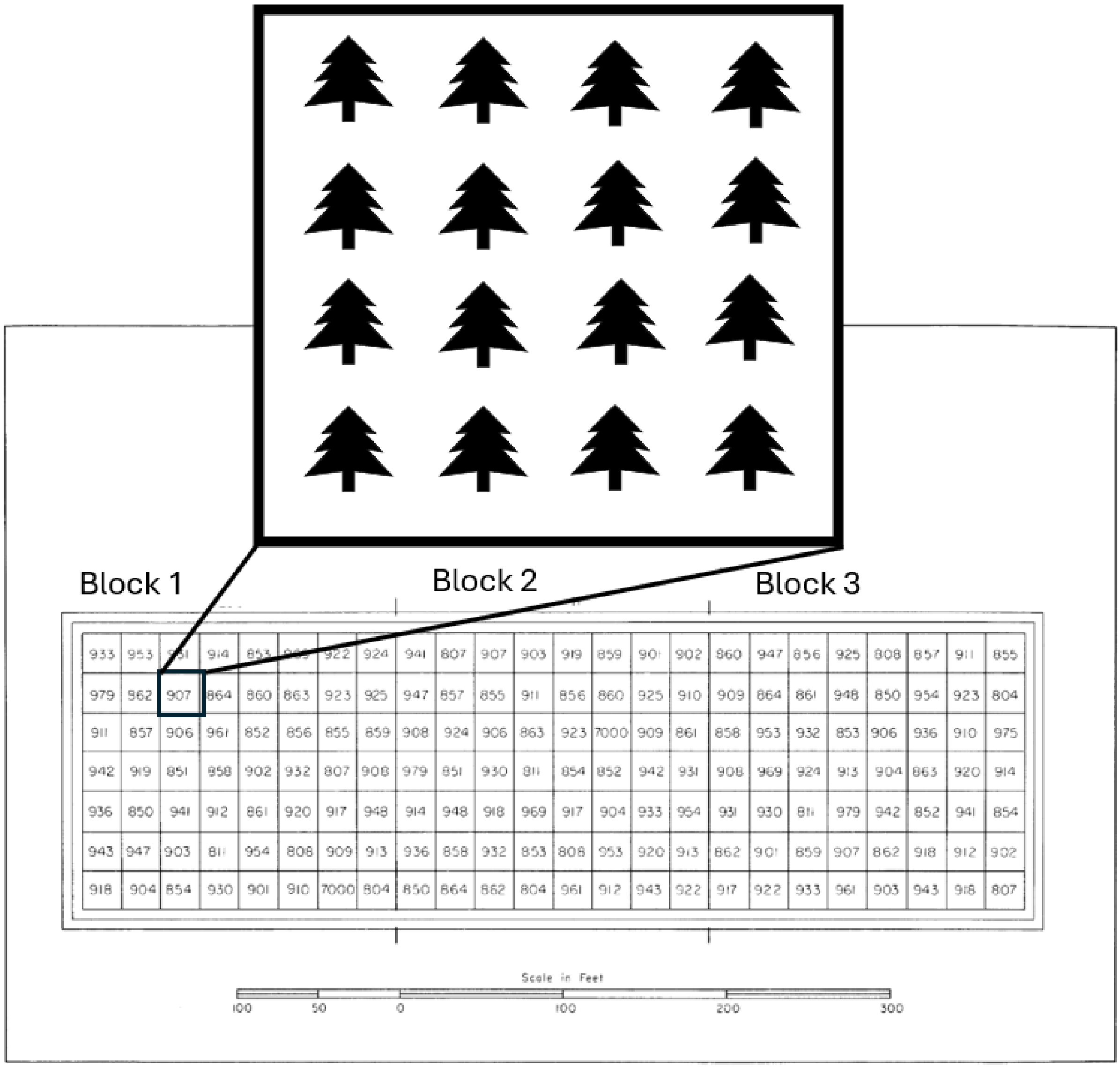


Figure 4. Visualization of the temperature (MAT) and water availability (CMI) between the sites used in this study.



933	953	951	914	853	969	922	924	941	807	907	903	919	859	901	902	860	947	856	925	808	857	911	855
979	962	907	864	860	863	923	925	947	857	855	911	856	860	925	910	909	864	861	948	850	954	923	804
911	857	906	961	852	856	855	859	908	924	906	863	923	7000	909	861	858	953	932	853	906	936	910	975
942	919	851	958	902	932	807	908	979	851	930	811	854	852	942	931	908	969	924	913	904	863	920	914
936	850	941	912	861	920	917	948	914	948	918	969	917	904	933	954	931	930	811	979	942	852	941	854
943	947	903	811	954	808	909	913	936	858	932	853	808	953	920	913	862	901	859	907	862	918	912	902
918	904	854	930	901	910	7000	804	850	864	862	804	961	912	943	922	917	922	933	961	903	943	918	807

Figure 5. Representation of provenance trial experimental set up (Morgenstern & Kokocinski, 1976). Numbers represent provenance IDs. Each provenance is planted once per block in a 4x4 grid of 16 trees.

Table 1. Table of site characteristics for PET, LAU and CHI.

Characteristic	PET	LAU	CHI
Mean Annual Temperature (ºC)	4.7	1.5	-0.4
Climate Moisture Index	-0.9	9.0	27.2
Total Annual Precipitation (mm)	841.6	842.3	975.5
Water Holding Capacity (%)	77.7	78.1	62.4
Spacing between trees (m)	1.8 x 1.8	1.8 x 1.8	2.4 x 3
Survival	42 % (n = 336)	65 % (n = 240)	78 % (n = 672)

GROWTH DATA

Height data was collected by Natural Resources Canada in 2022 for PET, 2023 for LAU and 2016 for CHI. The height of each individual tree was measured using a secant scale clinometer (Suunto, PM-5), commonly used in forestry to determine stand height. Relative growth rate (RGR; m/yr) over an individual's lifetime was calculated as the height of the tree divided by the age at the time of measurement.

TRAIT DATA

Individual trees were sampled from at least three blocks at each site. Branch samples were collected from PET in July 2022 and May 2023 (n = 143), from LAU in July 2023 (n = 156) and from CHI in July 2022 (n = 132). Since I only considered fully mature needles and some samples were not yet mature at the time of collection, needles that emerged during the year of collection (yr 0) were not considered. For tree branch sampling, it is common practice to sample the most sun-exposed branches of a tree in order to standardize the light environment however, the height and geometry of many trees prevented the collection of branches from the top of the crown. Therefore, I standardized for branch position in the crown. Each sampling morning, branches containing at least four years of complete growth were cut from the bottom of the top third of foliar branches using a 13.7 m telescopic pole pruner (HV-245 Tel-O-Pole). To keep the branches hydrated, the cut ends were placed in florist tubes filled with water. The branches were then placed in plastic bags with a damp paper towel, and stored in a cooler with ice until time-sensitive traits were measured indoors in the afternoon (Garnier *et al.*, 2001).

I measured 10 traits associated with tree response to temperature, water availability, or both. Three traits, Huber value (HV), water use efficiency (WUE) and needle carbon to nitrogen ratio (CN) were measured at the branch level. The other seven traits were measured for each of the four most recent years of mature growth. Branch level trait values were calculated from year-level trait values by taking an abundance-weighted average. The relative abundance was calculated from dry biomass, with needle biomass for needle traits and twig biomass for twig traits. For example, the branch-level mean needle length (NL) was weighted by the total dry needle biomass for each year of growth and twig specific density (TSD) was weighted by the total dry twig biomass for each year of growth. Traits were classified by association with structure, photosynthesis, or water use in plants (Table 2).

To characterize investment in structural support at the needle and branch levels, leaf dry matter content (LDMC; g/g) and twig specific density (TSD; g/cm^3) were measured (Poorter *et al.*, 2010; Bartlett *et al.*, 2012). The LDMC of 12 needles from each growth year was measured as needle dry mass divided by fresh mass, measured using analytical balances (10^{-4} g AG104 Metler Toledo from Switzerland, and 10^{-6} g XSR205 Metler Toledo, as needed). Needles were dried using a forced air oven at 60 ºC to a constant weight or for a minimum of 72 hours. To measure TSD, after removing the needles from the branch, the volume was measured for three fresh twigs per growth year. Since the twigs varied in size within a growth year, the three twigs were randomly sampled from a subset excluding the largest and smallest sizes. Twig fresh volume was measured using the water immersion method (Sukul *et.al.*, 1993). After fresh measurements, the twigs were dried at 60 ºC to constant weight for at least 72 hours and dry weight for three twigs was measured using analytical balances (10^{-4} g AG104 Metler Toledo from Switzerland, and 10^{-6} g XSR205 Metler Toledo, as needed). TSD was calculated for each of the three branches as twig dry mass (g) divided by twig fresh volume (cm^3) and averaged. Additionally, total dry twig biomass was measured for each growth year and used for abundance-weighted trait averaging.

Huber value (HV; mm/g), the ratio of sap-wood diameter to needle weight, was measured to characterize water supply per water demand at the branch level (Carter & White, 2009). Two perpendicular diameter measurements were taken at the base of the fourth oldest year of complete growth using electronic calipers (±0.01 cm, Series 500 ABSOLUTE Digimatic Caliper) and averaged. All needles were removed from the branch and dried at 60 ºC to constant weight. The total mass of needles for each branch was measured with the Mettler Toledo AG104 Analytical Balance. A high value for HV indicates a liberal water supply per needle weight whereas a low value for HV reflects conservative water supply per needle weight. HV was calculated as branch base diameter (mm) divided by the dry mass of the needles supplied by that branch (g).

To characterize water use and regulation at the needle level, water use efficiency (WUE; ‰) and stomatal density (SD; count/cm) were measured. To measure WUE, I used carbon isotope ratio ($\delta^{13}C$), which is commonly used to estimate intrinsic water use efficiency (Ma *et al.*, 2023).

During photosynthesis, $^{12}CO_2$ is preferentially fixed over $^{13}CO_2$ for various reasons, the main one being that the enzyme RuBisCO discriminates against $^{13}CO_2$ and only binds it when $^{12}CO_2$ is limited, which occurs when stomata are closed (Farquhar *et al.*, 1982; Lambers *et al.,* 2008). The ratio of ^{13}C to ^{12}C present in plant tissue, therefore reflects the amount of time leaves spent with their stomata closed, and $\delta^{13}C$ gives the ^{13}C isotope composition relative to the primary reference scale of Vienna Pee Dee Belemnite. Needles from all growth years were combined and ground into a fine powder using a ball mill grinder to ensure a homogenous mixture. Analysis of carbon isotopes was performed at the Environmental Isotope Laboratory at the University of Waterloo. The analysis for ^{13}C isotope measurements was done by combustion conversion of sample material to gas through a 4010 Elemental Analyzer (Costech Instruments, Italy) coupled to a Delta Plus XL (Thermo-Finnigan, Germany) continuous flow isotope ratio mass spectrometer (CFIRMS). To determine the homogeneity of the ground needle samples, duplicate measurements were performed for 34 samples, spaced at regular intervals throughout the measurement process. To measure SD images of needle abaxial surface were taken using Leica EZ4 W stereo microscope at 35X magnification and the microscope imaging software LAS X for Life Sciences (Leica Microsystems, 2021). Since stomata were not clearly visible over the full length of the needles, the number of stomata along the maximum length possible was recorded along with stomata count using WinSeedle Software (Regent Instruments, 2020).

Needle cooling (NC; ºC), the needle temperature relative to ambient temperature, was measured to assess needle thermal regulatory ability. Under the ‘limited leaf homeothermy’ hypothesis leaves buffer environmental variation by controlling internal leaf temperature to maintain the optimal temperature range for the photosynthesis reaction (Michaletz *et al.*, 2015). These measurements were taken while the branches were secured in a florist tub full of water to maintain needle transpiration. Needle temperature was measured indoors, on-site, a few hours after sample collection, using a thermal camera, TCAM-300 (Infrared Camera INC, 2021). To validate the thermal camera's measurements, a high accuracy temperature sensor (TS, ± 0.1 ºC, TMP117 High-Accuracy, Low-Power, Digital Temperature Sensor) was included in each image. The sensor plate of the TS was placed inside each thermal image and its temperature was recorded when each thermal picture was taken. The difference between the temperature recorded on the TS and the temperature of the sensor plate on the thermal camera was used as an adjustment for all temperature readings in each thermal image. Needle cooling was measured for each of the four most recent complete years of growth and was calculated as needle temperature minus ambient temperature.

To characterize photosynthetic ability of the needles, the concentration of chlorophyll (CHL; mg/m^2) was measured using a chlorophyll content meter: CCM-300 (Opti-Sciences). The CCM-300 uses the fluorescence ratio technique to measure total chlorophyll content (Gitelson *et al.*, 1999). A few hours after sample collection, CHL was measured for healthy needles from each of the four most recent years of mature growth.

Leaf mass per area (LMA; mg/cm^3) represents the leaf level cost of light interception and in global interspecific comparisons is an important indicator of plant carbon-use strategies (Gutschick & Wiegel, 1988; Grime, 2001; Westoby *et al.*, 2002). To measure needle fresh area (cm^3), 12 needles from each of the four most recent years of complete growth were haphazardly selected and scanned using the STD4800 Scanner for WinRhizo and WinSeedle and area was measured using WinSeedle software (Regent Instruments, 2020). Needles were dried in a VWR Forced Air Incubator at 60 ºC to a constant weight for a minimum of 72 hours and needle dry weight was measured using analytical balances (10^{-4} g AG104 Metler Toledo from Switzerland,

and 10^{-6} g XSR205 Metler Toledo, as needed). LMA was calculated for each growth year as the weight of the 12 needles over their area.

Needle length (NL; mm) is an indicator of the size of the needle and affects a plant's light capture, water balance, and thermal stability (Perez-Harguindeguy *et al*., 2013). To measure NL needles were scanned using the STD4800 Scanner for WinRhizo and WinSeedle and the length of the needle was measured using WinSeedle software (Regent Instruments, 2020). NL was measured for 12 needles from each of the four most recent full years of growth and the average length of the needles was calculated for each growth year.

Table 2. Traits measured, abbreviations, units, and associated physiological function(s).

Trait	Unit	Function
Leaf dry matter content (LDMC)	g g^{-1}	Structural investment
Twig specific density (TSD)	g cm^{-3}	Structural investment
Huber value (HV)	mm^2 g^{-1}	Water use and transport
Water use efficiency (WUE)	‰	Water use and transport
Stomata density (SD)	count cm^{-1}	Water use and transport
Needle cooling ability (NC)	ºC	Photosynthesis
Chlorophyll concentration (CHL)	mg m^{-2}	Photosynthesis
Needle carbon to nitrogen ratio (CN)	g g^{-1}	Photosynthesis
Leaf mass per area (LMA)	mg cm^{-3}	Structure + Photosynthesis
Needle length (NL)	mm	Structure + Photosynthesis + Water use and transport

STATISTICAL ANALYSIS

All statistical analyses were conducted in R version 4.4.0 (R Core Team, 2024). Two percent of all data was missing due to lost samples or measurement errors. In PET, 3% of the data was missing, in LAU, <1% of the data was missing and in Chibougamau, 3% of the data was missing. Missing values were imputed for each site using linear predictive models. Traits as predictors which yielded models with the highest predictive power for missing values were identified using the “dredge()” function from the “MuMIn” package. Data were only imputed when the prediction model R^2 value was above 0.6. Otherwise, the missing values were left as NA. After imputation, there was less than 0.01% data missing from each site for sample sizes of n = 142 trees in PET, n = 151 trees in LAU, and n = 132 trees in CHI.

To identify significant differences in survival among sites and among provenances within sites one-way ANOVAs were used. Due to missing provenances in LAU (6956 and 6979) a two-way ANOVA to accommodate both Site and Provenance as factors was not possible. Principal component analyses (PCAs) were conducted on trait data within each site using the “PCA()” function of the “FactoMineR” package to assess trait covariance strength and structure.

Standardized selection gradients were measured for each site by regressing relativized RGR onto all 10 standardized traits and their two-way interactions using multiple linear regression models using the function “lme()” from the “nlme” package (Connor 1988). Traits were standardized by taking the z-scores for all trait values within each site. Additionally, RGR was relativized by dividing RGR values within a site by the mean RGR value for that site. In this method, the partial regression coefficients represent the strength and direction of selection, referred to as selection gradients (β) (Lande and Arnold, 1983). To control for the effect of different lineages, provenance was included as a random factor in each model.

Differences in selection between the two most extreme sites, PET and CHI, were assessed using t-tests to determine statistical significance using the “tsum.test()” function from the “BDSA” library. Additionally, selection gradients that changed directionally with the climate gradient were interpreted as being driven by the climate gradient.

In order to test whether trait integration was aligned with the direction of selection, significant selection gradients in PET were used to create performance surfaces (trait1 x trait2 x RGR) using the “geom_contour()” function in “ggplot” library. The performance surface is a topographic map of selection and allows us to visualize the peaks and valleys of performance in relation to traits. Smooth contour lines were generated using the “interp()” function from the “akima” library. This helped to remove noise from the data so trends in the performance surface could be better identified. For each provenance, significant correlations between the residuals of the traits were determined using the Pearson Correlation Coefficient from the “cor.test()” function from the “stats” library. The residuals of the traits from the regression models were collected using the “residuals()” function from the “stats” library. Significant correlations between phenotypic traits were later assessed to determine if integration might facilitate a provenance’s response to selection.

RESULTS

SURVIVAL

Average survival was significantly lower in Petawawa (42%) than in the other two sites (LAU: 65%, CHI: 69%) (Figure 6). In terms of differences in provenance survival, in Petawawa there was no significant difference among the survival of provenances (One-way ANOVA, $F_{(6,14)} = 1.113$, $p = 0.403$). However, in Chapleau and Chibougamau the survival of some provenances differed. In Chapleau, it was significantly lower in provenance 6907 (39.58%) than in provenance 6855 and 6859 (83.33% and 79.17% respectively; One-way ANOVA, $F_{(4,10)} = 3.491$, $p = 0.0495$). In Chibougamau provenance 6979 had significantly lower average survival (45.00%) than provenances 6855, 6856 and 6907 (83.75%, 77.50%, and 77.50% respectively) (One-way ANOVA, $F_{(6,28)} = 2.492$, $p = 0.0466$).

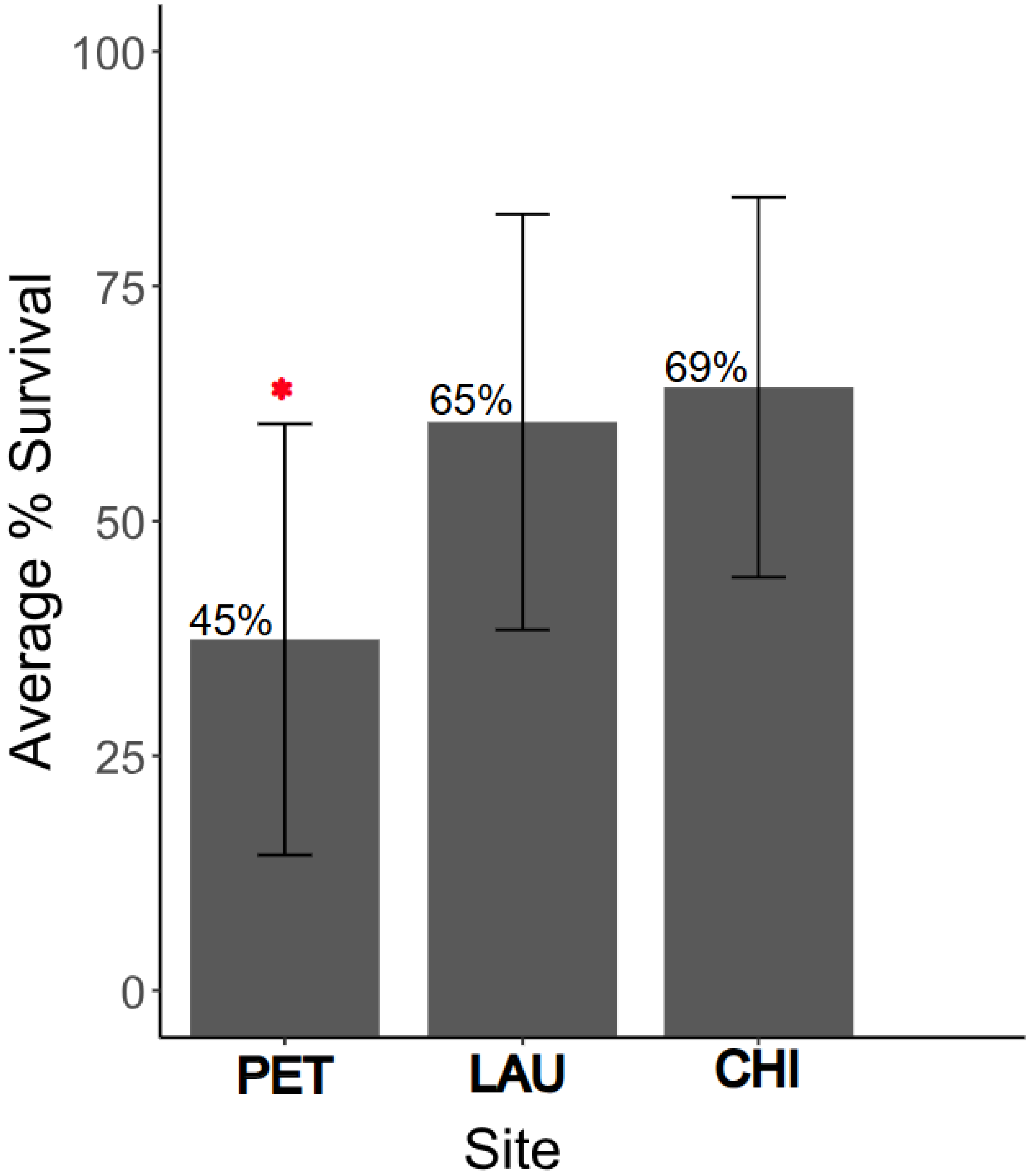


Figure 6. Average percent survival of individual trees in each of the three study sites. Red star represents significantly different site (PET: n = 336, LAU: n = 240, CHI: n = 672).

TRAIT SELECTION ALONG THE CLIMATE GRADIENT

All 10 traits measured experienced significant selection in at least one site, either alone or in interaction with another trait, hereafter referred to a trait interaction and represented by trait1*trait2 (Figure 7). Many traits were under selection, with a total of 17 significant selection gradients across all 3 sites. Across sites, most of the selection gradients (β) were for trait interactions (12 out of 17). In Petawawa, most β were positive (6 out of 7) and in Chibougamau most β were negative (7 out of 9). Here a positive trait interaction β indicates that individuals with high performance are associated with high values of both traits. For example, in PET high CHL is associated with high performance only in individuals that also have high LDMC. A negative trait interaction β indicates that individuals with high performance are associated with a high value in the first trait combined with low values in the second trait, and vice-versa (low value in the first trait combined with a high trait value for the second trait). For example, in PET individuals with high performance either had high NL and low CN values, or low NL and high CN values. The traits and trait interactions under selection differed among sites. In Petawawa, three traits were under significant or marginally significant selection: WUE ($\beta = 0.044$, $p < 0.01$) CN ($\beta = 0.029$, $p = 0.10$) and NL ($\beta = 0.028$, $p = 0.17$). Four trait interactions were under significant or marginally significant selection: WUE*HV ($\beta = 0.025$, $p = 0.01$) CHL*LDMC ($\beta = 0.023$, $p = 0.06$), CN*HV ($\beta = 0.021$, $p = 0.06$) and NL*CN ($\beta = -0.022$, $p = 0.01$) (Figure 7). In Chapleau selection only acted on LC*LMA ($\beta = -0.037$, $p = 0.04$) (Figure 7). In CHI only one trait was significantly under selection TSD ($\beta = -0.068$, $p = 0.03$) and 8 trait interactions were under significant or marginally significant selection: CHL*HV ($\beta = -0.097$, $p = 0.02$), CHL*TSD ($\beta = 0.083$, $p = 0.05$), NL*LC ($\beta = -0.069$, $p = 0.03$), NL*SD ($\beta = -0.087$, $p = 0.05$), LC*TSD ($\beta = 0.055$, $p = 0.03$), WUE*HV ($\beta = -0.068$, $p = 0.03$) and WUE*TSD ($\beta = -0.080$, $p = 0.03$) and LDMC*HV ($\beta = -0.068$, $p = 0.07$).

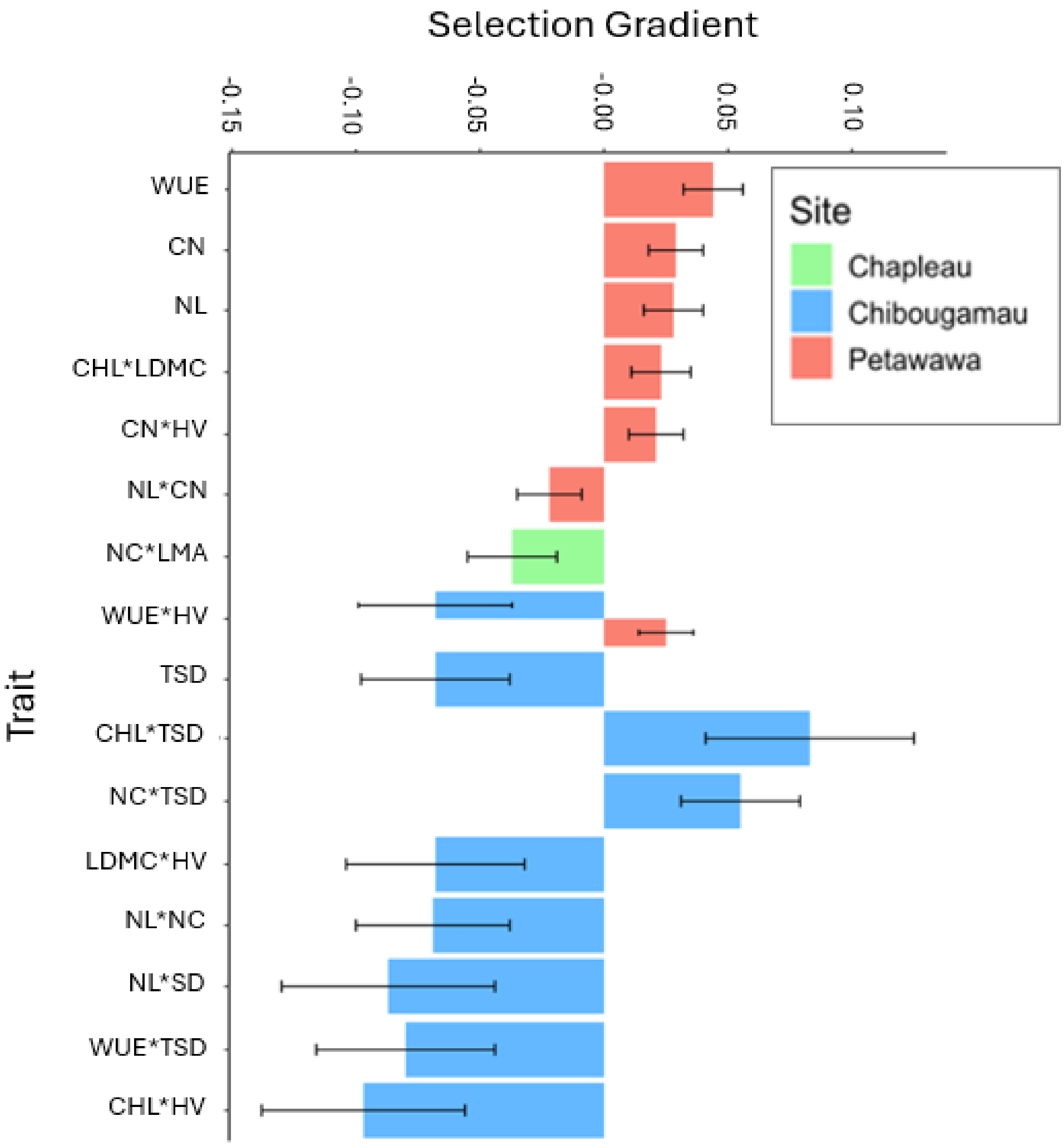


Figure 7. Significant and marginally significant selection gradients (β) for each of the three sites. Error bars represent standard error.

DIFFERENCES IN SELECTION ASSOCIATED WITH CLIMATE

To identify differences associated with climate, I identified the β changing directionally with the climate gradient among the three sites. Here I make the assumption that changes that occur directionally along our climate gradient are likely due to climate. While I acknowledge that there are many factors that vary among natural environments, directional changes along our gradient are most likely due to differences in climate, because the other factors known to differ among the sites do not differ directionally (Table 1). Selection gradients in Petawawa that varied directionally with climate are WUE, CN, WUE*HV, and CN*HV (Figure 8). The selection gradients for WUE and WUE*HV significantly differed between PET and CHI (two-sample t-test, $p = 0.046$; two-sample t-test, $p = 0.025$, respectively; Figure 8). The selection gradients for CN and CN*HV were marginally different between PET and CHI (two-sample t-test, $p = 0.060$, $p = 0.092$; Figure 8)

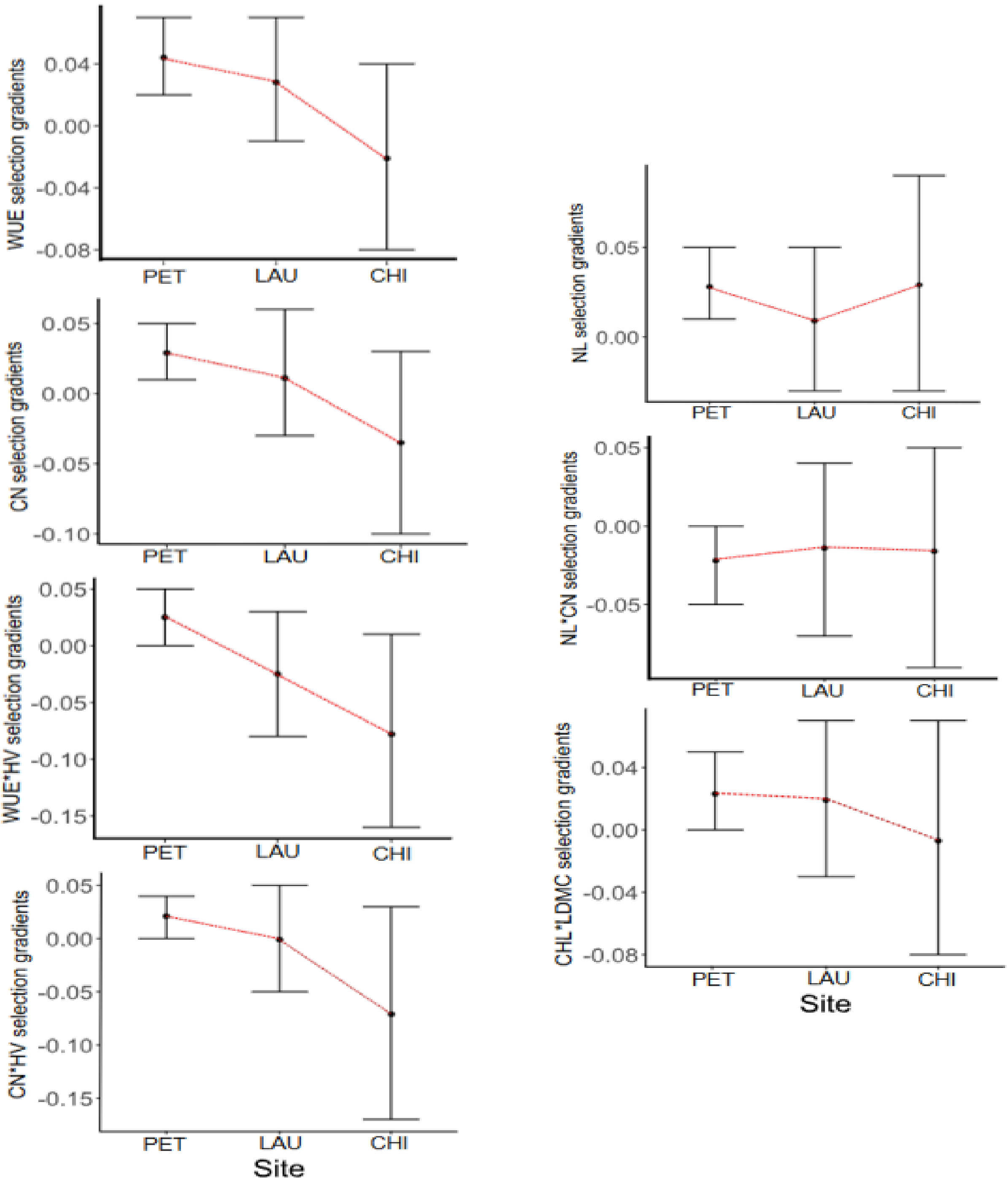


Figure 8. 95% Confidence intervals of βs in each site for βs under significant selection in Petawawa.

PHENOTYPIC INTEGRATION IN *P. MARIANA* PROVENANCES

In general, traits showed weak covariation. For the experiment wide PCA on trait values, together the first two principal components accounted for only 34.1% of total trait variation (Figure 9). The site-specific PCAs for PET and LAU are different from each other and from the experiment wide PCA. The amount of variance explained by the first two axes of the site-specific PCA remained low (PET: 32.5%; LAU 37.5%; CHI: 41.6%) (see Supplementary Information Appendix S1 Table S3 for loadings).

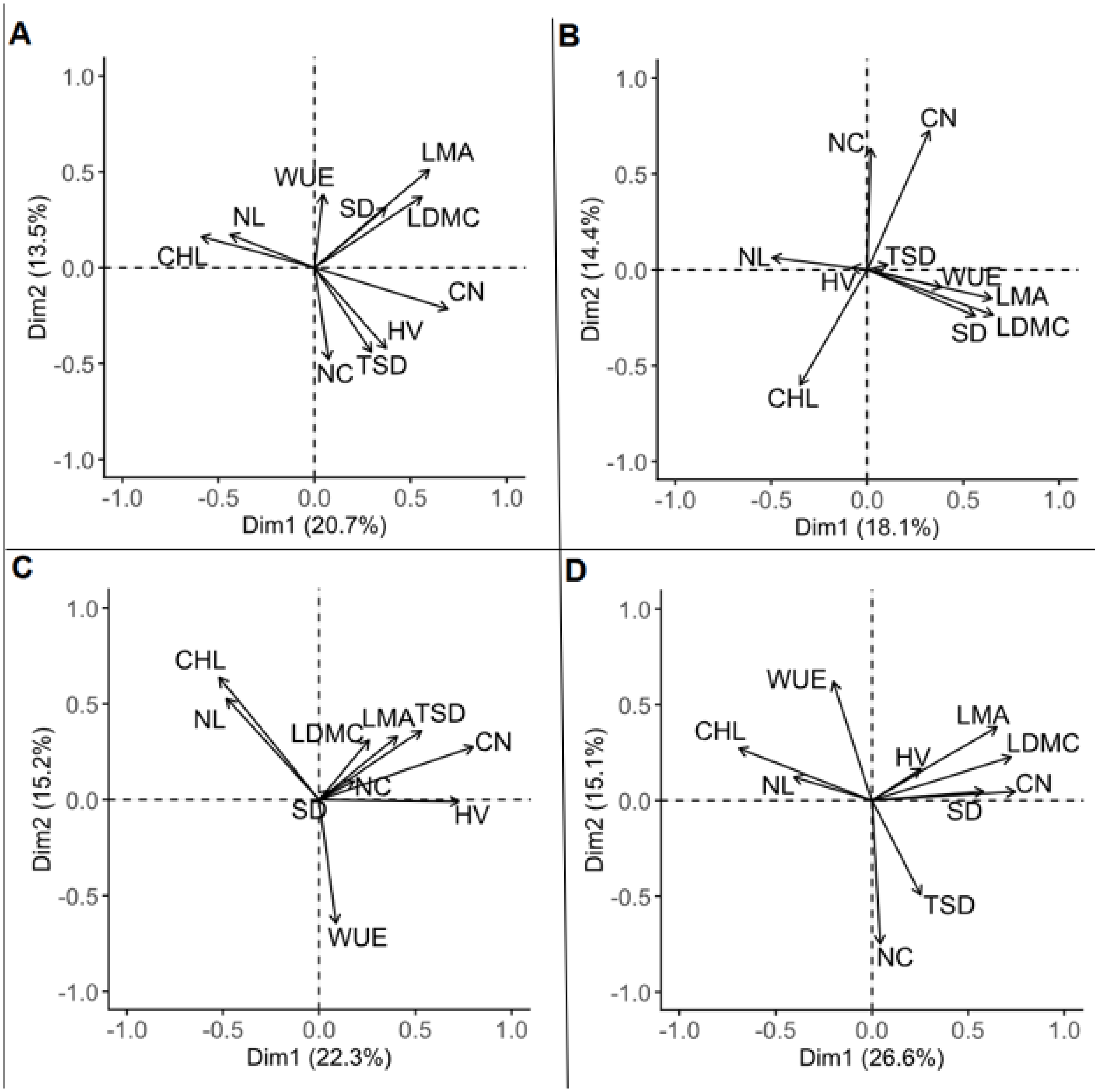


Figure 9. PCA of trait values among all the sites as well as for individual sites. Tell us what the circles mean. PCAs of trait values among all sites (A), in PET (B), in LAU (C) and in CHI (D).

Most traits under selection in PET are not correlated, except for three trait pairs with significant covariances in one or two provenances: WUE and NL in 6804, CN and HV in 6979 and 6855. The covariance between WUE and NL in provenance 6804 is largely perpendicular to the direction of selection (Pearson's correlation, t = -0.194, df = 20, p = 0.021, r = -0.53, Figure 10A). Similarly, the covariances between needle CN and HV for provenances 6855 and 6979 are largely perpendicular to the direction of selection (Pearson's correlation, t = -2.75, df = 20, p = 0.012, r = -0.52, Figure 10C & D) (Pearson's correlation, t = -2.30, df = 11, p = 0.042, r = -0.57).

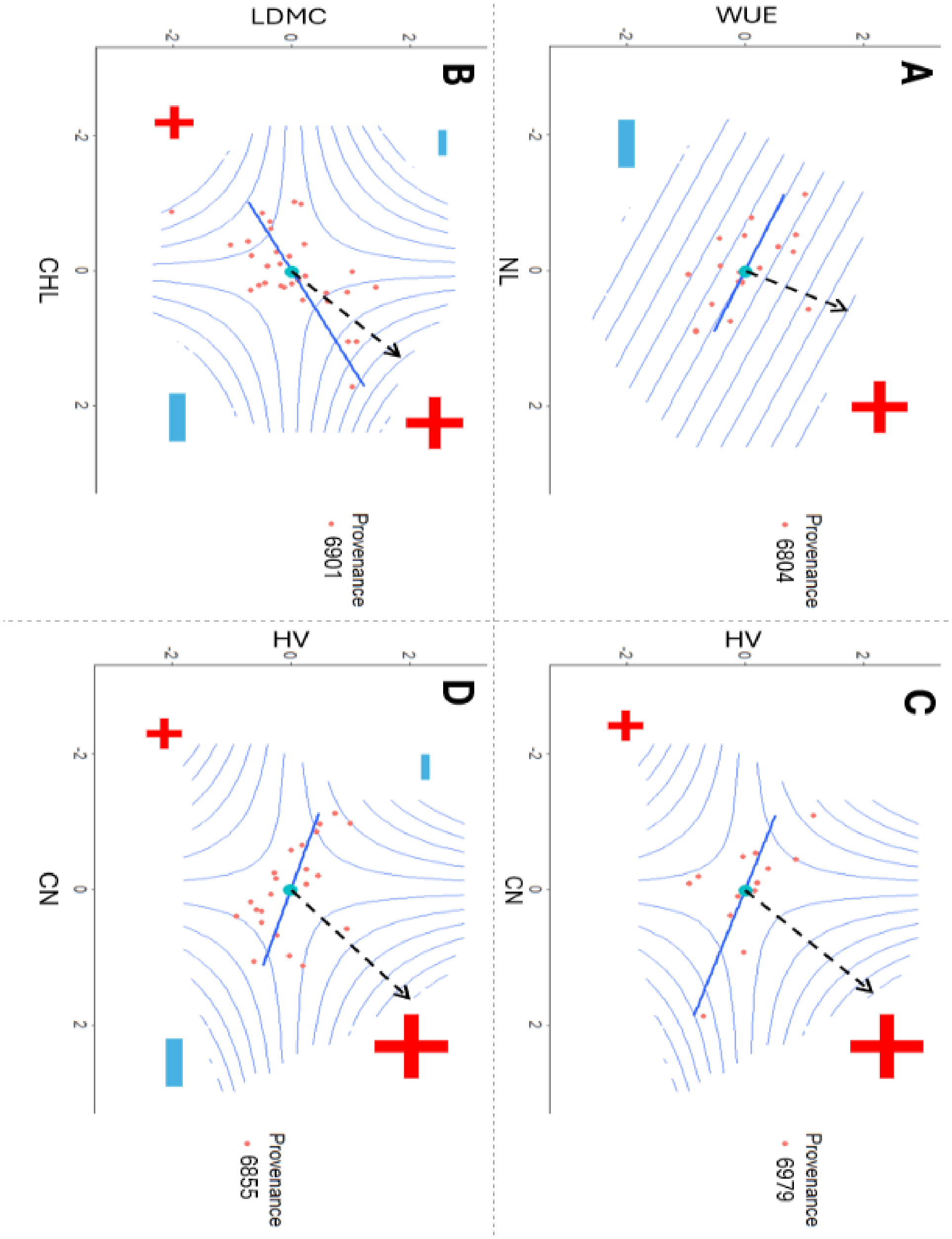


Figure 10. Significant intra-provenance trait covariances in traits under climate-linked selection.

DISCUSSION

The differences in climate among the sites in this study were large enough to adequately detect differences in selection. Further, the directional change in selection along the climate gradient are consistent with the expectation that selection at each site is partly driven by climate (Linhart & Grant, 1996). The lower survival of *P. mariana* individuals in the warmer and drier site (PET), suggests that the climate at his site is stressful for the trees and leads to stronger selection than in cooler climates. Additionally, the traits under selection in each site showed significant differences between selection gradients in the warmest site (PET) and the coldest site (CHI). These changes in selection on traits in these two sites confirm that the climate gradient used in this research is broad enough to register the influence of climate on patterns of selection.

P. mariana experienced lower survival in the hottest and driest site, indicating that the fitness of these trees is likely lower in a warm and dry environment. The low survival in a warm and dry environment provides insight into the strength of selection on the full phenotype before selection was measured for individual traits. In principle, within a generation, the adaptive plasticity of a population could help to maintain survival and thus fitness in the face of climate change (Bradshaw, 1965; C. D. Schlichting, 1986; Sultan, 1987; Van Tienderen, 1991; C. Schlichting, 1998; Kingsolver *et al*., 2001). Although the provenances did exhibit trait plasticity (Figure S1), the low survival rate in Petawawa indicates that the adaptive plasticity of the *P. mariana* provenances to hot and dry environments is insufficient to maintain survival at levels similar to those in cooler climates. If findings from this spatial climate gradient apply to the temporal effects of climate change on *P. mariana* in general, this will likely result in a lower abundance of *P. mariana* individuals as climates increase in temperature and decrease in water availability.

First, the lower survival in the warmer and drier site resulted in weaker selection gradients in Petawawa than at the other sites. Weak selection gradients despite strong selection can occur because of low variation in trait values (resulting in survivor bias) (Mitchell-Olds & Shaw, 1987; Wade & Kalisz, 1990). In other words, mortality of individuals led to an underestimate of the selection gradients. Further, since biomass is often allocated in priority to the most limiting resource a common response to water limitation is a shift in biomass allocation to belowground growth (Poorter *et al*., 2012). If belowground allocation increases plastically with water limitation, then height-based RGR would become an increasingly poor indicator of performance in increasingly water-limited sites. Thus, the weaker selection gradients in PET could be an artifact of aboveground relative growth rate becoming an increasingly imperfect indicator of performance at the drier site.

The magnitude of selection in this study is smaller than the values from the body of literature. Selection gradients for natural populations typically range from negative one to one, with a mean of 0.22 and median of 0.16 (Kingsolver *et al*., 2001), whereas the largest selection gradient in this study is 0.07 in CHI and the smallest is 0.021 in PET. To contrast this, experimental studies have been shown to detect stronger selection than observational studies since they can impose more extreme environmental conditions than are naturally present (Caruso *et al*., 2017). As such the pressures faced in the natural environment may be less severe resulting in lower selection pressures. However, selection in the present study was lower than what is typically observed in natural environments. One possible explanation is that all the provenances used in this study originated from the southern latitudes of *P. mariana*'s range, where environmental conditions may not differ drastically from those experienced in previous generations. As a result, the fitness of the present individuals may have been somewhat impacted but not to a large extent, leading to relatively moderate fitness levels for surviving individuals. This aligns with findings that lower fitness tends to result in larger selection gradients (Caruso et al., 2017). Therefore, the low selection gradients in this study indicate that the fitness of surviving individuals is high compared to other selection studies in the literature. Again, this is likely due to the mortality in the experiments, removing low performing individuals before this study took place.

Response to selection for the *P. mariana* provenances under study is largely unconstrained by phenotypic covariance. Phenotypic integration is unlikely to hinder or facilitate response to selection of *P. mariana* in warmer climates. Not only is the overall strength of trait integration weak, as shown by the PCAs performed within site, but very few of the provenances showed intra-provenance covariation for the four climate-linked selection gradients. A corollary of the lack of trait integration in all provenances is that their integration does not differ, and none of the studied provenances show higher adaptive potential compared to others. The three instances where trait covariation was present in fact showed integration that would slow down evolutionary response to selection. However, given the rarity of these instances, overall, I do not expect integration to play a meaningful role in black spruce response to selection from warming climates. Over the long term given unknown future environmental change, low integration is beneficial as is provides more flexibility for the phenotype to respond to selection.

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