Drought tolerance and growth in populations of a wide-ranging tree species indicate climate change risks for the boreal north

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Abstract

Choosing drought-tolerant planting stock in reforestation programs may help adapt forests to climate change. To inform such reforestation strategies, we test lodgepole pine (*Pinus contorta* Doug. ex Loud. var *latifolia* Englm.) population response to drought and infer potential benefits of a northward transfer of seeds from drier, southern environments. The objective is addressed by combining dendroecological growth analysis with long-term genetic field trials. Over 500 trees originating from 23 populations across western North America were destructively sampled in three experimental sites in southern British Columbia, representing a climate warming scenario. Growth after 32 years from provenances transferred southward or northward over long distances was significantly lower than growth of local populations. All populations were affected by a severe natural drought event in 2002. The provenances from the most southern locations showed the highest drought tolerance but low productivity. Local provenances were productive and drought tolerant. Provenances from the boreal north showed lower productivity and less drought tolerance on southern test sites than all other sources, implying that maladaptation to drought may prevent boreal populations from taking full advantage of more favorable growing conditions under projected climate change.

Introduction

As the glaciers of the last ice age retreated in western North America, tree species have slowly re-colonized from glacial refugia and have become adapted to local environments over generations (Aitken *et al.*, 2008). Such adaptations include drought tolerance mechanisms, which are important in areas like the interior plateaus of western North America, where climates are characterized by dry and hot summers. Tolerances of tree populations in these areas can potentially be exceeded as climates continue to warm (St. Clair & Howe, 2007; Allen *et al.*, 2010; Alberto *et al.*, 2013). Maladaptation may be an issue not only for the populations at the southern and low elevation range limits, but might be observed throughout the distribution of wide-ranging species due to climate adaptation of local sub-populations (Aitken & Whitlock, 2013). Already, reduced tree productivity and survival is considered to be a major threat in the Northern Hemisphere due to drought (Allen *et al.*, 2010; Peng *et al.*, 2011; Anderegg *et al.*, 2013). To mitigate such negative impacts, management strategies to increase the adaptive capacity of forests are urgently needed.

Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var *latifolia* Englm.) is one of the most widespread tree species in western North America. It is an ecologically and economically important tree and is therefore of particular concern for climate change adaptation. Lodgepole pine can grow in environments where mean annual temperatures are as low as −5 °C and as high as 12 °C, covering over 4000 km of latitude in western North America (Little, 1971): Subpopulations occurring within this range are adapted to very different climate environments (Rehfeldt *et al.*, 1999). Under projected climate change, populations that cannot migrate to matching climatic conditions within close distance, for example, up in elevation, may become increasingly maladapted to new climate environments (Aitken & Whitlock, 2013). The general increase in temperatures is expected to be associated with an increase in severe drought events across the interior plateaus of western North America. For example, what used to be a once in a 100-year drought event during the climate normal period from 1961 to 1990 might be expected to occur

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once every 5 years by the 2080s (Christidis *et al.*, 2014). Reforestation with more drought-tolerant planting stock may therefore be a prudent climate change adaptation strategy for this region.

Choosing appropriate planting material for reforestation is a tool that forest managers can use to adapt forests to changing conditions (St. Clair & Howe, 2007; O'Neill *et al.*, 2008a). Normally, reforestation programs geographically constrain their seed movement under the paradigm that local provenances are optimally adapted. However, moving planting stock northward or higher in elevation to re-align the population with the climate environments that they are adapted to is now being considered by some managers (O'Neill *et al.*, 2008b). This concept is known as assisted migration and has been suggested as a means to conserve species with declining populations or to maintain forest health and productivity. One major concern over assisted migration, however, relates to long transfer distances. If populations are moved to habitats far outside of their historical range, they may react in unpredictable or invasive ways, or they may introduce new pests and pathogens to an area (Marris, 2009; Ricciardi & Simberloff, 2009). Forest applications may pose fewer risks, however, because populations are primarily moved within their existing range or somewhat beyond the leading edge of the distribution. This is known as assisted migration, also referred to as assisted gene flow in this context (Aitken & Whitlock, 2013). Northward transfers may nevertheless result in planting stock being more susceptible to cold injury (e.g., Benito-Garzón *et al.*, 2013).

The most suitable provenances for reforestation efforts are often determined through provenance trials that have been established for the most important forest tree species. Provenance trials involve testing multiple populations from across a species range across the planting environments of interest, similar to common gardens in agriculture (Morgenstern, 1996). Through observation of the phenotype in a constant environment, these experiments can be used for assessing genetic differences and the interaction between the genotype and the environment. Beyond the initial intention, these trials have also emerged as opportune climate change laboratories (Mátyás, 1994; Schmidtling, 1994; Carter, 1996; Leites *et al.*, 2012): Testing a northern seed in a warmer climate in the south can indicate how northern forests will react under projected climate change. This now offers the opportunity to re-evaluate historic location-based seed transfer limits and select the best provenances for a warmer, more drought-prone climate.

The IUFRO-Illingworth lodgepole pine provenance trial (Illingworth, 1978) that we analyze in this study is arguably the largest provenance trial series in existence, and it has been previously used to infer potential climate change impacts. Rehfeldt *et al.* (1999) were the first to assess the optimal climatic niche space of provenances and potential consequences of climate change. Subsequently, complex universal response functions were used to assess growth responses (Wang *et al.*, 2006a, 2010; O'Neill *et al.*, 2008a), and tree-ring analysis on selected provenances to extend these response functions has also been carried out (McLane *et al.*, 2011a,b). These studies indicated that climate change will generally increase growth of lodgepole pine, especially in the northern regions of its distribution. Since then, the mountain pine beetle epidemic that has decimated millions of hectares of lodgepole pine forests in western North America has also destroyed many sites of this provenance trial, affording the opportunity to destructively sample trees from these experiments for whole-tree analysis of interannual variation in growth.

Here, we use height, diameter, and basal area increments in over 500 trees originating from 23 populations across western North America that were destructively sampled on three experimental sites in southern British Columbia, selected for representing the warmest and driest environments in the IUFRO trial series that comprises a total of 60 test sites. We focus on a 7-year period that includes an extended drought in 2002. The specific objectives were to (i) assess genotype-by-environment interactions by evaluating climate–growth relationships for each population; (ii) quantify drought resistance, resilience, and recovery of different populations using height and basal area growth to evaluate potential trade-offs among different populations; and (iii) suggest reforestation strategies by considering performance and trade-offs in all populations.

Materials and methods

Experimental design

When the Illingworth lodgepole pine provenance trial was developed over 40 years ago, it was designed for determining the best planting stock from a productivity perspective. Hence, not all of the original 153 provenances were tested at all 60 sites (Illingworth, 1978). We therefore selected 23 provenances that were widely planted, representing four climatic regions of western North America: the United States (US), British Columbia's Southern Interior (SI), British Columbia's Central Interior (CI), and the Northern region of British Columbia and Yukon (N). Five or six provenances were chosen to be climatically representative of these four regions (Fig. 1, Tables 1 and 2). To evaluate drought response under climate change, we focus on the three planting sites in the southern interior
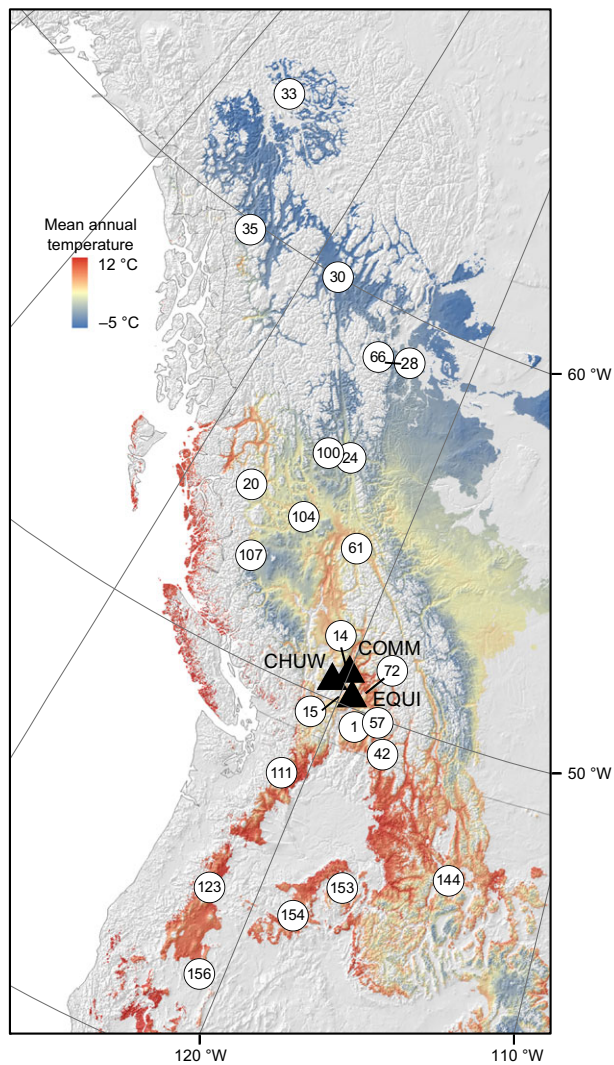
Fig. 1 Map of western North America showing the lodgepole pine (*Pinus contorta* Dougl. ex. Loud. Englm.) species distribution, colored by mean annual temperature. The planting sites are represented by black triangles. Each circle represents a provenance, numbered according to Illingworth (1978).

region of British Columbia with the warmest and driest climate conditions (Fig. 1).

Field and laboratory measurements

Each of the three test sites is represented by two blocks, where provenances are planted in 9-tree plots arranged in a randomized complete block design. The trees were planted in 2.5 × 2.5 m spacing. To minimize the effects of varying competition on growth, we tried to select trees that, by the time of death, had still been surrounded by neighboring trees. At each block, four trees were cut and measured per provenance for a total of 513 trees (a few blocks did not contain a sufficient number of dead trees for sampling). Because most trees were approximately 32–35 before being killed by the mountain pine

beetle, they were roughly mid-rotation age. After a tree was felled and de-limbed, we used an Eslon tape to measure tree length. Stem disks were collected at 0.3 and 1.3 m above ground and at each tree's half-height. As the exact year of tree death at each site was not known, a few living trees from each site were cut and stem disks taken for cross-dating purposes.

All of the approximately 1400 stem disks were first sanded with a large belt sander (LZG-S 10/7/14; Langzauner GmbH, Lambrechten, Austria) and then scanned (ScanMaker 9800XLplus; Microtek, Hsinchu, Taiwan). The scanned images were then imported for analysis in WinDendro (WinDendro, Reg 2012b, Regent Instruments Canada Inc., 2012). Tree-ring width, earlywood width, and latewood width were measured for four radii per disk. Automatic measurements generated by the software were inspected and manually corrected as necessary. Cross-dating was also conducted in WinDendro using a reference based primarily on living trees to date each tree and to align the tree-ring series.

Calculation of drought indices

This study focuses on the years of 1999–2005, which covers an extended drought period that occurred in 2002. Tree-ring widths were transformed into basal area increments using the *bai.out* function of the *dplr* package (Bunn, 2008) in the *R* programming environment (R Development Core Team, 2013). This transformation removes the dimension-related trend in tree-ring width series. The 3 years prior to the year 2002 were used as pre-drought normal basal area growth conditions, while a 3-year post-drought period allows the evaluation of population recovery and resilience (Lloret *et al.*, 2011). Specifically, drought resistance is the ability of a tree to resist growth loss due to drought and is calculated by dividing each tree's basal area increment in 2002 by its average basal area increment during the pre-drought period. Drought recovery represents the ability of a tree to recover after drought and is estimated by dividing each tree's basal area increment during the post-drought period by its increment in the drought year. Drought resilience is the ability to achieve pre-drought performance and is calculated by division of post-drought growth by the pre-drought performance. Similarly, relative resilience accounts for the damage that the tree incurred during drought, and is calculated by subtracting resistance from resilience (Lloret *et al.*, 2011).

Statistical analysis

As our field work was conducted in 2013 and 2014, but most trees had died between 2006 and 2008, some trees had begun to rot at the lower part of the trunk and sometimes taking a stem disk at 1.3 m height was not possible. Occasionally, the top annual height increments were missing because the brittle, dry top was broken while felling the tree in the dense stand. If mortality was low in a particular provenance, it was also not always possible to sample four trees in a block. Due to these missing values and a consequently slightly unbalanced design, we calculated best linear unbiased estimates (BLUEs)

Table 1 Average source climate variables from the year 1961 to 1990 normal period are shown for provenances

Region	Prov.	Lat.	Long.	Elev.	MAT	MWMT	MCMT	TD	MAP	MSP	AHM	SHM	Eref	CMD
N	33	63.30	−136.47	876	−4.3	13.8	−24.6	38.4	423	249	14	55	369	131
N	30	59.98	−128.55	640	−2.7	14.5	−23.5	38.0	449	236	16	62	442	197
N	35	59.80	−133.78	789	−0.4	12.6	−15.0	27.6	361	186	27	68	410	203
N	28	58.67	−124.17	762	−1.3	13.4	−15.4	28.8	689	491	13	27	446	7
N	66	58.65	−124.77	1173	−1.7	10.8	−13.6	24.4	675	482	12	22	336	0
CI	24	55.95	−123.80	686	2.1	14.6	−11.3	25.9	469	226	26	65	504	246
CI	100	55.80	−124.82	762	1.3	13.6	−12.0	25.6	522	251	22	54	470	181
CI	20	54.13	−127.23	937	1.8	12.7	−10.4	23.1	551	243	21	52	484	208
CI	104	54.02	−124.53	732	2.7	14.3	−10.9	25.2	506	236	25	61	545	267
CI	61	53.87	−121.80	838	2.7	14.1	−10.1	24.2	750	331	17	43	530	155
CI	107	52.50	−125.80	1311	1.0	10.7	−9.4	20.1	822	209	13	51	486	211
SI	14	50.97	−120.33	1059	3.9	15.0	−7.6	22.6	466	221	30	68	580	304
SI	72	50.70	−119.18	777	5.7	17.1	−6.3	23.4	735	312	21	55	681	256
SI	15	50.05	−119.65	1067	4.4	15.2	−6.5	21.7	665	268	22	57	588	247
SI	57	49.90	−118.20	579	5.9	17.4	−5.8	23.2	659	258	24	67	687	329
SI	1	49.58	−119.02	1006	4.6	15.9	−6.5	22.4	547	226	27	70	609	319
SI	42	49.18	−117.58	998	5.3	16.9	−6.1	23.0	858	285	18	59	672	265
US	111	47.78	−120.93	762	7.4	17.3	−1.5	18.8	1535	237	11	73	663	261
US	144	46.67	−113.67	1524	4.6	16.0	−5.7	21.7	408	189	36	85	670	426
US	153	45.63	−117.27	1311	5.7	16.2	−3.9	20.1	510	217	31	75	795	439
US	154	44.53	−118.57	1494	6.5	17.1	−2.6	19.7	676	167	24	102	801	491
US	123	44.38	−121.67	1006	7.4	16.8	−1.0	17.8	427	73	41	230	909	692
US	156	42.30	−120.78	1615	7.4	17.6	−0.4	18.0	583	125	30	141	881	560

Region refers to the assigned population based on geographical origin (N = North, CI = Central Interior, SI = Southern Interior, US = United States). *Prov* refers to the provenance corresponding to the Illingworth provenance trial's numbering system (Illingworth, 1978). Latitude (*Lat.*) and longitude (*Long.*) are given in decimal degrees, and elevation is given in meters above sea level (*Elev.*). Climate variables include mean annual temperature in °C (*MAT*); mean warmest month temperature in °C (*MWMT*); mean coldest month temperature in °C (*MCMT*); temperature difference is a measure of continentality and is given in °C (*TD*); mean annual precipitation is given in mm (*MAP*); mean summer precipitation is given in mm (*MSP*); annual heat–moisture index (*AHM*); summer heat–moisture index (*SHM*); Reference Evaporation (*Eref*); and climate moisture deficit is given in mm (*CMD*).

Table 2 Planting site climate variables from the year 1961 to 1990 normal period are shown for all field tests

Site code	Lat.	Long.	Elev.	MAT	MWMT	MCMT	TD	MAP	MSP	AHM	SHM	Eref	CMD
CHUW	50.58	−120.62	1430	3.1	14.0	−7.1	21.1	482	241	27.2	58.1	527	232
COMM	50.92	−120.07	1370	3.1	13.9	−7.5	21.4	522	256	25.1	54.3	532	217
EQUI	50.37	−119.60	1370	3.3	14.2	−7.3	21.5	686	301	19.4	47.2	557	188

Site code refers to the abbreviated site name from the Illingworth lodgepole pine provenance trial (Illingworth, 1978). Latitude (*Lat.*) and longitude (*Long.*) are given in decimal degrees, and elevation is given in meters above sea level (*Elev.*). Climate variables include mean annual temperature in °C (*MAT*); mean warmest month temperature in °C (*MWMT*); mean coldest month temperature in °C (*MCMT*); temperature difference is a measure of continentality and is given in °C (*TD*); mean annual precipitation is given in mm (*MAP*); mean summer precipitation is given in mm (*MSP*); annual heat–moisture index (*AHM*); summer heat–moisture index (*SHM*); Reference Evaporation (*Eref*); and climate moisture deficit is given in mm (*CMD*).

of height, basal area increments and drought tolerance indicators of regions and provenances within regions. When estimating BLUEs for regions, block and provenance effects were defined as random. When estimating provenance means, block was random. The mixed model was implemented with the *asreml* package (Butler *et al.*, 2009) for the R programming environment (R Development Core Team, 2013). For the analysis and illustration of the region and provenance main

effects, blocks within sites were considered as replicates. Subsequent *post hoc* tests were carried out using the *ghlt* function from the *multcomp* package (Hothorn *et al.*, 2008), applying Bonferonni's adjustments to control experiment-wise α-levels.

To infer adaptation with respect to source climate of provenances, we ran regression analyses of height and drought indices as a function of relevant climate variables of the provenances' source locations. Source and planting site climate vari-

Table 3 Height and diameter at 1.3 m of four lodgepole pine populations after 32 years of growth

Variable	North	Central interior	Southern interior	United States
Height (m)	10.4 a (0.76)	12.9 b (0.75)	13.6 b (0.75)	11.2 a (0.75)
Diameter (cm)	13.2 a (0.75)	16.5 b (0.73)	16.4 b (0.73)	15.1 b (0.73)

Standard error of the mean is provided in parentheses. Different letters behind the values indicate significant differences between groups ($\alpha = 0.05$).

ables were derived using version 4.62 of the CLIMATEWNA software package (Wang *et al.*, 2006b; Hamann *et al.*, 2013), which interpolates climate based on the parameter-elevation regressions of independent slope models (Daly *et al.* 2008). We used the 1961–1990 period as a baseline climate normal which we assume to represent each population's adapted climate. This period precedes a significant anthropogenic warming signal and is also preferred as a reference climate because of an abundance of weather station data for this period. Tested climate variables include mean annual temperature (°C), mean summer temperature from June to August (°C), mean coldest month temperature (°C), minimum winter temperature (°C), minimum spring temperature (°C), summer heat–moisture index (SHM), mean annual precipitation (mm), and mean growing season precipitation from May to September (mm).

Results

Source climate and growth of populations

Populations varied significantly in height and diameter at 1.3 m after 32 years until dying by mountain pine beetle between 2006 and 2008 (Table 3). The northern population and US population had significantly lower height and smaller diameters than the central interior and southern interior populations. In contrast, the mean heights of the southern and central interior populations were not significantly different from each other. Furthermore, the central population transferred to a warmer climate at the southern sites slightly underperformed the local source, although not significantly (Table 3).

The strongest predictors of population growth were temperature variables, especially variables indicating cold (Fig. 2). Relationships were generally parabolic in shape as expected from niche theory, and the top three source climate predictor variables were mean annual temperature ($R^2 = 0.64$, $P < 0.001$), mean coldest month temperature ($R^2 = 0.49$, $P = 0.001$), and minimum winter temperature ($R^2 = 0.41$, $P = 0.004$). The populations from the cold and warm extremes of the range (northern and US populations, respectively) represent the tails of the parabola, where poor growth is associated with high and low temperatures at the population's origin. The best lodgepole pine performance in southern British Columbia appears to be associated with mean annual temperatures of approximately 2–3 °C. Prove-
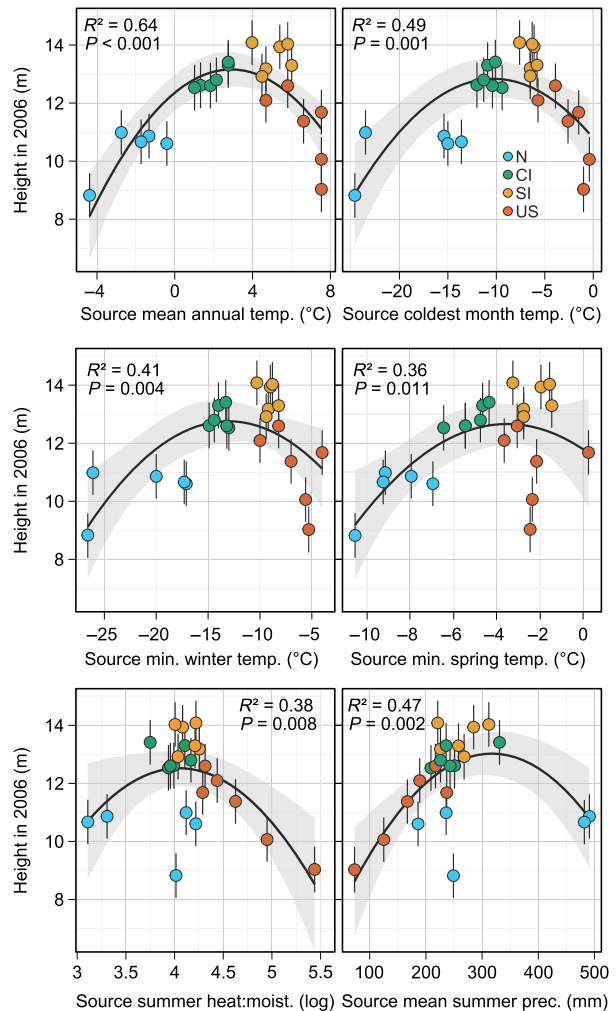

Fig. 2 Height of lodgepole pine provenances at three test sites in southern British Columbia and the relationship to their climate of origin. Each data point represents a provenance replicated on 6 blocks, and it is colored by origin (North = blue, Central Interior = green, Southern Interior = orange, and United States = red). Climate variables here represent the mean annual temperature (°C), mean coldest month temperature (°C), coldest temperature in winter (°C), coldest temperature in spring (°C), summer heat–moisture index, and mean summer precipitation (mm). Error bars represent the standard error of the mean, while gray ribbons outline the 95% confidence intervals.

nances from the central and southern interior regions represent these climates well, as they occur at the top of these parabolas. A significant nonlinear relationship

was also found between height and a logarithmically transformed source summer heat–moisture index ($R^2 = 0.38$, $P = 0.008$) and mean summer precipitation ($R^2 = 0.47$, $P = 0.002$).

Population differences in drought tolerance

The drought event of 2002 was initiated by low precipitation during June, July, and August and led to a drop in basal area increments in all populations (Fig. 3). We found significant differences in drought response between populations for all four drought tolerance indices (Table 4). Differences in drought resistance, recovery, and relative resilience can be mainly attributed to the US and N populations. The US provenances unexpectedly showed a greater decrease in growth than the other provenances, but showed a better rate of recovery and the ability to achieve a higher level of pre-drought basal area growth (Table 4). The opposite trend is seen in the northern population, which exhibits higher drought resistance than the US population, but showed the slowest recovery, resilience, and relative resilience of all four populations (Table 4). The central and southern interior populations were not significantly different from each other and generally appeared comparatively drought tolerant: They showed higher drought resis-

tance, medium recovery, higher resilience, and medium resilience relative to their resistance (Table 4).

Drought tolerance and source climates

The relationship between source climate of populations and their drought tolerance was found to be linear (Fig. 4). Populations originating in regions with warmer winters have higher relative drought resilience. Mean annual temperature had an R^2 of 0.64 ($P < 0.001$), but provenance mean coldest month temperature showed the highest R^2 of 0.69 ($P < 0.001$). The minimum temperature in winter and minimum temperature in spring demonstrated similar predictive power ($R^2 = 0.67$, $P < 0.001$). Relative drought resilience showed a significant relationship with the average source summer heat–moisture index when log-transformed. The provenances from drier climates, indicated by a higher index value, showed higher relative resilience ($R^2 = 0.42$, $P < 0.001$). The average source mean summer precipitation showed a weak, negative linear relationship, indicating that provenance's relative resilience decreased for populations originating from wetter climates ($R^2 = 0.29$, $P = 0.008$). As the points are colored by region, it is also possible to see how these trends hold true at broader regional scales (Fig. 4).
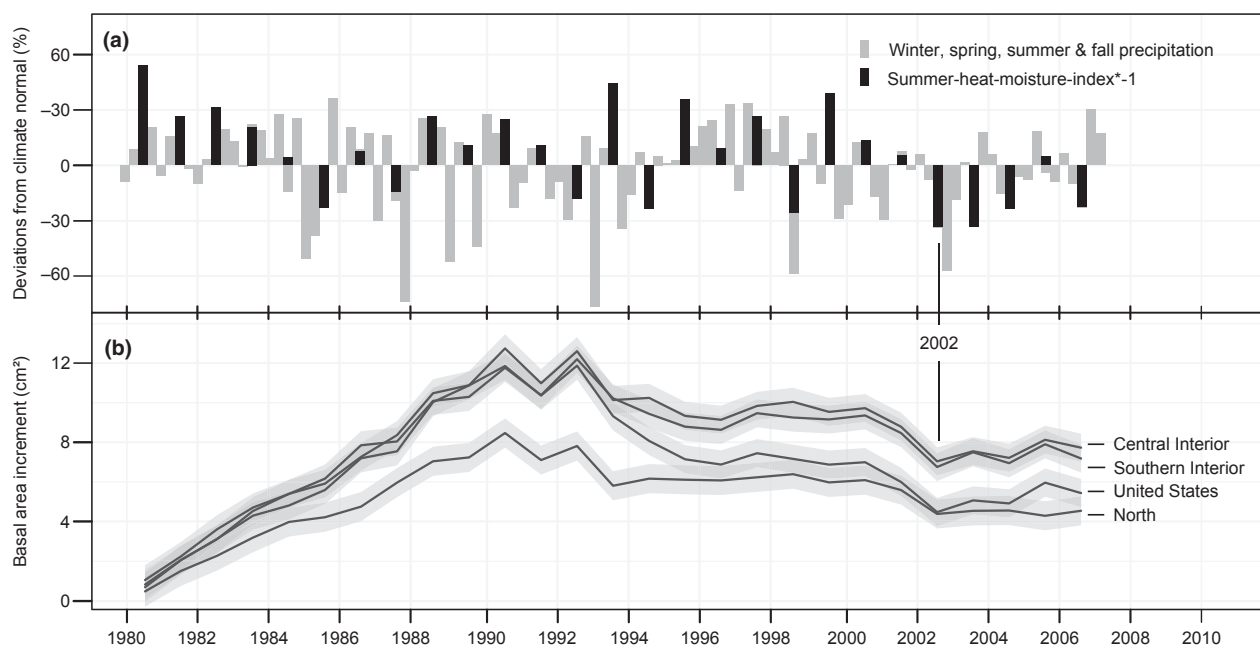

Fig. 3 Climate anomalies and basal area increments. Panel (a) shows anomalies in moisture conditions over the study period. Grey bars represent deviations in winter, spring, summer, and fall precipitation (mm) and black bars overlying summer precipitation represent deviations in the summer heat–moisture index as negative index values, both relative to their respective mean values during the 1961–1990 baseline period. Panel (b) shows basal area increments, or the area represented by the new ring's formation, in cubic centimeters for the four regions over the lifetime of the provenance trial.

Table 4 Drought indicator values (larger values are better) for resistance, recovery, resilience, and relative resilience for four regions ordered by latitude

Drought index	North	Central Interior	Southern Interior	United States
Resistance	0.73 a (0.019)	0.74 a (0.018)	0.75 a (0.019)	0.64 b (0.019)
Recovery	1.03 a (0.021)	1.09 ab (0.019)	1.11 b (0.019)	1.23 c (0.020)
Resilience	0.75 a (0.019)	0.80 b (0.018)	0.83 b (0.018)	0.78 ab (0.019)
Relative Resilience	0.02 a (0.012)	0.06 b (0.010)	0.08 b (0.011)	0.14 c (0.011)

Standard error of the mean is provided in parentheses. Different letters behind the values indicate significant differences between provenances ($\alpha = 0.05$).
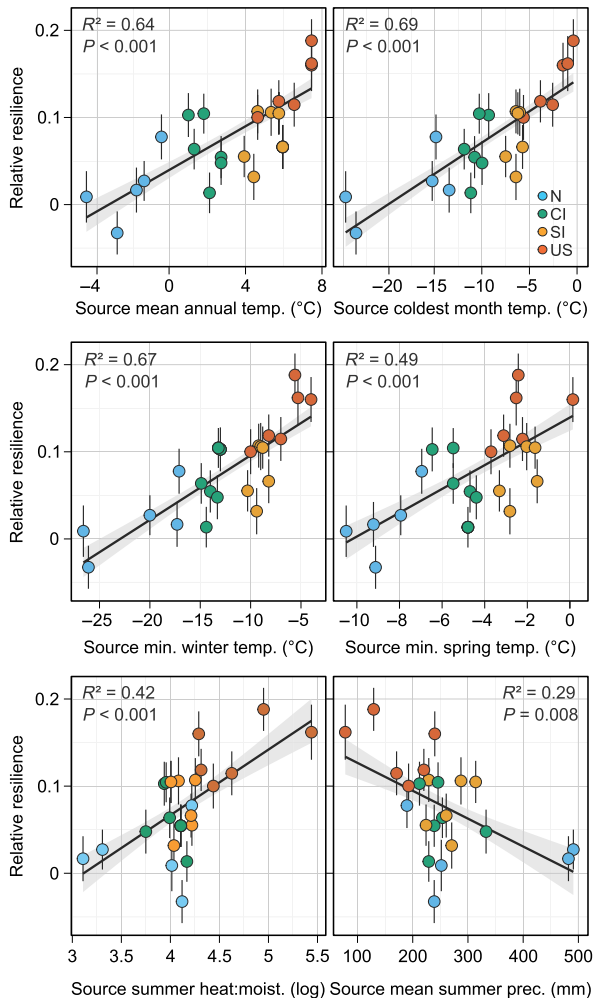

Fig. 4 Relative drought resilience of four lodgepole pine populations compared to source climate (1961–1990 climate normal). Each data point represents a provenance, and it is colored by population (North = blue, Central Interior = green, Southern Interior = orange, and United States = red). Climate variables here represent the mean annual temperature (°C), mean coldest month temperature (°C), coldest temperature in winter (°C), coldest temperature in spring (°C), summer heat–moisture index (SHM), and mean summer precipitation (MSP, mm). Error bars represent the standard error of the mean, while gray ribbons outline the 95% confidence intervals.

Relationship between growth and drought tolerance

Productivity as indicated by height by the end of 2006 shows an unexpected parabolic relationship with relative drought resilience (Fig. 5). The provenances from the US region had lower productivity, but higher drought tolerance, indicating an expected trade-off between tolerance to drought at the cost of growth. The northern provenances show no evidence of a trade-off with both low growth and low drought tolerance. Both the central and southern interior populations again show high similarity in their response, both with a surprising ability to withstand long-term consequences of drought while being comparatively productive.

Discussion

Source temperature predicts productivity

In the southern part of British Columbia's interior, water limitation is a defining factor for plant growth, especially in the desert-like valleys (Nelson *et al.*, 2011). As latitudes increase in the interior, climates become colder and less dry. The lack of significant differences in height and drought tolerances between the southern and central interior populations was therefore unexpected, and indicates adaptation to temperature rather than water availability. The central and southern interior populations occur at the top of the parabolas in Fig. 2, which suggests that these provenances show the optimal growth and drought tolerance in southern British Columbian planting environments. This response could relate to the climatic transfer distance, as the central and southern populations both did not show large climatic differences to the planting sites. Although the central interior population showed slightly lower height growth (Table 3), it did not show smaller basal area increments (Fig. 3).

Anomalously dry periods have occurred several times over the lifetime of the provenance trial (Fig. 3a), but they have not always been associated with a corresponding decrease in basal area growth (Fig. 3b). Most of these dry periods did not occur during the critical part of the
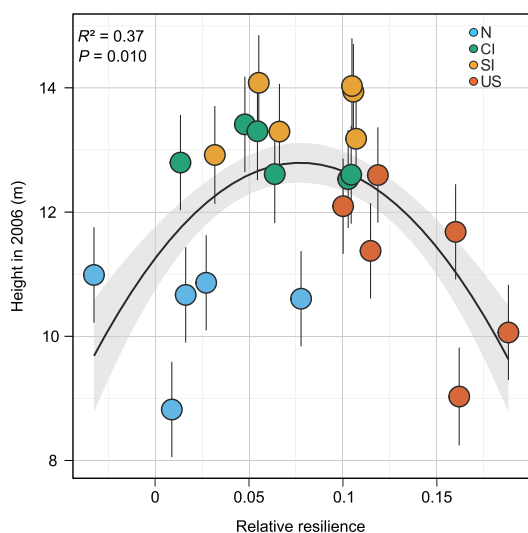
Fig. 5 The trade-off relationship height and relative resilience to drought in lodgepole pine. Productivity is measured by height in meters by the end of the study period (2006), and drought tolerance is represented by relative drought resilience, or the ability to recover to previous growth levels relative to the damage incurred during drought. Each data point represents a provenance, and it is colored by population (North = blue, Central Interior = green, Southern Interior = orange, and United States = red). Error bars represent the standard error of the mean, while gray ribbons outline the 95% confidence intervals.

year when growth is underway: Summer droughts can have greater impact than dry periods that happen outside of this time. Given the high predictive power of cold-driven climate variables, some visible drops can likely be attributed to cold conditions, or a combination of cold and dry conditions. The drought in 2002, however, was a summer drought and led to a clear drop in basal area growth across all populations (Fig. 3b).

Trade-offs indicate differing adaptive strategies

Drought resilience is arguably the most important drought response index because the failure of a tree to regain its previous potential after an extreme event often precedes mortality (Scheffer *et al.*, 2001; Allen *et al.*, 2010). On the other hand, low resilience might point to an effective adaptive strategy that shuts down growth under unfavorable conditions, but prevents structural damage that might compromise long-term productivity. If such a mechanism existed, it should lead to better performance under future droughts, which could not be assessed in this study due to mortality. Relative resilience is also important, because it captures both the damage incurred during drought as well as the ability to return to pre-drought growth-levels. Negative values of relative resilience would indicate a decreasing growth trend after drought,

which is often preceding mortality (Lloret *et al.*, 2011). The ability of how fast a tree can recover may become more important with drought events expected to become increasingly frequent under projected climate change (Christidis *et al.*, 2014).

To more effectively interpret the drought response results, it is important to consider productivity before choosing seed sources for reforestation. Our results indicate that a typical trade-off only applies to the most southern (US) lodgepole pine population. The results in Fig. 5 suggest comparatively good relative resilience at the expense of height growth. This type of strategy could involve investments into a more safety-oriented stem hydraulic system (Hacke & Sperry, 2001; Hacke *et al.*, 2001), with increased tracheid wall thickness, reduced cell lumen size, and more resistant pit membranes in order to reduce risk of cavitation that can permanently disrupt the water supply to the crown (Tyree & Zimmermann, 2002). The response of the US population in the post-drought period appears plastic, with comparatively fast recovery and high relative resilience. A high degree of stomatal control appears to be a likely alternative mechanism, while a combination of both strategies is also possible (Hartmann, 2011).

Contrary to expectations of substantial trade-offs between drought tolerance and productivity, the central and southern interior populations showed an unexpected ability to tolerate drought and to maintain comparatively good long-term growth (Fig. 5). Guy & Holowachuk (2001) concluded that the most productive and water-use-efficient genotypes come from more moderate climates, which appears to also be the case in this study. This strategy might, however, nevertheless involve a trade-off that has not yet been revealed for lack of a truly exceptional drought during the study period. Maladaptation could become more significant if drought events increase in frequency and severity under expected climate change (Bréda *et al.*, 2006).

Boreal provenances appear at risk

As productivity and drought tolerance was negatively related in the US population, we had expected a similar growth versus drought tolerance trade-off in the northern population. Recent research has indicated a link between cold adaptation and drought adaptation in seedlings (Bansal *et al.*, 2015a,b) and mature trees of Douglas-fir (Montwé *et al.*, 2015). Cold-adapted trees also invest into thicker cell walls and narrower lumen sizes that are more resistant to freeze-thaw-induced embolisms (Schreiber *et al.*, 2013a,b). Northern populations might also be genetically preprogrammed to flush later in spring, to reduce risk from late spring frosts (O'Reilly & Owens, 1989), but having the added benefit

of avoiding early summer droughts. Instead, the most northern population showed no evidence of such benefits in this study, as they had both poor drought resilience and low height and diameter growth.

An important inference of this study is therefore that boreal populations may not be able to take advantage of more favorable growing conditions under projected climate change. Although previous research has suggested that northern populations may benefit disproportionally from climate warming (Wang *et al.*, 2006a, 2010; O'Neill *et al.*, 2008a), the lack of drought tolerance shown in this study appears to put these populations at high risk.

Implications for assisted migration

Because provenances from the central interior, southern interior, and the United States regions appear generally drought tolerant, our results suggest that they could be used for reforestation under a warming climate. However, the result that height growth can be predicted by temperature variables hints at the need for cautious interpretation. Although warmer source location's winter and spring temperatures predict increased height growth (Fig. 2), cold or frost may still limit northward movement of planting stock. Several drops in basal area growth visible in Fig. 3 were not associated with early summer drought, for example, in 1991. This could be the effect of a frost event that damaged the cambial tissue, or a freeze–thaw event that causes cellular embolisms (Mayr *et al.*, 2006). A similar event seems to have occurred in 1993. The US population had been a top performer until this event, but a rank change occurred in 1993, and the US population never recovered such competitive growth levels. This is also suggesting that results from young provenance trials should be assessed carefully. The population-specific response to frost appears to be an important follow-up study, and we propose using micro-sections of tree rings to search for poorly lignified or damaged cells due to frost damage (Piermattei *et al.*, 2015). Tree growth can also be influenced by differences in photoperiod (Wheeler, 1979). A shorter photoperiod could potentially negatively influence the success of seed transfers. This should be tested before transfers across long latitudinal distances are implemented.

In British Columbia's southern interior, the paradigm that local is best appears to remain valid, at least temporarily. Southern provenances planted in southern British Columbia represent good drought tolerance and productivity and can be recommended for continued planting. The US provenances were incorporated into our sampling design to test the viability of an assisted migration prescription, should the southern interior

region be shown to need it. Although it appears that it might not be currently necessary, our sample material missed recent dry summers. With increasing frequency of dry growing seasons, forest managers may wish to consider using a small percentage of more drought resilient planting stock (Prober *et al.*, 2015). Such a drought-averse strategy reduces the risk of mortality and forest health issues, but represents a compromise with productivity.

Conflict of interest

The authors declare that they have no conflict of interest.

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