

Local adaptation of balsam fir seedlings improves growth resilience to heat stress

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Abstract

Increasing frequencies of heat waves and drought are expected to shift the range and growth of balsam fir (*Abies balsamea* (L.) Mill.), a widely distributed cold-adapted boreal species. However, our ability to predict this species response to these climate anomalies remains limited, especially when considering how trees can exhibit delayed and persistent growth responses to these stressors, or legacy effects. Here, we assess the growth response of balsam fir seedlings from four populations following 60 treatment combinations of temperature and water deficit in the previous year. Although we observed moderate water deficit legacy effects on growth, there were no resilience or recovery responses. We did, however, observe considerable negative legacy effects on growth proportional to the level of warming, with average legacy growth declines reaching 45% under the highest warming treatment. Furthermore, the southern populations displayed a 28% higher average growth resilience to temperature stress compared with the northern populations, indicating a higher tolerance to warming. When comparing legacy effects on balsam fir populations at moderate warming conditions relative to the current local baseline climate, we report limited growth declines for southern populations and growth increases for the northern populations. While our results highlight the importance of legacy effects from heat stress in seedlings, they also provide evidence that careful selection of warm-adapted genotypes for reforestation efforts may help offset some of these legacy effects.

Key words: *Abies balsamea* (L.) Mill., climate change, water deficit, provenance, legacy effects

1. Introduction

Projected shifts in global precipitation and temperature patterns (Zhang et al. 2019; IPCC 2021) are anticipated to greatly influence global forest mortality rates and composition by the end of this century (McKenney et al. 2007; Allen et al. 2010; McDowell et al. 2016). However, there is still uncertainty in projecting these changes due to varying tree responses and climate model uncertainties (Loehle and Leblanc 1996; Devi et al. 2018). The duration and severity of tree growth suppression due to drought and high temperatures have been reported to vary based on a multitude of interacting factors such as age, species, and the intensity and timing of the initial stressor events (Anderegg et al. 2015; Peltier et al. 2016; Gao et al. 2018; Huang et al. 2018; McDowell et al. 2022). In addition, these effects can carry on beyond the duration of the climate event. The importance of these legacy effects is increasingly acknowledged, as they have been observed to promote tree mortality through declines in plant resistance to subsequent abiotic and biotic stressors (Anderegg et al. 2013a; Cailleret et al. 2017; Kannenberg et al. 2019; DeSoto et al. 2020; Peltier and Ogle 2020; McDowell et al. 2022). However, we still lack sufficient knowledge to account for their influence when projecting tree growth responses under climate change.

Some of the main physiological symptoms of drought and high temperature legacy effects are xylem cavitation, decreased sapwood area, growth inhibitions (Anderegg et al., 2013b, 2015; Trugman et al. 2018), and shifts in carbon reserves due to increased demand for the restoration and preservation of hydraulic and photosynthetic structures (McDowell et al. 2008; Anderegg et al. 2013a, 2013b; Klein et al. 2018; DeSoto et al. 2020; Peltier and Ogle 2020). Drought-induced xylem cavitation and lagged growth reductions can increase susceptibility to cumulative cavitation, likely in part due to reduced hydraulic transportation and weakened xylem (Anderegg et al. 2013a, 2013b; Hacke et al. 2001). Further, initial damages in photosynthetic and hydraulic systems can reduce future tree growth and resistance capacity through reduced carbon assimilation, which limits structural repair and growth of new sapwood and leaves (Anderegg et al. 2013a, 2013b; Sevanto et al. 2014; Kannenberg et al. 2019; Chang et al. 2020).

To better quantify the climate tolerance of plants, Lloret et al. (2011) proposed the separation of tree growth responses to stressor events into three time-related components: resistance, recovery, and resilience. Under this framework, *resistance* is defined as the ability of a plant to maintain growth during a stressor event; *recovery* is the ability of a tree to re-

cover from damages incurred from a stressor event; and *resilience* is the ability of a tree to resume pre-stressor growth rates, thus integrating the elements of recovery and resistance (Lloret et al. 2011). The key functional traits that dictate the magnitude of tree resilience to heat and drought mostly relate to its hydraulic framework and ability to maintain a positive water balance, thereby ensuring continuous carbohydrate production and distribution throughout the entire system (Aubin et al. 2016; DeSoto et al. 2020; McDowell et al. 2022). Functional traits such as deep rooting habit increase water access, while a higher stomatal sensitivity allows for effective stomatal regulation, enabling greater control over transpiration rates. These traits, along with a thinner tracheid aperture, can enable greater xylem tension, decreasing the risk of runaway xylem cavitation and subsequent growth declines (Sperry and Tyree 1990; Anderegg et al., 2013b; Aubin et al. 2016). For instance, legacy growth declines in a shallow-rooted conifer with low hydraulic safety margins, such as balsam fir (*Abies balsamea* (L.) Mill), were associated with increased aridity in the summer and autumn of the prior year (Goldblum and Rigg 2005; D'Orangeville et al. 2013). Indeed, the occurrence and intensity of legacy effects are primarily associated with late-season drought events and drought severity to a lesser extent (Huang et al. 2018; Gao et al. 2018; Kannenberg et al. 2019). While the bulk of literature addresses drought legacy effects in mature trees, our understanding of how heat and drought legacy effects impact both trees and seedlings is limited. Compared with mature trees, seedlings have limited ability to acquire water and minimal carbon production (McDowell et al. 2008), thereby hindering their resilience and recovery capacity.

The climatic tolerance of a species is determined in part by its ability to adapt to stressors through phenotypic plasticity. Phenotypic plasticity can vary between populations of a species due to local adaptation, and this variation can be assessed with provenance trials, where trees from different populations, or provenances, are planted together across climate gradients and compared (Carter 1996; Mátyás 1996; Ghalambor et al. 2007; Risk et al. 2021). For example, in a mature balsam fir provenance trial, water-use efficiency was positively correlated with size (Akalusi and Bourque 2021), while balsam fir seedlings from warm-adapted origins demonstrated higher photosynthetic acclimation in response to increasing temperatures (Ravn et al. 2022). While useful, much of this research has focused on growth response to extreme growing conditions (e.g., Atzmon et al. 2004; McLane et al. 2011) and the overall provenance response to growing conditions (e.g., Carter 1996; Garzón et al. 2011; Lu et al. 2014), two approaches that assume a stable effect of climate on growth over time (Astigarraga et al. 2020; Wilmking et al. 2020). However, growth response to climate is often affected by legacy effects from the previous year's growing season (McDowell et al. 2008; Huang et al. 2010; Levanič et al. 2011; Anderegg et al. 2013a; Camarero et al. 2015; Peltier et al. 2016; Peltier and Ogle 2020). Therefore, by limiting tree stress in the pre- and post-stressor growing seasons, assessing the multi-year growth response of provenances to a specific stressor year should yield a clearer relationship between legacy growth and climate (Olesinki et al. 2011;

Taegar et al. 2013; Peltier et al. 2016), increasing our understanding of species-level responses to climate change and informing potential management solutions, such as assisted migration.

During the 2021 growing season, we subjected 2-year-old seedlings of four balsam fir provenances to a combination of temperature (seasonal average of 13.9 °C to 30.9 °C) and water deficit (0 to -2.5 mPa) treatments. We reported marginal changes in growth across all treatment combinations and observed moderate intraspecific variance of phenotypic plasticity in seedling root:shoot ratios and photosynthesis (Ravn et al. 2022). In this study, we describe the resilience, growth, and survival responses of these same seedlings grown under non-stressful, ambient conditions in the following year to observe potential legacy effects and assess differences in resilience and recovery among provenances. Our research objectives were to (1) determine the extent and direction of legacy growth effects across treatment gradients and (2) assess variation in the severity of legacy effects between provenances. We hypothesized that (i) seedlings exposed to higher intensities of temperature and water deficit treatments will experience the lowest rates of growth in the following season due to the stress imposed in the prior year and (ii) balsam fir provenances from southern locations will have the highest levels of resilience and recovery to treatments due to local physiological adaptations.

2. Materials

2.1. Experimental design

In our previous study (Ravn et al. 2022), we conducted a controlled greenhouse experiment in 2021 (May 1–September 16) to assess the direct response of balsam fir provenances to large gradients of temperature and late-summer water deficit treatments. Our split-split plot design had 240 unique treatments: four provenances selected from a wide climate gradient within the species natural range, nested within five levels of water deficit intensity ranging from 0 to -2.5 mPa, and nested within 12 temperature treatments ranging from an average of 13.9 °C to 30.9 °C. During the 2022 growing season (April 11–August 16), all seedlings were subjected to the same treatment conditions that ensured adequate moisture, sufficient nutrients, and ambient temperatures to best isolate the lagged effects on growth from the previous growing season. This experiment was conducted at the Atlantic Forestry Centre (AFC) Greenhouse operated by Natural Resources Canada—Canadian Forest Service (CFS; Fredericton, NB, Canada).

2.2. Provenance selection

We selected among the available provenances to maximize the range of temperature from which they originated, while choosing only eastern provenances to minimize differences in adaptation to moisture stresses. We used climatic norms (1981–2010) provided by the CFS (Environment Canada 2011) to describe climate ranges for each of the 126 balsam fir provenances available from the National Tree Seed Center (NTSC; <https://cfs.nrcan.gc.ca/publications?id=36773>).

Table 1. Description of the seedlots used in the experiment.

	Roddickton, NL	Georges Brook, NL	Honeydale, NB	Carleton, NS
Code	North	Mid-north	Mid-south	South
NTSC PID	8800430	20090231	9810240	8810054
Collection year	1988	2009	1998	1988
Coordinates	50.98, -56.23	48.27, -53.98	45.35, -67.15	44.02, -65.93
Summer TMAX (1981–2010)	18.8	20.9	22.8	23.8
Winter TMIN (1981–2010)	-22.7	-19.2	-13.7	-8.0
TMAX (1961–1990)	19.6	22.4	24.6	21.3
TMIN (1961–1990)	-16.0	-11.0	-15.1	-7.8
CMI (1961–1990)	87.4	77.2	72.5	86.1
Seed collection type	Bulk	Single	Bulk	Bulk

Note: PID indicates provenance identification number from the NTSC records.

Based on this data, the mean maximum summer temperature and mean minimum winter temperature gradient amongst our four selected provenances spanned 5 °C and 14 °C, respectively (Table 1). In addition, to account for the potential influence of climate during seed formation on the heritability of climate tolerance in seedlings, we compared the 1961–1990 climate normals and seed collection-year climate for each provenance but did not find any climate anomalies during seed collection years. Finally, during our experiment, our mid-north provenance was determined to originate from a single, open-pollinated tree, unlike our other provenances (Table 1), thus limiting the genetic variation of these seedlings and our ability to extrapolate growth responses to the entire population.

2.3. Treatments

In 2020 (year 1), we started our experiment with the germination and growth of our seedlings under ambient environmental conditions existing in the greenhouse. In 2021 (year 2), we used 12 climate-controlled phytotrons to expose these 3,600 seedlings in their second year to 12 different temperature treatments at intervals of 1.81 °C to ensure that each provenance experienced a minimum of +11 °C above and -3 °C below their origin summer climate. To simulate seasonal temperature growth, temperature regimes were adjusted weekly, while daily temperature levels were set to adjust every two hours (Ravn et al. 2022). In August of that same year, we exposed seedlings to a water deficit trial consisting of five levels of intensity, here measured as soil water potential (SWP; mPa). For our most extreme water deficit level, seedlings experienced a SWP of -2.5 mPa, associated with complete photosynthetic and transpirative shutdown in certain conifers (Havranek and Benecke 1978). Between our control and maximum treatment, each successive water deficit level increased at evenly spaced intervals of -0.625 mPa. The duration of each treatment level varied according to temperature treatments due to differences in evapotranspiration. For instance, the most severe water deficit level (-2.5 mPa) was obtained with watering intervals of 15 and 31 days in the warmest and coldest treatments, respectively. In the present study, we grew these seedlings under non-stressful, ambi-

ent conditions in greenhouse for their third year to measure legacy effects.

2.4. Response variables

We measured the annual height growth (cm) of seedlings for each of their three years of existence to test our first hypothesis. Height growth was used in these analyses as it is a useful predictor of seedling establishment and survival, generally related to vigour, photosynthetic, and transpirational potential (Grossnickle 2012). To test our second hypothesis, we used the annual height growth measurements to calculate the resilience and recovery to temperature and water deficit treatments. Considering the potential confounding effect of differing interannual growth rates among provenances, we conducted a preliminary growth analysis of each provenance under non-stressful treatment conditions and found no differences between groups. Finally, given the non-stationary growth patterns of seedlings, we calculated the relative resilience and recovery rates rather than absolute rates using the following equations (Lloret et al. 2011):

$$\text{Recovery} = \frac{G_3}{G_2} \quad \text{and} \quad \text{Resilience} = \frac{G_3}{G_1}$$

where G_1 , G_2 , and G_3 represent annual seedling height growth for years 1, 2, and 3, respectively.

In year 2, we measured the length (cm) of each apical and lateral Lammas branch of 15 seedlings for the north and south provenances each to compare Lammas growth. Although this data was limited and insufficient for testing our two hypotheses, we analyzed these data to supplement our discussion section, as this observed variation could influence resilience and recovery levels.

2.5. Statistical analysis

We used linear-mixed effect models to assess the impacts of temperature and water deficit on height growth in the following year of balsam fir seedlings from four contrasting provenances. Separate models were fitted to predict height growth, recovery, resilience, and Lammas growth. We used provenance, average treatment temperature, and level of water deficit intensity as factors in our three main models. For

our Lammas growth model, we did not use water deficit intensity because measurements were conducted prior to our water deficit treatments. We standardized our temperature variable through scaling to allow for better model interpretation due to the different value ranges between our predictor variables. Finally, to account for potential heterogeneity between treatment blocks, we assigned a random intercept for the phytotrons within each model.

For each response variable, we started with a full model including all measured variables and relevant interactions between the main variables. Except for the model-specific hypothesized interactions, we removed all non-significant ($p > 0.05$) explanatory variables as well as non-significant two-way and three-way interactions within each model iteration to avoid overfitting and to simplify model interpretation. Our hypothesized interactions for the three main models are water deficit and provenance, and temperature and provenance. In the height growth model, we added a “year” term along with “year” interactions with temperature and water deficit to test for different treatment effects between years. To improve interpretation for our height growth model only, all 12 temperature levels were grouped into pairs of closely related treatments during analysis. We did not include a “year” variable for our resilience and recovery models since these two variables inherently compare growth between years. For the variable “year” in our height model and temperature in our Lammas, resilience, and recovery models, we observed non-linear, binomial relationships; therefore, both variables were fit with orthogonal polynomial terms. Our height growth model takes the following form:

$$y_j = \beta_0 + \beta_1 T + \beta_2 P + \beta_3 D + \beta_4 Y^2 + \beta_5 P \times D + \beta_6 Y^2 \times T \times P + \epsilon_j$$

where T is the average temperature treatment in Year 2, P is the provenance, D is the water deficit intensity, Y is the growing year, fit with an orthogonal polynomial term, β is the slope of the fixed effects, and ϵ is the intercept of the phytotron j random effects.

Our recovery and resilience model takes the following form:

$$y_j = \beta_0 + \beta_1 T^2 + \beta_2 P + \beta_3 D + \beta_4 P \times T^2 + \beta_5 P \times D + \epsilon_j$$

Our Lammas growth model takes the following form:

$$y_j = \beta_0 + \beta_1 T^2 + \beta_2 P + \beta_3 P \times T^2 + \epsilon_j$$

All analyses were run using the R package “lme4” (R Development Core Team 2022; Bates et al. 2015). To test linear mixed-effect model assumptions, we conducted a Breusch–Pagan test to assess levels of heteroscedasticity, calculated generalized variance inflation factors to test for multicollinearity, and visually analyzed Q–Q plots for linearity. We used the “emmeans” package with the “emtrends” function to conduct pairwise comparisons with the least-squares means method to test for statistically significant differences

in height, recovery, and resilience trends between provenances and temperature treatments (Lenth 2021).

3. Results

3.1. Legacy treatment effects

While seedling height growth in year 2 was not affected by the temperature treatments or water deficit treatments applied that year, we observed significant legacy effects on height growth in the following year (i.e., year 3; Fig. 1 and Table A1). For all provenances in year 3, mean height growth declined at an average rate of 4% per degree increase in mean treatment temperature, with a 45% growth reduction between the hottest and coldest treatments. However, provenances differ in their legacy effects. For the two lowest mean temperature treatments (15 °C and 17 °C), notable differences emerged in trends among the provenances. The two southern provenances displayed significantly higher trends compared with the two northern provenances (Fig. 1 and Tables A2 and A3). At 30 °C, the mid-south provenance exhibited trends similar to the two northern provenances, while the southern provenance maintained a significant growth difference (Fig. 1 and Tables A2 and A3). In the warmest treatment conditions, the southernmost provenances exhibited a 29% higher growth rate than the other provenances (Fig. 1). Compared with temperature, the legacy effects of the water deficit treatments were moderate, although significant, with growth declines only noted in the mid-north and mid-south provenances (Table A1). This weak water deficit effect was noted in the prior growing season, suggesting that our treatments did not reach low enough levels.

3.2. Comparison of resilience and recovery between provenances

Apart from the mid-north provenance, seedling resilience responses to average treatment temperatures were positively correlated with the provenance origin temperature, while there were fewer distinctions in recovery responses (Table 2 and Fig. 2). Further, we observed limited effects of our water deficit treatments for both resilience and recovery (Table 2 and Fig. 2). Across the experimental temperature gradient, southern provenances demonstrated, on average, 28% higher resilience than the northern provenances. However, pairwise comparisons indicate that such higher resiliency in the mid-southern provenance and the southernmost provenance was no longer significant above average treatment temperatures of 27.5 °C and 28.5 °C, respectively (Fig. 2). Unlike resilience, recovery values were more similar among provenances, with only the mid-northern provenance demonstrating lower recovery rates compared with the other provenances (Table 2 and Fig. 2).

4. Discussion

The large, negative effect of temperature on legacy height growth observed here supports our first hypothesis. Relative to same-year effects on growth, we find significantly stronger legacy effects, which highlights the importance of

Fig. 1. Interaction plot illustrating the modelled effect of temperature treatment (year 2) on the height growth of four balsam fir provenances over 3 years. The coloured bands represent 95% confidence intervals.

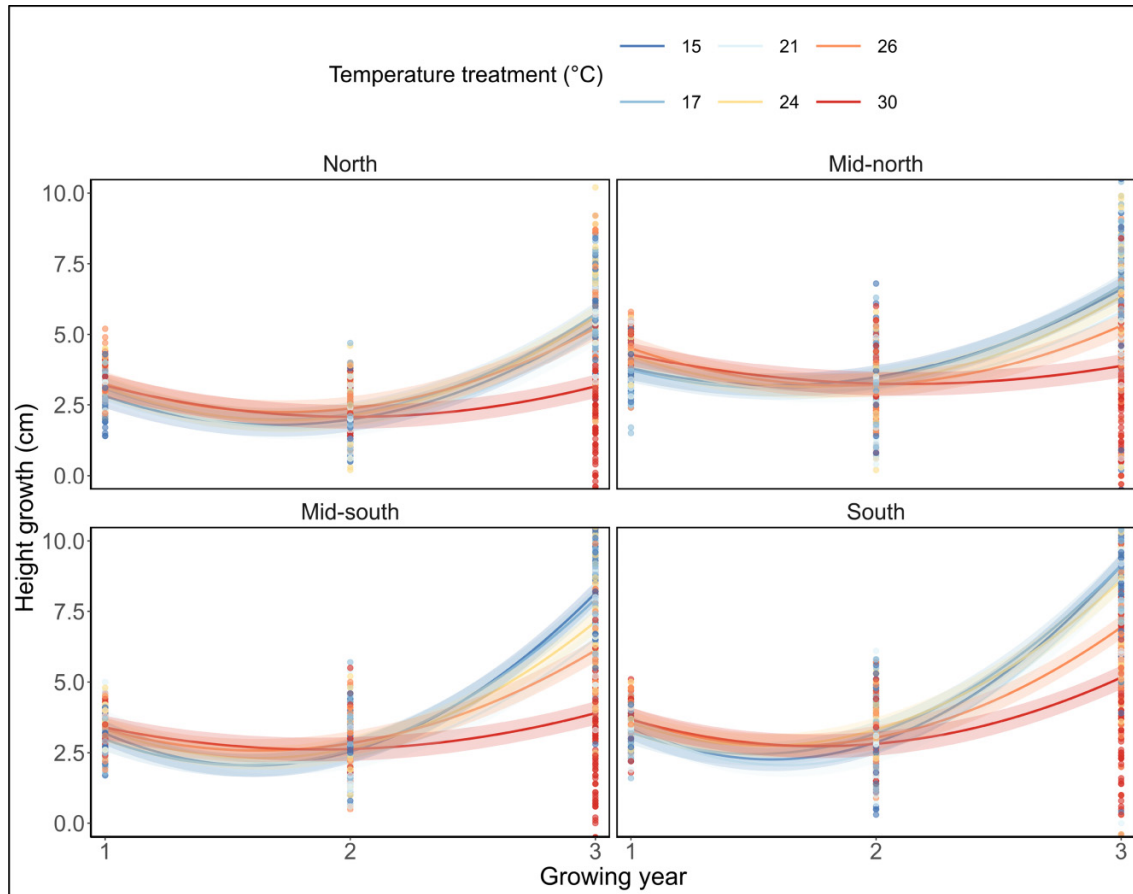
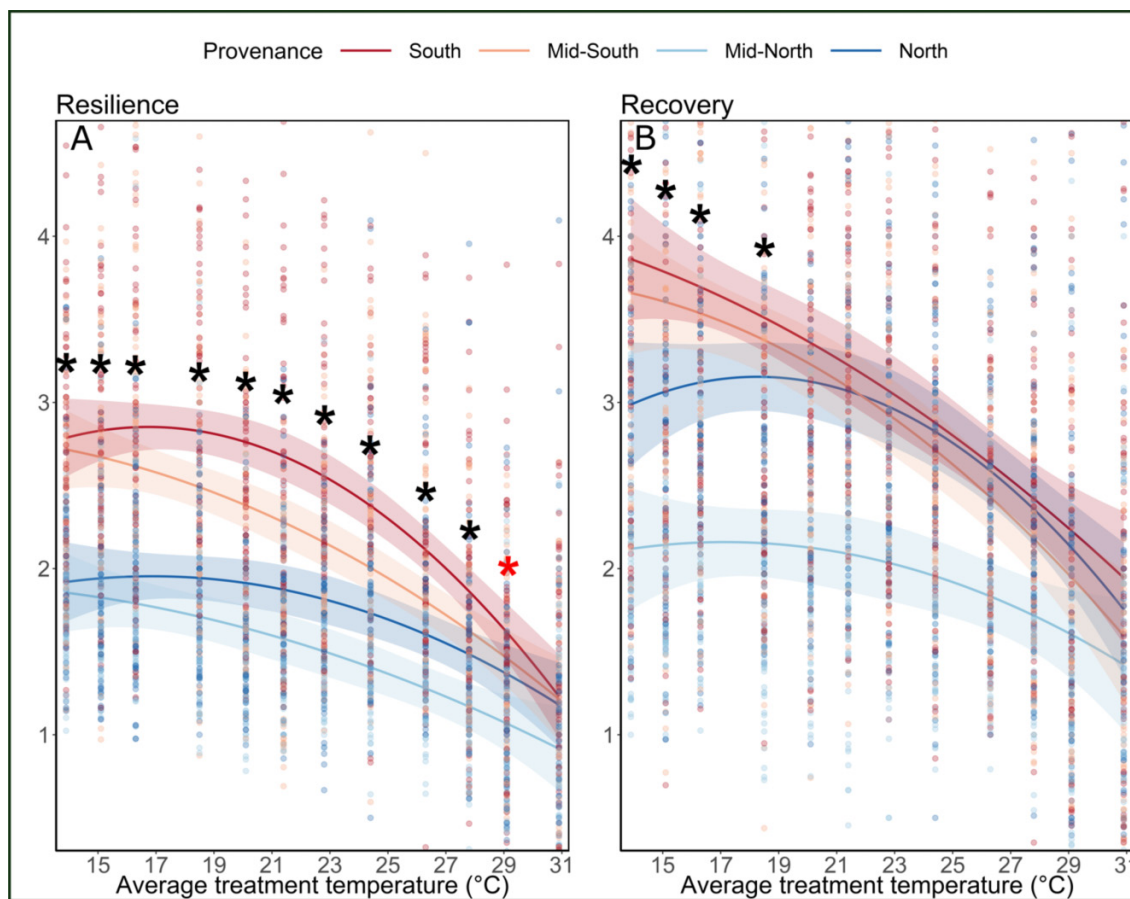


Table 2. General linear mixed-effects model coefficients for recovery and resilience models.

Coefficient	Recovery (<i>n</i> = 3026)	Resilience (<i>n</i> = 3026)
Intercept	2.87 (2.60–3.15)	1.68 (1.53–1.83)
Temperature [1]	–20.45 (–28.86–12.04)	–12.4 (–17.74–7.04)
Temperature [2]	–11.6 (–20.58–3.78)	–5.45 (–10.78–0.11)
Water deficit	–0.04 (–0.11–0.04)	0.02 (–0.02–0.05)
Provenance [MN]	–0.85 (–1.19–0.5)	–0.21 (–0.39–0.04)
Provenance [MS]	0.21 (–0.13–0.56)	0.58 (0.41–0.75)
Provenance [S]	0.57 (0.22–0.92)	0.79 (0.62–0.96)
Water deficit × Provenance [MN]	0.01 (–0.10–0.11)	–0.01 (–0.06–0.04)
Water deficit × Provenance [MS]	–0.04 (–0.14–0.07)	–0.06 (–0.11–0.01)
Water deficit × Provenance [S]	–0.09 (–0.20–0.01)	–0.05 (–0.10–0.01)
Temperature [1] × Provenance [MN]	8.79 (0.73–16.85)	–3.71 (–7.73–0.31)
Temperature [2] × Provenance [MN]	6.78 (–1.28–14.84)	2.79 (–1.23–6.81)
Temperature [1] × Provenance [MS]	–14.84 (–22.88–6.81)	–13.33 (–17.33–9.32)
Temperature [2] × Provenance [MS]	5.49 (–2.55–13.53)	1.07 (–2.94–5.08)
Temperature [1] × Provenance [S]	–12.54 (–20.62–4.46)	–13.74 (–17.77–9.91)
Temperature [2] × Provenance [S]	8.13 (0.02–16.25)	–5.78 (–9.82–1.73)
Marginal <i>R</i> ² /Conditional <i>R</i> ²	0.176/0.192	0.345/0.371

Note: Values in bold indicate statistically significant responses (*p* < 0.05). The values in parentheses are the 95% confidence intervals. Coefficients labelled as “M-N”, “M-S”, and “S” signify mid-north, mid-south, and south locations, respectively. The “1” and “2” for the “treatment temperature” variable indicate the order of the polynomial.

Fig. 2. Interaction plot illustrating the modelled effect of average treatment temperatures in year 2 on (A) provenance-specific resilience and (B) provenance-specific recovery. The coloured bands represent 95% confidence intervals. Black asterisks indicate where values differ significantly ($p < 0.05$) between the two northern and two southern provenances, while red asterisks indicate where values differ significantly between the two northern provenances and the southernmost provenance only.



considering legacy effects when evaluating the interactions between plant growth and climate. However, the moderate legacy effect of our water deficit treatments on seedling height growth, along with the lack of resilience and recovery response, indicates that our treatments were insufficient in severity. The observed distinctions in growth response to temperature treatments between years 2 and 3 may be partially explained by environmental stresses in year 2, affecting the production of leaf primordia during bud formation, thereby reducing the potential for shoot growth in year 3 (Morris 1951; Clements 1970; Powell 1977). Further, seedlings face heightened climate sensitivity due to their limited ability to acquire resources (McDowell et al. 2008; Fisichelli et al. 2014; Gray and Brady 2016). Reduced foliage production likely compounds this sensitivity through the inhibition of stem and root growth, potentially limiting seedling recovery from legacy effects and resilience to future stressors (McDowell et al. 2011; McDowell et al. 2022).

Our results also show substantial variations in heat tolerance among balsam fir provenances, with greater resilience and recovery in warm-adapted southern provenances. While the southern provenances had higher overall resilience and resistance to temperature treatments, treatment conditions

were much warmer for the northern provenances than the southern provenances when considering the climate transfer distance, i.e., the difference between temperature treatments relative to the provenance origin climate. Similarly, year 2 warming treatments induced positive legacy growth responses in the northern provenances and minimal growth declines in the southern provenances. While the level of growth response observed here differs from previous single-year experimental studies on warming effects on balsam fir (Vaughn et al. 2021), recent observational and modelling research also demonstrates positive to neutral relationships between temperature and balsam fir growth with adequate moisture (Collier et al. 2023; Wang et al. 2023).

Considering the low hydraulic safety margins of balsam fir (Sperry and Tyree 1990), the large differences in regional water balances and temperature regimes between the highest and lowest performing provenances may have influenced adaptive selection in the southern provenances. This, in turn, could explain the observed variation in seedling resilience among provenances. Previous observations have revealed higher photosynthetic plasticity and lower rates of severe damage under heat stress for these southern provenances (Ravn et al. 2022). While these observed trends in

phenotypic plasticity likely influence the observed resilience trends through the mitigation of moisture and heat stress, additional adaptation in unmeasured traits such as xylem anatomy could also reduce hydraulic damages resulting from increases in evapotranspiration (Sperry and Tyree 1990; Levanič et al. 2011; Bryukhanova and Fonti 2013; Moran et al. 2017; Schönbeck et al. 2022), thereby enabling higher growth and performance in post-stressor years. Finally, while the mid-north provenance exhibits similar growth behaviour as the north provenance, the observed growth response may not be scalable to the population due to the limited genetic representativeness resulting from a single-tree collection.

Indeed, provenance-specific recovery and resilience trends support our second hypothesis in that the warmer-adapted southern provenances of balsam fir may be better able to mitigate temperature stress, thereby maintaining growth rates and remaining competitive. The improved resilience and growth of the southern provenances could also be explained by their increased propensity for secondary flushing (see *Supplementary material*) or Lammas growth, enabling greater growth compensation for reduced bud investment in the prior stressor year (Pollard and Logan 1974; Soolanayakanahally et al. 2013). While short, cold growing seasons tend to favour quick and conservative growth behaviour in northern provenances to avoid stressors such as early-fall frost damage (Johnsen et al. 1996; Silvestro et al. 2019), longer, warmer growing seasons can promote plastic growing strategies such as secondary flushing to improve competitiveness when conditions are favourable (Cannell and Jonstone 1978; Johnsen et al. 1996).

Environmental stress can select individuals with phenotypic plasticity closer to the local phenotypic optimum, thereby increasing chances of persistence and facilitating genetic adaptation (Via and Lande 1985; Kelly 2019). For balsam fir, studies have found relatively high levels of genetic isolation across different populations due to low levels of pollen spread (Jackson et al. 1997; Shea and Furnier 2002), a trait that may explain the observed phenotypic variation between the provenances observed in this study (Sexton et al. 2014). However, considering the range-limiting effects of the relatively recent Wisconsin glaciation, current levels of genetic and phenotypic deviation may not represent the complete adaptative capacity of balsam fir to climate within its current natural range due to low post-glacial generational turnover in these regions (Hewitt 1999; Shea and Furnier 2002).

While the bulk of current research focuses on legacy effects in mature trees (Anderegg et al. 2013a, 2013b; Kannenberg et al. 2019; Wu et al. 2018), our understanding of legacy effects in seedlings is limited (Junttila 1986; Pikkarainen et al. 2022), a critical knowledge gap that hinders our capacity to predict and mitigate the impacts of climate change. For example, regional forest simulation model projections oversimplify the growth response of seedlings to climate and neglect the concept of legacy effects and intraspecific trait variation, undermining model credibility and forecasting accuracy (Boulanger et al. 2017; Taylor et al. 2017). Considering the climate sensitivity of seedlings, amplification of legacy effects in the regenerative layer may significantly alter future forest structure and composition (Werner et al. 2020). For instance,

legacy growth declines could be exacerbated by increased competitive stress from climate-resilient species (Hille Ris Lambers et al. 2013). Moreover, increased seedling mortality could lower recruitment rates into the upper canopy (Lloret et al. 2009), causing changes in forest composition (Hanson and Welzlin 2000; Lloret et al. 2009; Werner et al. 2020). As such, the integration of legacy effects and seedling growth dynamics into forest simulation models may improve the accuracy of growth and compositional projections.

5. Conclusions

Despite differences among balsam fir provenances in their immediate response to temperature stress (Ravn et al. 2022), our results reveal that the legacy growth response to temperature is even stronger for this species. Further, our results suggest that southern, warm-adapted provenances are more resilient to climate change-induced warming, which supports the careful selection of warm-adapted provenances and assisted migration programs to help offset some of the negative impacts of climate warming. Under moderate warming compared with the current local baseline climate, we found minimal legacy growth effects for the southern provenances and potential growth benefits for the northern provenances. However, the addition and interaction of legacy effects under increasing heat and drought stress may limit seedling resilience, potentially minimizing the observed intraspecific variation and resilience to climate change. Our results highlight the necessity of considering legacy effects and population origin in research regarding plant and climate interactions. Since the implications of our experiment are limited due to the controlled nature of our project and the limited impact of our water deficit treatments, future research should aim to assess how overall provenance resilience is influenced by interacting factors such as ontogeny, biotic stressors, severe drought, and competition.

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mits unrestricted use, distribution, and reproduction in any medium, provided the original author(s) and source are credited.

Data availability

The raw data supporting the conclusions of this article will be made available by the authors without undue reservation.

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Formal analysis: JR

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Investigation: JR, ART, MBL, LD

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Project administration: JR

Resources: MBL

Supervision: ART, LD

Writing – original draft: JR

Writing – review & editing: JR, ART, MBL, LD

Competing interests

The authors declare there are no competing interests.

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Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2023-0128>.

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Appendix A

Table A1. General linear mixed-effects model coefficients for the height growth model.

Coefficient	Height growth ($n = 9165$)
Intercept	3.52 (2.85–3.65)
Growing year [2]	99.03 (86.47–111.59)
Growing year [2]	94.35 (81.79–106.91)
Temperature [17 °C]	0.28 (–0.26–0.82)
Temperature [21 °C]	–0.09 (–0.63–0.45)
Temperature [24 °C]	0.25 (–0.29–0.79)
Temperature [26 °C]	0.24 (–0.30–0.78)
Temperature [30 °C]	–0.57 (–1.11–0.03)
Water deficit	0.04 (0.01–0.08)
Provenance [MN]	1.41 (1.17–1.65)
Provenance [MS]	1.49 (1.25–1.73)
Provenance [S]	1.88 (1.64–2.13)
Provenance [MN] × Water deficit	–0.05 (–0.11 to –0.00)
Provenance [MS] × Water deficit	–0.08 (–0.13 to –0.03)
Provenance [S] × Water deficit	–0.04 (–0.10 to –0.01)
Growing year [1] × Temperature [17 °C]	4.72 (–12.63–22.07)
Growing year [2] × Temperature [17 °C]	5.58 (–11.77–22.93)
Growing year [1] × Temperature [21 °C]	–17.99 (–35.65 to –0.34)
Growing year [2] × Temperature [21 °C]	5.06 (–12.59–22.72)
Growing year [1] × Temperature [24 °C]	–1.85 (–19.33–15.63)
Growing year [2] × Temperature [24 °C]	–7.42 (–10.06–24.9)
Growing year [1] × Temperature [26 °C]	–21.69 (–39.41 to –3.96)
Growing year [2] × Temperature [26 °C]	–10.33 (–28.06–7.40)
Growing year [1] × Temperature [30 °C]	–100.18 (–117.57 to –82.80)
Growing year [2] × Temperature [30 °C]	–45.06 (–62.44 to –27.69)
Growing year [1] × Provenance [MN]	10.52 (–6.83–27.87)
Growing year [2] × Provenance [MN]	–16.83 (–34.18–0.52)
Growing year [1] × Provenance [MS]	94.76 (77.41–112.11)
Growing year [2] × Provenance [MS]	46.63 (29.28–63.98)
Growing year [1] × Provenance [S]	125.58 (108.23–142.93)
Growing year [2] × Provenance [S]	58.45 (41.10–75.80)
Temperature [17 °C] × Provenance [MN]	–0.29 (–0.54 to –0.04)
Temperature [21 °C] × Provenance [MN]	–0.22 (–0.47 to –0.04)
Temperature [24 °C] × Provenance [MN]	–0.26 (–0.52 to –0.01)
Temperature [26 °C] × Provenance [MN]	–0.52 (–0.78 to –0.27)
Temperature [30 °C] × Provenance [MN]	–0.25 (–0.5–0.00)
Temperature [17 °C] × Provenance [MS]	–0.4 (–0.65 to –0.15)
Temperature [21 °C] × Provenance [MS]	–0.38 (–0.63 to –0.12)
Temperature [24 °C] × Provenance [MS]	–0.51 (–0.63 to –0.12)
Temperature [26 °C] × Provenance [MS]	–0.77 (–1.02 to –0.51)
Temperature [30 °C] × Provenance [MS]	–0.74 (–1.00 to –0.49)
Temperature [17 °C] × Provenance [S]	–0.22 (–0.48–0.03)
Temperature [21 °C] × Provenance [S]	–0.18 (–0.42–0.05)
Temperature [24 °C] × Provenance [S]	–0.22 (–0.47–0.04)
Temperature [26 °C] × Provenance [S]	–0.81 (–1.07 to –0.56)
Temperature [30 °C] × Provenance [S]	–0.67 (–0.93 to –0.42)
Growing year [1] × Temperature [17 °C] × Provenance [MN]	3.13 (–21.11–27.37)
Growing year [2] × Temperature [17 °C] × Provenance [MN]	–0.84 (–25.07–23.40)
Growing year [1] × Temperature [21 °C] × Provenance [MN]	–24.43 (–48.88–0.03)
Growing year [2] × Temperature [21 °C] × Provenance [MN]	0.61 (–23.84–25.07)
Growing year [1] × Temperature [24 °C] × Provenance [MN]	–51.75 (–74.25 to –29.25)
Growing year [2] × Temperature [24 °C] × Provenance [MN]	7.28 (–15.21–29.78)

Table A1. (concluded).

Coefficient	Height growth (<i>n</i> = 9165)
Growing year [1] × Temperature [26 °C] × Provenance [MN]	-56.57 (-81.08 to -32.06)
Growing year [2] × Temperature [26 °C] × Provenance [MN]	9.65 (-14.86-34.16)
Growing year [1] × Temperature [30 °C] × Provenance [MN]	-25.4 (-49.68 to -1.11)
Growing year [2] × Temperature [30 °C] × Provenance [MN]	5.1 (-19.19 to -29.38)
Growing year [1] × Temperature [17 °C] × Provenance [MS]	-4.87 (-29.11-19.37)
Growing year [2] × Temperature [17 °C] × Provenance [MS]	-17.6 (-41.84-6.63)
Growing year [1] × Temperature [21 °C] × Provenance [MS]	-60.05 (-84.51 to -35.60)
Growing year [2] × Temperature [21 °C] × Provenance [MS]	-23.39 (-47.85 to -1.06)
Growing year [1] × Temperature [24 °C] × Provenance [MS]	-42.45 (-66.81 to -18.10)
Growing year [2] × Temperature [24 °C] × Provenance [MS]	-33.34 (-57.69 to -18.10)
Growing year [1] × Temperature [26 °C] × Provenance [MS]	-62.79 (-87.30 to -38.28)
Growing year [2] × Temperature [26 °C] × Provenance [MS]	-43.82 (-66.3 to -21.33)
Growing year [1] × Temperature [30 °C] × Provenance [MS]	-73.73 (-98.02 to -49.45)
Growing year [2] × Temperature [30 °C] × Provenance [MS]	-50.09 (-74.37 to -25.81)
Growing year [1] × Temperature [17 °C] × Provenance [S]	2.35 (-22.08-26.78)
Growing year [2] × Temperature [17 °C] × Provenance [S]	-23.13 (-47.56-1.30)
Growing year [1] × Temperature [21 °C] × Provenance [S]	-0.17 (-24.62-24.29)
Growing year [2] × Temperature [21 °C] × Provenance [S]	1.5 (-22.96-25.95)
Growing year [1] × Temperature [24 °C] × Provenance [S]	-25.42 (-49.94 to -0.89)
Growing year [2] × Temperature [24 °C] × Provenance [S]	-35.6 (-60.12 to -11.07)
Growing year [1] × Temperature [26 °C] × Provenance [S]	-75.75 (-100.26 to -51.24)
Growing year [2] × Temperature [26 °C] × Provenance [S]	-39.57 (-64.08 to -15.06)
Growing year [1] × Temperature [30 °C] × Provenance [S]	-66.18 (-90.61 to -41.75)
Growing year [2] × Temperature [30 °C] × Provenance [S]	-35.62 (-60.05 to -11.20)
Marginal R ² /Conditional R ²	0.675/0.688

Note: Values in bold indicate statistically significant responses (*p* < 0.05). The values in parentheses are the 95% confidence intervals. Coefficients labelled as “M-S”, “M-N”, and “N” signify mid-southern, mid-northern, and northern locations, respectively. The “1” and “2” for the ‘Growing year’ variable indicate the order of the polynomial.

Table A2. Pairwise trend comparison results for the height growth model.

Temperature treatment	Provenance comparison	Estimate	SE	df	t-Ratio	p-Value
15	North-Mid-north	0.612	0.409	9083	1.498	0.4387
15	North-Mid-south	-3.281	0.409	9083	-8.028	<0.0001
15	North-South	-4.199	0.409	9083	-10.276	<0.0001
15	Mid-north-Mid-south	-3.893	0.399	9083	-9.766	<0.0001
15	Mid-north-South	-4.811	0.399	9083	-12.07	<0.0001
15	Mid-south-South	-0.919	0.399	9083	-2.304	0.0971
17	North-Mid-north	0.609	0.399	9083	1.528	0.4205
17	North-Mid-south	-2.437	0.399	9083	-6.115	<0.0001
17	North-South	-3.203	0.405	9083	-7.907	<0.0001
17	Mid-north-Mid-south	-3.047	0.399	9083	-7.643	<0.0001
17	Mid-north-South	-3.812	0.405	9083	-9.411	<0.0001
17	Mid-south-South	-0.766	0.405	9083	-1.89	0.2323
21	North-Mid-north	0.898	0.406	9083	2.211	0.1203
21	North-Mid-south	-1.475	0.406	9083	-3.632	0.0016
21	North-South	-4.264	0.406	9083	-10.502	<0.0001
21	Mid-north-Mid-south	-2.372	0.399	9083	-5.951	<0.0001
21	Mid-north-South	-5.161	0.399	9083	-12.947	<0.0001
21	Mid-south-South	-2.789	0.399	9083	-6.996	<0.0001

Table A2. (concluded).

Temperature treatment	Provenance comparison	Estimate	SE	df	t-Ratio	p-Value
24	North–Mid-north	0.678	0.403	9083	1.682	0.3334
24	North–Mid-south	–1.259	0.403	9083	–3.127	0.0096
24	North–South	–2.295	0.408	9083	–5.622	<0.0001
24	Mid-north–Mid-south	–1.937	0.401	9083	–4.831	<0.0001
24	Mid-north–South	–2.973	0.407	9083	–7.312	<0.0001
24	Mid-south–South	–1.036	0.406	9083	–2.553	0.0522
26	North–Mid-north	0.908	0.408	9083	2.226	0.1163
26	North–Mid-south	–0.465	0.408	9083	–1.142	0.6637
26	North–South	–1.475	0.408	9083	–3.617	0.0017
26	Mid-north–Mid-south	–1.373	0.399	9083	–3.444	0.0032
26	Mid-north–South	–2.382	0.399	9083	–5.976	<0.0001
26	Mid-south–South	–1.009	0.399	9083	–2.532	0.0552
30	North–Mid-north	0.711	0.4	9083	1.777	0.2846
30	North–Mid-south	–0.115	0.4	9083	–0.288	0.9917
30	North–South	–1.772	0.405	9083	–4.376	0.0001
30	Mid-north–Mid-south	–0.826	0.4	9083	–2.065	0.1648
30	Mid-north–South	–2.483	0.405	9083	–6.131	<0.0001
30	Mid-south–South	–1.657	0.405	9083	–4.091	0.0003

Note: Comparisons were conducted with the ‘emtrends’ function from the “emmeans” package (Lenth 2021).

Table A3. Estimated marginal mean trend results for the height growth model.

Temperature treatment	Provenance	Trend	SE	df	Lower CL	Upper CL
15	North	5.45	0.296	9083	4.873	6.03
15	Mid-north	4.84	0.282	9083	4.288	5.39
15	Mid-south	8.73	0.282	9083	8.181	9.29
15	South	9.65	0.282	9083	9.099	10.2
17	North	5.76	0.282	9083	5.208	6.31
17	Mid-north	5.15	0.282	9083	4.598	5.7
17	Mid-south	8.2	0.282	9083	7.645	8.75
17	South	8.96	0.291	9083	8.393	9.53
21	North	5.45	0.292	9083	4.874	6.02
21	Mid-north	4.55	0.282	9083	3.997	5.1
21	Mid-south	6.92	0.282	9083	6.369	7.47
21	South	9.71	0.282	9083	9.158	10.26
24	North	5.76	0.286	9083	5.197	6.32
24	Mid-north	5.08	0.284	9083	4.523	5.64
24	Mid-south	7.02	0.283	9083	6.462	7.57
24	South	8.05	0.291	9083	7.483	8.62
26	North	4.72	0.295	9083	4.139	5.29
26	Mid-north	3.81	0.282	9083	3.257	4.36
26	Mid-south	5.18	0.282	9083	4.63	5.73
26	South	6.19	0.282	9083	5.639	6.74
30	North	2.17	0.283	9083	1.617	2.73
30	Mid-north	1.46	0.283	9083	0.906	2.02
30	Mid-south	2.29	0.283	9083	1.733	2.84
30	South	3.94	0.29	9083	3.376	4.51

Note: These results were generated using the “emtrends” function from the “emmeans” package (Lenth 2021).