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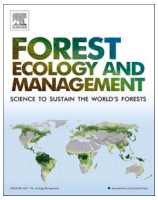

Selective breeding for growth does not compromise drought resistance in western larch seedlings

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ABSTRACT

As the impacts of drought intensify with climate change, adaptation to drought is becoming an increasingly important consideration for tree breeding and forest management. This elevates the need to understand how breeding for faster growth affects drought tolerance and if breeding to improve drought tolerance could help mitigate the impacts of drought on forest health and productivity. To understand the implications for tree breeding in future climates, we studied how selective breeding of western larch (*Larix occidentalis*) for faster growth affects drought resistance (a component of drought tolerance); the quantitative genetics of drought resistance traits; and the effects of drought on genetic variation in growth and phenology. We established a seedling common garden experiment in a warm climate outside the natural range with 23 natural populations and 29 selectively-bred families from two breeding zones in British Columbia. We imposed two drought treatments of varying duration and severity with a control treatment in the third growing season. Height growth, bud phenology and drought resistance traits were phenotyped. We found that selective breeding for faster growth has not compromised drought resistance in seedlings. Weak correlations between drought resistance and height growth or bud phenology among family phenotypes suggest that breeding for improved drought resistance may be possible without affecting other traits relevant to adaptation to local climates. However, we detected limited genetic variation and low heritability for drought resistance, as well as diminished genetic variation in growth and phenology traits under drought, indicating potential barriers to breeding for improved drought resistance in seedlings.

1. Introduction

Global temperatures have risen rapidly over recent decades, accompanied by increases in the frequency, duration, and severity of droughts in many regions around the world (IPCC, 2021). Extreme drought events have been linked to elevated forest mortality and declines in forest health, including increased susceptibility to pathogens and other disturbance agents (Anderegg et al., 2020; DeSoto et al., 2020; Hartmann et al., 2022). In addition to dieback and declining health of adult trees, drought is also a primary limiting factor for seedling establishment and growth (Moles and Westoby, 2004; Padilla and Pugnaire, 2007). As climates change and the impacts of drought intensify, adaptation to drought stress is becoming an important consideration for tree breeding programs and forest management. In addition to understanding how local adaptation in natural populations may be used to mitigate maladaptation to drought through assisted migration, there is an elevated need to understand how tree breeding for faster growth affects drought tolerance and if breeding to improve drought tolerance could help reduce the impacts of drought on forest health and productivity in future climates.

Traditional tree breeding programs aim to increase growth and productivity by selecting faster growing genotypes within regional breeding zones established to maintain local adaptation. In some conifer species, evidence of trade-offs between growth and drought tolerance have been found among natural populations (Bansal et al., 2015; Candido-Ribeiro and Aitken, 2024; De La Mata et al., 2014; Kerr et al., 2015; Montwé et al., 2015) but correlated responses associated with selection for faster growth and drought tolerance have not been well studied. Selective breeding for faster growth could compromise drought tolerance through negative genetic correlations or trade-offs expected based on physiological or morphological constraints. For example, selection for faster growth could be achieved through greater hydraulic

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conductivity, which in turn could compromise embolism resistance of the xylem based on expected trade-offs (Gleason et al., 2016; Sperry, 2003). However, evidence for a trade-off between growth rates and embolism resistance within tree species is mixed (Hajek et al., 2014; Schuldt et al., 2016; Sterck et al., 2012) and is not well studied in the context of tree breeding.

Selective breeding for faster growth can lengthen the growing period by causing delayed growth cessation, which could lead to greater drought vulnerability if earlier growth cessation is adaptive to avoid late-season drought stress as has been found in Douglas-fir (*Pseudotsuga menziesii*) (Joly et al., 1989; Kaya et al., 1994; White, 1987). On the other hand, the ability to resume growth later in the season if moisture conditions become favorable could be an advantage for drought recovery (Zlobin, 2024). Selective breeding for growth could also advance bud flush and increase early-season growth before drought becomes limiting, which could provide an advantage under late-season drought conditions. Earlier bud flush has been associated with drier source climates and latitude in Douglas-fir populations, indicating that it could be an adaptation to summer drought (Campbell and Sugano, 1979; St Clair et al., 2005). Understanding how selective breeding for growth affects phenology and drought tolerance is important for maintaining productivity and adaptation to local climates.

For selective breeding to improve drought tolerance, genetic variation and control of traits relevant to drought tolerance need to be understood. While field trials in adult trees can provide valuable insight into the genetics of growth responses to drought by measuring tree rings (Azcona et al., 2024; Depardieu et al., 2020; Laverdière et al., 2022), experimental drought can be more controlled and evenly applied in common garden studies of seedlings, which can be used to assess genetic effects on traits relevant to drought tolerance that may be more difficult to measure in adult trees. Dark-adapted chlorophyll fluorescence (F_v/F_m) is a trait that can be rapidly assessed in seedlings to track declines in photosynthetic efficiency under drought stress (e.g., Candido-Ribeiro and Aitken, 2024). Declines in chlorophyll fluorescence are a late-stage signal of drought stress, occurring after plants have reached a point of no return in terms of hydraulic failure (Trueba et al., 2019). Fluorescence declines have been previously identified as one of the best predictors of survival under drought in Scots pine (*Pinus sylvestris*) (Garcia-Forner et al., 2015). Therefore, fluorescence declines are an informative trait for detecting genetic variation in drought resistance, or the ability to survive and grow during a drought event (a component of drought tolerance).

The economic and ecological significance of the deciduous conifer species western larch (*Larix occidentalis*) makes it a good candidate for studying the effects of selection on drought tolerance and the potential for breeding to improve drought tolerance. Western larch is abundant in western North America in areas of moderate moisture availability in mid-elevation forests, and it also co-occurs in dry forests in association with ponderosa pine (*Pinus ponderosa*) and Douglas-fir (Schmidt and Shearer, 1990). Like many conifers, western larch is isohydric and maintains a wide hydraulic safety margin between tissue and soil water potentials typically experienced in the field (Baker et al., 2019; Piñol and Sala, 2000). While its distribution is smaller than widespread conifers of the region, climate niche modeling projects that suitable habitat will dramatically decline within the current natural range but expand beyond the current range in British Columbia under projected future climates this century (Rehfeldt and Jaquish, 2010). Based on these projections and on trial plantings that demonstrated reforestation potential outside the natural range, policy was changed in British Columbia to allow operational planting of western larch on public lands outside of its contemporary range restricted to 10 % of trees in a stand (Jaquish, 2010; O'Neill et al., 2017).

To test the effects of selective breeding for faster growth on drought resistance, the quantitative genetics of drought resistance traits, and the effects of drought on the quantitative genetics of growth and phenology in western larch seedlings, we established a seedling common garden experiment at a warm study site outside the natural range. The experiment included seedlings from 23 natural populations and 29 selectively-bred families from two breeding zones in British Columbia. We imposed two drought treatments of varying duration and severity compared to a control treatment in the third year of growth. We measured height growth, bud phenology and drought resistance traits (chlorophyll fluorescence, canopy loss, and mortality) to address the following questions: 1) How does selective breeding for faster growth affect drought resistance in seedlings? 2) Do seed sources from drier, more continental climates of the eastern zone have greater drought resistance compared to the western zone? 3) Are drought resistance traits correlated with height growth or bud phenology among families? 4) How heritable are drought resistance traits? 5) How does drought affect genetic variance and heritability of height growth and bud phenology?

2. Materials and methods

2.1. Study design

We obtained 23 open-pollinated seedlots from natural populations and 29 seedlots of second-cycle full-sib families from the western larch breeding program of the British Columbia Ministry of Forests which began in 1990, originating from two breeding zones established in southern British Columbia (Fig. 1). Seedlots representing natural populations were obtained from appropriately stored seed collections from the British Columbia Tree Seed Centre, and each open-pollinated seedlot comprised a minimum of 10 maternal parent trees. Second-cycle full-sib families included 32 parents total, 29 of which were represented in more than one family in a factorial mating design, allowing for estimation of additive genetic variation and narrow-sense heritability of traits. Families consist of parents selected from natural stands within breeding zones; both parents of 15 families originate from the western breeding zone (Nelson) and 14 families consist of both parents from the eastern breeding zone (East Kootenay). Natural populations and selectively-bred families from the eastern zone originate from higher elevations, on average, with shorter growing seasons, colder winter minimum temperatures, greater continentality, less annual precipitation, and more arid summers compared to the western zone (Figure S1).

The common garden design was also used to study local adaptation to climate in natural populations of western larch from across the range in the US and Canada, described in detail in (Roskilly and Aitken, 2024). Briefly, seedlings were grown in a greenhouse for one growing season and moved to controlled chambers set at 4°C in the dark to simulate winter and meet chilling requirements to break bud dormancy. In April 2020, we transplanted seedlings into raised outdoor beds at Totem Research Field at the University of British Columbia, Vancouver, BC. The beds contained a sandy loam soil with good drainage over a layer of gravel to prevent water moving up through capillary action from soil below. The common garden experiment included a well-watered control and two drought treatments (described below). Thick sheets of polyethylene were stapled to the wood walls as a moisture barrier separating adjacent control and drought treatment beds. Seedlings were planted in four blocks of 240 plants in a complete randomized block design, with 3 randomly assigned individuals per seed source within each block, for a total of 12 plants per seed source per treatment, 960 seedlings per treatment and 2880 seedlings in total. Seedlings were spaced 4 cm apart. To minimize edge effects, each block was surrounded by a row of buffer seedlings that were not measured.

2.2. Drought treatments

We subjected seedlings to drought treatments in their third year of growth in summer 2021, an exceptionally hot and dry year across the Pacific Northwest, with record-breaking heat events in June and a prolonged drought (Thompson et al., 2022). We used transparent rain covers suspended on PVC hoops over the beds to exclude any

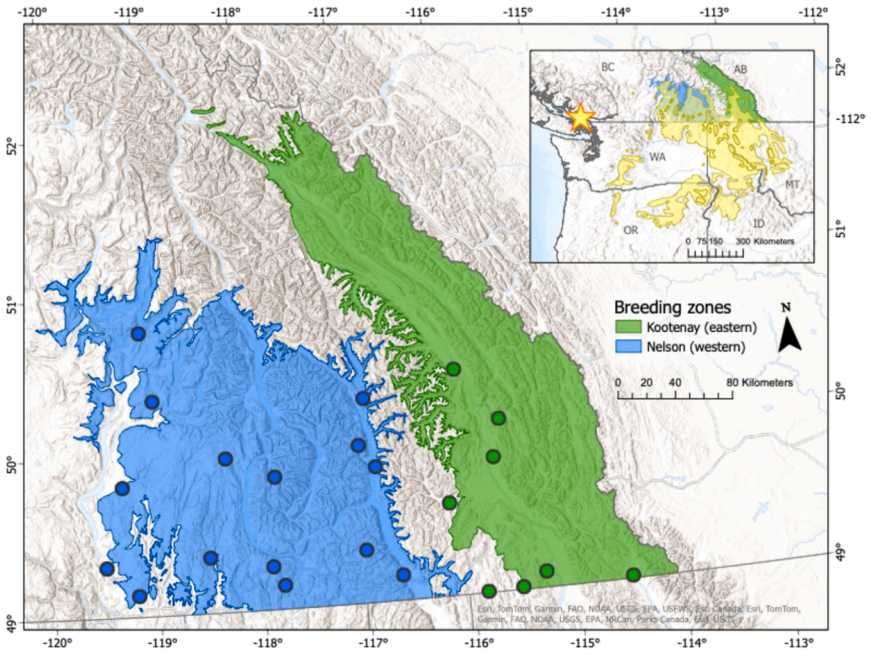

Fig. 1. Map showing the origins of the 23 natural populations (circles) sampled from two breeding zones (polygons) of western larch in British Columbia. Inset shows the natural range of western larch in yellow and location of the common garden test site (gold star).

precipitation during the growing season. Rain covers did not reach the soil surface to allow for air flow (Figure S2). The moderate and severe drought treatments began on May 18th, 2021, when rain covers were erected over the raised beds. The severe drought treatment ended on October 14th, 2021, when temperatures became too cool to continue the treatment (nearly five months without water). The moderate drought treatment was rewatered on August 13th, 2021, after almost 3 months without water. The amount and frequency of watering in the control treatment was determined by monitoring soil volumetric water content (VWC) with a portable soil moisture probe (Fieldscout TDR 150 with rods 20 cm long). The sandy loam soil in the beds had a maximum capacity of 15 % VWC and the control treatment beds were always watered to maintain VWC above 5 %. The drought treatments included a drought pre-acclimation phase in summer 2020, the growing season preceding the drought treatments, in which soil volumetric water content (VWC) was gradually reduced from 15 % to 0 % from July 15th to August 25th and rewatered on September 15th, 2020. In 2021, the soils in the drought treatments reached 0 % VWC by June 4th, beyond which changes in soil VWC could not be detected. We measured midday water potentials four times during the drought treatment between July 1st and August 28th to estimate the level of drought stress, relative to the control treatment, using branch samples of three edge plants per bed with a Scholander pressure bomb (Figure S3). Briefly, between 12 pm and 2 pm, we wrapped branches in tin foil to acclimate to stem water potentials for at least 30 mins, then cut branch samples with a clean razor blade and immediately measured water potentials as the pressure at which water started to release at the cut end of the branch. In 2022, the recovery year, all treatments were watered to maintain VWC above 5 % (watered weekly or biweekly as needed).

2.3. Trait data

We collected data for seven traits in 2021: height growth, bud flush and bud set phenology, fluorescence declines, final fluorescence, canopy loss, and mortality. Height was measured five times throughout the 2021 growing season and final height was measured on September 6th, 2021, after growth cessation and final bud set. We also measured bud flush and early height growth in 2022 as recovery responses in the growing season following the drought treatment. Early growth was estimated as the height on July 7th, 2022 minus the initial height measured at the beginning of the growing season on May 9th, 2022. We did not use growth or phenology data collected beyond this date in the recovery season because the effects of competition due to tight spacing in the raised beds caused reduced vigor and elevated mortality in both the control and drought treatments.

Visual assessments of the timing of terminal bud flush and bud set were collected to analyze the timing of initiation and cessation of height growth, respectively. A binary system was used to record observations. Bud flush was determined as the date on which bud scales separated and emerging needles were visible, and bud set was recorded as the date on which brown bud scales were visible on apical buds. Some seedlings set bud multiple times due to lammas growth in the control treatment, and final bud set was determined as the date after which no reflushing was observed. Observations of terminal bud phenology of all seedlings were recorded once per week at the beginning of the 2021 and 2022 growing season until all seedlings had fully flushed (March 8th - April 13th, 2021 and March 11th - April 28th, 2022). Bud set was monitored weekly from July 1st to September 6th, 2021. Bud flush and bud set dates were analyzed as day of the year starting January 1st.

We measured dark-adapted chlorophyll fluorescence (F_v/F_m) to assess declines in photosynthetic efficiency in response to drought using a chlorophyll fluorometer (FluorPen Z990, Qubit Systems, Inc.). Fluorescence measurements were taken on mid-canopy needles after seedlings were exposed to dark conditions for at least 30 mins (Murchie and Lawson, 2013). We covered the beds with plastic blackout sheets and shade tarps in naturally low-light conditions (at dusk) to acclimate the seedlings to the dark prior to measurements. We measured fluorescence on all seedlings in the drought treatments seven times beginning with an initial measurement on June 16th, 2021 to establish an unstressed baseline (no differences between control and drought treatments) and a final measurement on October 13th, 2021. Initially, we measured all seedlings in control treatment, but eventually we subsampled 144 seedlings (36 per block) in the control treatments for efficiency as variation was low among seedlings. As the drought treatments progressed, we measured a subset of 144 seedlings per treatment (36 per block) biweekly to determine when to take the next round of full

measurements based on changes in fluorescence values.

We observed needle shedding in response to drought stress and so visually estimated percent canopy loss for each seedling in the drought treatment scored as 0, 25, 50, 75 or 100 % on September 6th, 2021. Mortality was estimated as the proportion of seedlings that were identified as dead (no growth since previous measurement with foliage damage and loss) during the final height measurement on September 6th, 2021 and confirmed as dead the following season (no new growth) on May 9th, 2022.

2.4. Analyses

To test for the effects of treatment while accounting for genetic variation among families and populations, we used a linear mixed-effect model using residual maximum likelihood to estimate best linear unbiased estimates (BLUEs) of treatments with ASReml-R version 4.0 (Butler et al., 2017). The following mixed-effects model was used:

$$Y_{ijkl} = \mu + T_k + P_j + (P * T)_{jk} + B_l + \epsilon_{ijkl} \quad (1)$$

where Y_{ijkl} is the phenotype corresponding to individual i from population or family j, treatment k and block l; μ is the phenotypic global mean across all individuals (fixed intercept); T is the fixed effect of kth treatment; P is the random effect of the jth population or family (seedlot); P*T is the random interaction effect of the jth seedlot and treatment k; B is the random effect of the lth block; and ϵ_{ijkl} is the random residual error term. To account for spatial effects on traits, row and column positions within the experiment were incorporated into the random residual term with a correlation structure. Models including the spatially correlated residual term consistently improved model fit and reduced AIC values. We tested for differences between BLUEs of treatments using pairwise t-tests with the *asremlPlus* package for ASReml-R version 4.0 and adjusted p-values using Tukey's method for multiple comparisons. To assess the significance of seedlot-by-treatment interactions for each trait, we conducted a likelihood ratio test using nested models with and without the random effect of seedlot × treatment.

For fluorescence declines, F_v/F_m values for each individual plant at a given date of measurement were first corrected for spatial autocorrelation based on an autoregressive model of residuals (Candido-Ribeiro and Aitken, 2024). A beta regression model (Ferrari and Cribari-Neto, 2004) with spatially-corrected individual F_v/F_m values was then used to estimate the linear rate of decline (slope) of fluorescence over time (date of measurement) using the R package *betareg* (Cribari-Neto and Zeileis, 2010). The slopes of fluorescence declines were then used in the following mixed-effects models. When needed, we used a cubed root transformation of slope values (after adding a constant to make values positive) and a log transformation of F_v/F_m values to meet model assumptions of normality of residuals and homoscedasticity of variances.

To test for difference between natural populations and selectively-bred families (seed source type) for each breeding zone and treatment, phenotypes were estimated as BLUEs using the following mixed-effects model:

$$Y_{ijklm} = \mu + T_i + S_{j(k)} + (S * T)_{i(j(k))} + b_l + r_{m(kl)} + \epsilon_{ijklm} \quad (2),$$

where Y_{ijklm} is the response phenotype; T is the fixed effect of the ith treatment; S is the fixed effect of the jth seed source type nested within breeding zone k; S*T the fixed interaction effect of the seed source type j nested within breeding zone k and treatment i; b is the random effect of block l; r is the random effect of seedlot m nested within seed source type j nested within breeding zone k; and ϵ_{ijklm} is the random residual error term including the spatial autocorrelation of individual seedling position in the experiment. We tested for pairwise differences between BLUEs of seed source type for each breeding zone and treatment using pairwise t-tests with the *asremlPlus* package (ASReml-R version 4.0) and adjusted p-values using Tukey's method. Models including the spatially correlated residual term consistently reduced Akaike's information criterion (AIC) values. For the estimation of phenotypes for drought resistance traits (fluorescence declines and canopy loss) measured only in the severe drought treatment, a mixed-effects model following Eq. (2) without the fixed effect of treatment was used.

To test for correlations among traits, Pearson correlation coefficients were estimated with BLUPs of family phenotypes for each treatment from Eq. (1). We also estimated genetic correlations among traits using a bivariate animal model. However, due to low additive genetic variance and heritability of traits under drought, the genetic correlation estimates had large standard errors and were not statistically significant, limiting their interpretability. Therefore, we focus on phenotypic correlations among family BLUPs, which provide more informative insights into trait relationships in this study.

To estimate additive genetic variance and heritability in full-sib families by treatment, we used the individual (animal) model approach using the following mixed-effects model:

$$Y_{ijk} = \mu + B_j + G_k + \epsilon_{ijk} \quad (3),$$

where Y_{ijk} is the phenotype corresponding to individual i from block j and individual additive genetic value k; μ is the phenotypic global mean across all individuals, B is the random effect of block j, G is the random effect of the kth individual additive genetic value derived from the relationship matrix based on the pedigree of the full-sib family structure, and ϵ_{ijk} is the random residual error term. Models including the spatially correlated residual term consistently reduced Akaike's information criterion (AIC) values.

Narrow-sense heritability (h^2) for each trait was estimated as:

$$h^2 = \frac{\sigma_a^2}{\sigma_p^2} \quad (4),$$

where σ_a^2 is the additive genetic variance estimated from Eq. (3) and σ_p^2 is the total phenotypic variance following the individual model.

3. Results

3.1. Drought treatment effects

Annual growth in both natural populations and selectively-bred families was reduced in the 2021 drought year by an average of 30 % (8.1 cm) in the moderate and 38 % (10.4 cm) in the severe drought relative to the control ($P = 0.003$, 0.0001, respectively; Fig. 2). Bud set in the drought year was on average 6.8 days earlier in the moderate and 8.7 days earlier in the severe drought treatment relative to the control treatment ($P \leq 0.0001$; Fig. 2). Only 1 % of seedlings reflushed after initial bud set in the moderate and severe drought treatments compared to 12 % of seedlings that reflushed at least once in the control treatment. Bud flush in the spring of the drought year and the recovery year did not differ in the severe drought treatment relative to the control (Figure S4). Seedlings responded to drought by shedding needles, with average estimated canopy loss of 30 % in the moderate and 45 % in the severe drought treatment ($P < 0.0001$; Figure S5). The effect of seedlot-by-treatment interaction was not significant for any traits except for bud set phenology ($\chi^2 = 19.51$, df = 1, $p < 0.0001$).

Fluorescence (F_v/F_m) values in the severe drought treatment began to decline at the beginning of August, coinciding with declines in stem water potential (Fig. 3, Figure S3). Fluorescence declined by 22 % on average by the end of the severe drought treatment compared to the healthy baseline measured prior to onset of drought (Fig. 3). At the end of the severe drought treatment, average mortality was 12 % (Figure S6) in the severe drought treatment relative to 3 % in the moderate drought and 1 % in the control treatment. Early growth in the recovery year following drought was reduced by an average of 10 % (1.47 cm) and

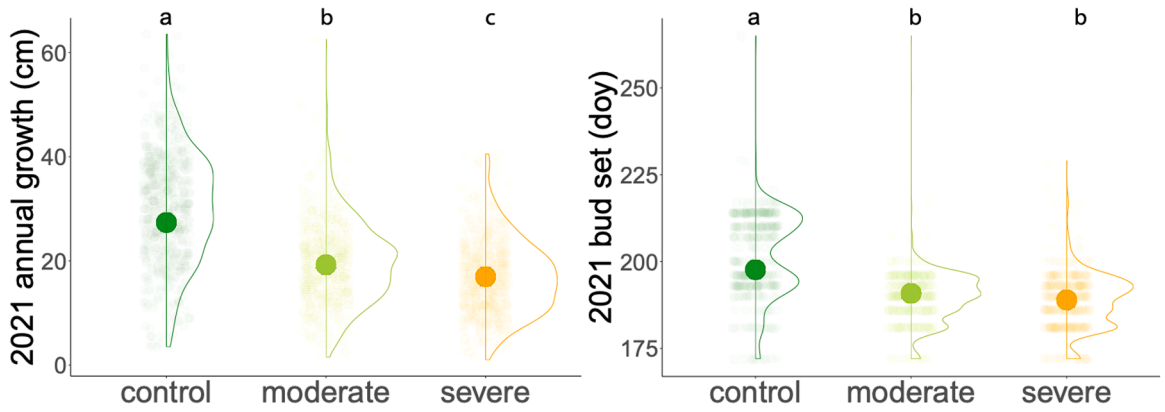

Fig. 2. Annual growth and bud set phenology for the control, moderate, and severe drought treatments in western larch seedlings in the drought year (2021). Bold points represent the BLUEs for each treatment and lighter points represent individual data. Letters indicate statistically significant differences between groups (Tukey's HSD test, $\alpha = 0.05$).

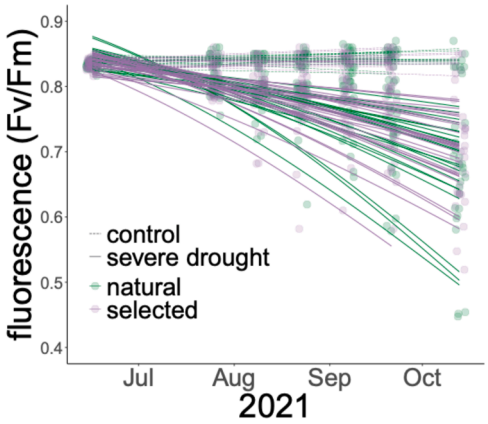

Fig. 3. Dark-adapted chlorophyll fluorescence (F_v/F_m) values over time in western larch seedlings in the control and severe drought treatment in the drought year (2021). Points and lines represent natural population or selectively-bred family phenotypes.

22 % (3.2 cm) in the moderate and severe drought treatment, respectively (Figure S7).

3.2. Comparisons between selectively-bred families and natural populations

Selectively-bred families averaged 20 % greater annual growth compared to natural populations in the drought year in both the control and severe drought treatment, corresponding to an average gain of 4.74 cm and 3.24 cm, respectively (Fig. 4). Natural populations from the eastern zone had greater annual growth compared to the western zone. However, annual growth in selectively-bred families did not differ between zones in the control treatment, leading to greater annual growth gains for selectively-bred families in the western zone (Fig. 4). Bud set was delayed in selectively-bred families compared to natural populations by an average of 4 days in each breeding zone in the control treatment (Fig. 4). Differences in bud set timing between selected and natural seed sources were reduced in the severe drought treatment; bud set was 1.8 days later in selectively-bred families from the western zone but did not differ in the eastern zone (Fig. 4). Bud flush did not differ between natural populations and selectively-bred families or between zones in the control treatment (Figure S8). However, after exposure to mild drought acclimation in 2020, selectively-bred families had earlier bud flush in spring 2021 compared to natural populations; 2.9 days earlier in selectively-bred families from the western zone and 1.8 days earlier in the eastern zone (Figure S8). In spring of 2022, the recovery year, bud flush did not differ between selectively-bred families and natural populations in the severe drought treatment (Figure S8). Early growth in the recovery year was 51 % greater on average in the selectively-bred families compared to the natural populations in the control and the severe drought treatment, corresponding to an average gain of 6.34 cm and 4.73 cm respectively (Figure S9).

Fluorescence declines and final fluorescence under severe drought did not differ between selectively-bred families and natural populations in either breeding zone, though final fluorescence was slightly higher in selectively-bred families from the eastern zone compared to the western (Fig. 5; Figure S10). Canopy loss also did not differ between selectively-bred families and natural populations (Figure S10).

3.3. Trait correlations

Fluorescence declines, final fluorescence, and canopy loss were all correlated with mortality among family phenotypes (Fig. 6). Fluorescence declines and mortality were strongly correlated among families ($r = -0.77$; $p < 0.001$; Fig. 6). Families with greater canopy loss also had faster fluorescence declines and higher mortality (Fig. 6). Annual growth in the drought year (2021) was not correlated with final fluorescence, fluorescence declines, or mortality among family phenotypes (Fig. 6). Annual growth was negatively correlated with canopy loss ($r = -0.4$; $p = 0.03$; Fig. 6). Families with slower fluorescence declines had greater early growth in the recovery year ($r = 0.44$; $p = 0.01$; Fig. 6). Bud flush and bud set phenology were also not correlated with final fluorescence, fluorescence declines, or canopy loss among family phenotypes in the drought or recovery year (Fig. 6). Families with earlier bud set had greater mortality ($r = -0.47$; $p = 0.01$; Fig. 6).

3.4. Heritability and additive genetic variance of traits by treatment

Heritability of both annual growth and bud set timing was lower in the drought treatments than in the control. Annual growth in the drought year had moderately low heritability in the control treatment ($h^2 = 0.17$) which was reduced in the drought treatments, with the lowest heritability in the severe drought treatment ($h^2 = 0.09$; Table 3). Heritability of bud set timing was strongly reduced by the drought treatments, with moderately high heritability in the control treatment ($h^2 = 0.36$) and the lowest heritability in the severe drought treatment ($h^2 = 0.03$; Table 3). Bud flush timing in spring of the drought year following mild drought acclimation the previous year was moderately heritable and had a higher heritability than the control treatment (Table 3). Bud flush phenology in the spring of the recovery year had the greatest heritability in the control treatment and lowest for the moderate

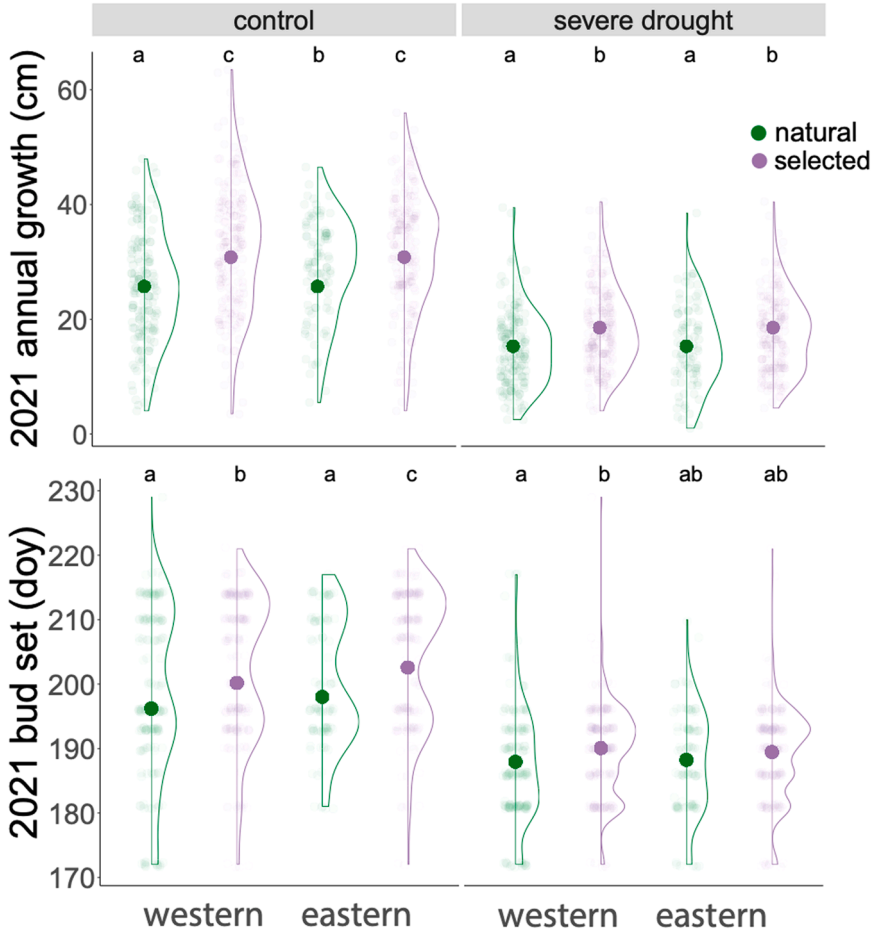

Fig. 4. Annual growth and timing of bud set in the drought year (2021) between natural populations and selectively-bred families of western larch from two breeding zones in British Columbia in the control and severe drought treatment. Bold points represent natural population and selectively-bred family phenotypes (BLUEs) and lighter points represent individual values. Letters indicate statistically significant differences between groups (Tukey's HSD test, $\alpha = 0.05$).

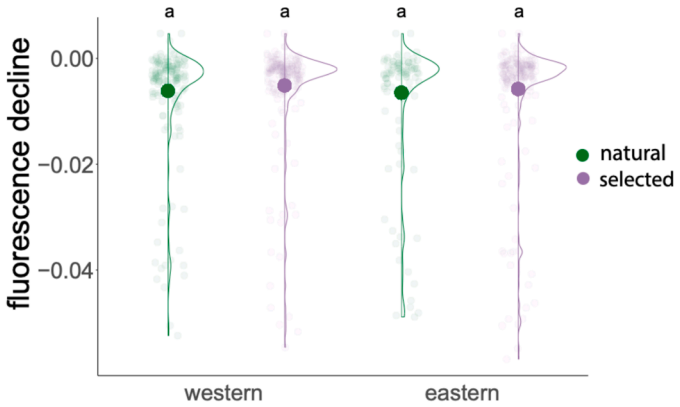

Fig. 5. Decline in dark-adapted chlorophyll fluorescence (F_v/F_m) in selectively-bred families and natural populations of western larch from two breeding zones in British Columbia in the severe drought treatment. Bold points represent natural population and selectively-bred family phenotypes (BLUEs) and lighter points represent individual values. Differences between natural populations and selectively-bred families were not significant in either breeding zone. Letters indicate statistically significant differences between groups (Tukey's HSD test, $\alpha = 0.05$).

treatment (Table 3). Early growth in the recovery year following drought had the lowest heritability in the severe drought treatment compared to moderate values in the moderate and control treatment (Table 3).

Final chlorophyll fluorescence values, fluorescence declines, and canopy loss had low heritability values in the severe drought treatment ($h^2 \leq 0.06$; Table 3). Canopy loss had the lowest heritability in the moderate drought treatment due to lower additive genetic variance and greater phenotypic variance relative to the severe drought treatment.

4. Discussion

We studied the effects of selective breeding for faster growth on drought resistance, the quantitative genetics of drought resistance traits, and the effects of drought on the genetics of growth and phenology in western larch seedlings to better understand the implications for tree breeding under increasing drought. Seedlings responded to the severe drought treatment with reduced annual growth, earlier bud set and greater needle shedding relative to the control treatment. Western larch seedlings were more drought resistant than expected, with only 12 % mortality and 22 % reduction in chlorophyll fluorescence, on average, after five months without water during an exceptionally hot and dry summer. We found that selective breeding has increased growth relative to natural populations under both drought and control conditions at a warm study site located outside of the natural range and established breeding zones. While selective breeding delayed bud set under well-watered conditions, both natural populations and selectively-bred families responded to drought treatments by setting bud earlier. Bud flush phenology did not differ between selectively-bred and natural genotypes in the control treatment but bud flush was slightly earlier in

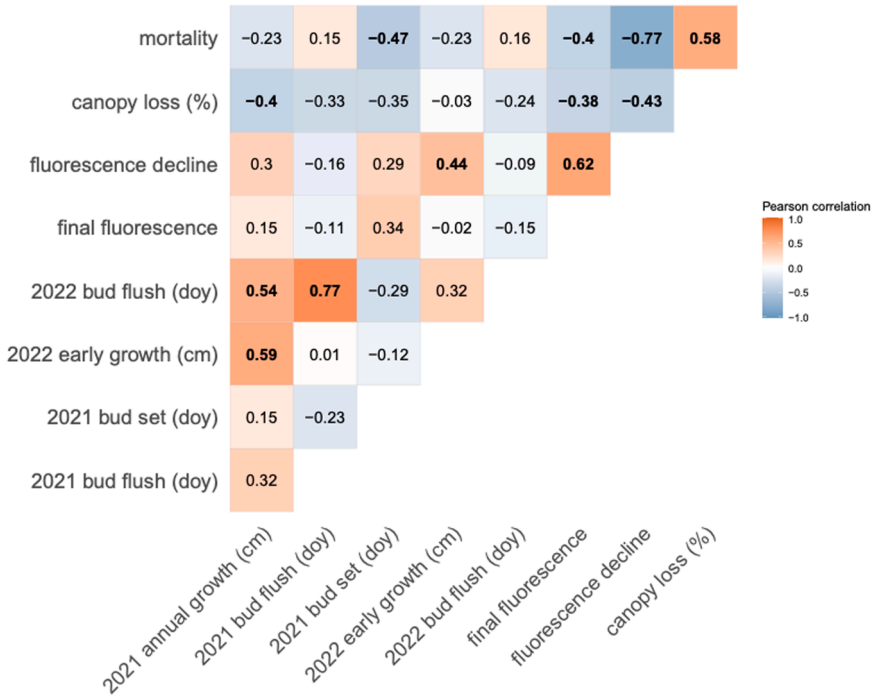

Fig. 6. Trait correlation coefficients among family phenotypes (BLUPs) in the severe drought treatment in the drought year (2021) and in the recovery year (2022). Pearson correlation coefficients significant at $P < 0.05$ are in bold.

Table 3
Heritability and variance components of traits in selectively-bred families. σ_a^2 = additive genetic variance estimated from pedigree, σ_p^2= total phenotypic variance for the trait, and narrow-sense heritability (h^2) for growth and bud phenology traits estimated from 29 full-sib breeding families in the drought year (2021) and recovery year (2022). Fluorescence decline and final fluorescence were measured in the severe drought treatment of the drought year (2021). Canopy loss was measured in the moderate and severe drought treatment of the drought year.

	control			moderate			severe		
Trait	σ_a^2	σ_p^2	h^2	σ_a^2	σ_p^2	h^2	σ_a^2	σ_p^2	h^2
2021 annual growth (cm)	10.94	62.67	0.17	6.28	47.54	0.13	4.51	47.86	0.09
2022 early growth (cm)	14.57	71.98	0.20	14.78	60.30	0.25	7.39	51.00	0.14
2021 bud set (doy)	41.84	115.98	0.36	7.23	35.59	0.20	1.37	52.71	0.03
2021 bud flush (doy)	4.80	42.88	0.11	2.54	35.89	0.07	6.52	30.04	0.22
2022 bud flush (doy)	24.95	69.70	0.36	2.49	72.83	0.03	6.73	39.69	0.17
canopy loss (%)				7.32	715.12	0.01	25.27	647.30	0.04
final fluorescence							0.06	1.68	0.03
fluorescence decline							0.00014	0.005	0.03

selectively-bred families in the severe drought treatment. We found weak correlations among family phenotypes between drought resistance and both annual growth and bud phenology, suggesting that breeding for drought resistance may be possible without altering traits relevant to adaptation to local climates. Importantly, selective breeding for faster growth did not compromise drought resistance in seedlings. However, we detected limited genetic variation and low heritability in drought resistance, along with diminished genetic variation in growth and phenology traits under drought, indicating potential barriers to breeding for improved drought resistance in seedlings.

While annual growth in natural populations and selectively-bred families was reduced under severe drought, growth gains under drought for selectively-bred families were similar to the control treatment, with an average of 21 % greater annual height growth relative to natural populations. This is consistent with reported genetic gains in growth (Forest Genetics Council of British Columbia, 2021), despite the warmer and less continental climate of test site located outside of established breeding zones. Natural populations from the eastern zone had greater annual growth compared to the western zone in the control treatment, consistent with a longitudinal cline detected among 52 natural populations, potentially reflecting an adaptation of faster growth in response to shorter growing seasons (Roskilly and Aitken 2024). However, annual growth differences between zones were eliminated in the severe drought treatment. Notably, growth gains of selectively-bred families relative to natural populations under drought were achieved without significant differences in bud phenology or duration of the growth period. Bud set was delayed in selectively-bred families compared to natural populations in the control treatment for both breeding zones. However, both selectively-bred families and natural populations responded to moderate and severe drought treatments by advancing bud set by more than a week, diminishing phenological differences associated with artificial selection or breeding zones. Bud flush timing did not differ between natural populations and selectively-bred families in the control treatment and did not differ between breeding zones. However, selectively-bred families had slightly earlier bud flush compared to natural populations in response to mild drought acclimation in the year prior to the drought treatments. This difference in bud flush timing may have been an effect of greater growth in selectively-bred families under mild drought acclimation in 2020 resulting in fewer resources allocated to buds and slightly earlier bud flush in spring of the drought year.

The lack of strong differences in bud phenology and earlier bud set

under drought suggests that growth gains from selective breeding were achieved through faster early-season growth, likely free growth. We could not distinguish determinate and free growth in this study because preformed and neoformed leaves are not readily distinguishable based on morphological differences. However, free growth is a form of indeterminate growth that occurs before bud set and remains a significant component of growth potential beyond the juvenile stage in western larch (Schmidt and Shearer, 1990).

The capacity for faster growth early in the season could provide a growth advantage without compromising drought resistance, particularly when drought occurs later in summer. Indeed, selectively-bred families had similar drought resistance to natural populations and faster growth in the drought treatment. We found no differences in fluorescence declines, final fluorescence, or canopy loss between selectively-bred families and natural populations. Selectively-bred families from the eastern zone had slightly higher final fluorescence values compared to the western zone, however, there was no difference in fluorescence declines. In other words, we did not find strong evidence for greater drought resistance in natural populations or selectively-bred families from the drier and more continental climates of the eastern zone. Given the similarities in bud phenology between natural populations and selectively-bred families under drought conditions, this suggests a lack of tradeoffs or genetically correlated responses between growth rates and drought resistance within these second-cycle breeding populations. However, differences among seed sources in drought resistance traits may change in response to future selection for growth or in more advanced generation breeding programs.

While the results of this study are informative for tree breeding programs concerned about seedling performance under increasing drought risks, this was a relatively short-term drought experiment conducted in outdoor raised beds. Experimental drought can be more controlled and evenly applied in common garden studies of seedlings and used to assess genetics of traits relevant to drought tolerance that may be more difficult to measure in adult trees. Greenhouse studies offer more controlled but less realistic environmental conditions that may not be relevant to field conditions. However, it can be challenging with outdoor experiments to impose realistic yet strong enough drought treatments to detect genetic differences in drought resistance in a single growing season. In this study, we used transparent rain covers to exclude precipitation during the growing season. Rain covers did not reach the soil surface to allow for air flow and prevent excessive heat. A barrier of gravel and landscape cloth at the bottom of the raised beds was used to prevent water moving up through capillary action from the soil below. While it is possible that seedling roots penetrated the ground below the soil in the raised beds (60 cm in height), summer 2021 was exceptionally hot and dry and it is unlikely they obtained a significant amount of extra moisture from the unirrigated soil below the beds. For outdoor drought experiments with seedlings, it is important to consider planting in a soil with good drainage, preventing precipitation and withholding water early in the season, and planning for a multi-year drought experiment, which can also be used to monitor drought recovery.

It is important to note that performance of seedlings under imposed drought in raised beds could differ from responses to drought conditions in the field or in older trees, and breeding programs select trees based on growth at older ages in field trials. Studies that directly evaluate differences in drought responses between selectively-bred and natural populations in adult trees are limited but in 26-year-old realized growth genetic gain trials of coastal Douglas-fir in British Columbia, no genetic differences in drought resistance or resilience were detected using growth ring data (Damen et al., 2025). It is possible that selection for faster growth is achieved by mechanisms that do not compromise hydraulic vulnerability. For example, in maritime pine (*Pinus pinaster*) and Douglas-fir, selective breeding for fast growth and stem traits improved hydraulic conductivity but did not compromise embolism resistance of the xylem (Song et al., 2023; Wang et al., 2003). Another possibility is that faster growth could increase hydraulic vulnerability in the xylem but is compensated by larger seedling size, for example, by providing more access to water through a larger root system. Studying the effects of selective breeding for growth on physiological and morphological traits related to drought responses, such as xylem hydraulics, stomatal sensitivity, leaf-to-sapwood area or root-to-shoot ratios, could help elucidate how selectively-bred families achieve faster growth without compromising drought resistance.

The traits we considered as indicators of drought resistance in this study, i.e., fluorescence declines, final fluorescence, canopy loss, and mortality, were strongly intercorrelated among families. Fluorescence declines and mortality were strongly correlated, indicating that faster fluorescence declines increased the likelihood of mortality in families by the end of the season. Fluorescence declines were previously identified as one of the best predictors of survival under drought in Scots pine (Garcia-Forner et al., 2015). A strong association between fluorescence and mortality was expected given that fluorescence declines are a late-stage signal of drought stress that occurs after plants have reached the point of no return in terms of hydraulic failure (Trueba et al., 2019). The strong correlation with mortality confirms that fluorescence declines are an informative trait for detecting genetic variation in drought resistance. Canopy loss and final fluorescence values were also correlated with mortality among families, though less so than fluorescence declines. Canopy loss was positively correlated with mortality and negatively correlated with fluorescence declines, suggesting that greater leaf shedding in response to drought stress did not prevent critical water loss in the severe drought treatment, as has also been found in some drought-deciduous tropical tree species (Wolfe et al., 2016). The function of drought-induced leaf shedding may not be limited to preventing critical water loss, and may vary by species and with drought conditions. It may reduce respiration, facilitate nutrient re-utilization, or re-balance leaf-to-root ratios (Wolfe et al., 2016). Leaf shedding in western larch seedlings occurred in older leaves first, and leaves lost chlorophyll before abscising, turning yellow or orange, suggesting that senescence occurred before leaf shedding, which may indicate a role for nutrient re-utilization.

Drought resistance traits were not strongly correlated with growth or bud phenology among family phenotypes in either the severe drought or control treatment. Annual growth under severe drought in 2021 was not correlated with fluorescence declines, final fluorescence or mortality. It was negatively correlated with canopy loss, indicating that faster growing families had less canopy loss. These results are consistent with the weak correlations between growth and drought resistance found among Douglas-fir families (Anekonda et al., 2002; Nuhu, 2022) and suggest that selection for greater drought resistance in seedlings may be possible without compromising growth. Similarly, bud flush and bud set phenology in the drought year were not strongly correlated with fluorescence declines or canopy loss (Fig. 6). Bud flush phenology in the recovery year was not correlated with drought resistance traits. Families with slower fluorescence declines had greater early growth in the recovery year. There was a negative correlation between bud set and mortality in the drought year, indicating that families with earlier bud set in the severe drought treatment had higher mortality. Given that drought stress induced earlier bud set, it is possible that families with later bud set may have had access to water for a longer duration, perhaps due to greater allocation to roots, leading to less drought stress and mortality. The weak correlations between drought resistance and annual growth or bud phenology in this study suggests that breeding for improved drought resistance within regional breeding populations may be possible without compromising traits relevant to adaptation to local climates.

An important finding from this study is the limited additive genetic variance and heritability for drought resistance traits of fluorescence declines, final fluorescence, and canopy loss among families. Similarly low heritability of dark-adapted chlorophyll fluorescence after 5 and 10 months of drought stress were also detected in seedlings of radiata pine (*Pinus radiata*) families from the breeding program in New Zealand

(Ismael et al., 2022). Low heritability of drought resistance traits, which were strongly correlated with mortality, is consistent with classical theory of life history traits, which posits that traits closely related to fitness should be under strong directional selection and therefore exhibit less genetic variance (Falconer and MacKay, 1995). Additionally, microsite variability in soil moisture and interannual differences in precipitation may promote phenotypic plasticity over genetic adaptation in traits related to drought resistance. However, in a drought experiment of 4-year-old coastal Douglas-fir families conducted in adjacent raised beds simultaneously with this study, heritability of fluorescence declines was higher among families ($h^2 = 0.15$; Nuhu, 2022) than found in this study, suggesting greater genetic variance in drought resistance than in western larch.

While drought is more challenging to study or apply evenly in the field, genetic trials of adult trees can help evaluate which components of drought responses have the most potential for breeding for drought tolerance (Moran et al., 2017). Studies of the quantitative genetics of drought responses in adult trees are limited, but in genetic trials of white spruce and lodgepole pine, drought resistance was found to be the least heritable component of the drought response estimated using tree ring indices (Azcona et al., 2024; Depardieu et al., 2020; Laverdière et al., 2022). Moreover, xylem hydraulic vulnerability should be strongly linked to drought resistance and studies have detected limited genetic variation in xylem hydraulic vulnerability among populations and families of maritime pine, Norway spruce (*Picea abies*), and Douglas-fir (Chmura et al., 2015; Lachenbruch et al., 2022; Lamy et al., 2012 but see Chauvin et al., 2019). On the other hand, higher heritability for drought recovery and resilience in white spruce (*Picea glauca*) families and for a longer-term growth decline index in lodgepole pine (*Pinus contorta*) suggests potential for genetic improvement in these species (Azcona et al., 2024; Depardieu et al., 2020; Laverdière et al., 2022). Nonetheless, the limited additive genetic variation and low heritability for drought resistance traits we found in this study suggests a potential barrier to selective breeding for drought resistance in seedlings.

Additive genetic variance for growth and bud set phenology was significantly reduced under drought, while treatment effects on bud flush phenology were more variable. Heritability was reduced by the duration and severity of the drought treatment for annual growth and bud set phenology, driven by decreases in both additive genetic variance and phenotypic variance. Reduced genetic variance and heritability persisted for early growth in the recovery year following the severe drought treatment but not in the moderate treatment, indicating that rewatering late in the growing season of the drought year promoted recovery of expressed genetic variance for growth the following season. Importantly, the seedlot-by-treatment interaction was only significant for bud set phenology, suggesting relatively stable family rankings across treatments for height growth and bud flush phenology. Our findings are consistent with the diminished genetic variation among provenances for growth sensitivity to drought in Norway spruce grown in stressful marginal habitat (Klisz et al., 2019) and reduced heritability in growth and phenology traits of Douglas-fir families grown in a dry test environment (Kaya, 1992). Heritability in canopy and root morphology traits was also reduced in seedlings of Scots pine families under drought conditions, though it was higher in natural populations compared to selectively-bred families (Gil-Muñoz et al., 2023). On the other hand, heritability and genetic variance for bud flush phenology were more variable between treatments due to high phenotypic plasticity, with lower heritability for bud flush compared to average heritability estimates for other temperate tree species such as Douglas-fir, white spruce, Norway spruce, and balsam poplar (*Populus balsamifera*) (Howe et al., 2003). High plasticity is consistent with bud flush that was nearly a month earlier in seedlings at the warm study site relative to average bud flush date of seedlings from a provenance trial located within the species range in a colder climate (Rehfeldt, 1992). While the effects of drought on quantitative genetics of bud flush were less consistent, the diminished genetic effects on growth and bud set phenology under drought in this study could lead to less predictable genetic gains for tree breeding programs as droughts become more prevalent in the future.

This study provides valuable information on the effects of selective breeding for growth on drought resistance, the quantitative genetics of drought resistance traits, and the effects of drought on the genetics of growth and bud phenology in western larch seedlings. We found that selective breeding for faster growth has not compromised drought resistance in western larch seedlings. Correlations among families between growth and both bud phenology and drought resistance are weak. However, limited genetic variation in drought resistance traits and diminished genetic effects of selection on growth and phenology under drought indicate potential barriers to breeding for improved drought resistance in seedlings. Studying the effects of selective breeding for growth on physiological and morphological traits related to drought responses help determine how selectively-bred families achieve faster growth without compromising drought tolerance. Some promising new phenotyping tools are available, including high throughput imaging for canopy and root morphology traits in seedlings (Gil-Muñoz et al., 2023) and drone-based remote sensing techniques for detecting genetic variation in spectral traits of adult trees in the field, though more studies are needed to link spectral indices to morphological and physiological traits relevant to drought responses (D'Odorico et al., 2020; Grubinger et al., 2023; Ludovisi et al., 2017; Sapes et al., 2024). It is also important to understand patterns of local adaptation to determine if assisted migration of natural or genetically improved seed sources could mitigate maladaptation to drought. Finally, understanding the effects of silvicultural decisions such as site selection, site preparation, planting season and density will also be increasingly important for mitigating the impact of drought on tree breeding programs and managed forests.

CRediT authorship contribution statement

Roskilly Beth A: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Martin R. Henry:** Writing – review & editing, Visualization, Methodology, Investigation. **Sally N. Aitken:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123064.

Data availability

Data will be publicly archived on the Dryad digital repository upon publication.

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