Pest defences under weak selection exert a limited influence on the evolution of height growth and drought avoidance in marginal pine populations

Yang Liu1,2,3, Nadir Erbilgin3, Blaise Ratcliffe1, Jennifer G. Klutsch4, Xiaojing Wei4, Aziz Ullah4, Eduardo Pablo Cappa5,6, Charles Chen7, Barb R. Thomas4 and Yousry A. El-Kassaby1

1Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia V6T 1Z4, Canada
2McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK
3Wolfson College, University of Cambridge, Barton Road, Cambridge CB3 9BB, UK
4Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton, Alberta T6G 2E3, Canada
5Instituto Nacional de Tecnología Agropecuaria (INTA), Instituto de Recursos Biológicos, Centro de Investigación en Recursos Naturales, De Los Reseros and Doctor Nicolas Repetto s/n, 1686, Hurlingham, Buenos Aires, Argentina
6Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina
7Department of Biochemistry and Molecular Biology, 246 Noble Research Center, Oklahoma State University, Stillwater, OK 74078, USA

While droughts, intensified by climate change, have been affecting forests worldwide, pest epidemics are a major source of uncertainty for assessing drought impacts on forest trees. Thus far, little information has documented the adaptability and evolvability of traits related to drought and pests simultaneously. We conducted common-garden experiments to investigate how several phenotypic traits (i.e. height growth, drought avoidance based on water-use efficiency inferred from $\delta^{13}C$ and pest resistance based on defence traits) interact in five mature lodgepole pine populations established in four progeny trials in western Canada. The relevance of interpopulation variation in climate sensitivity highlighted that seed-source warm populations had greater adaptive capability than cold populations. In test sites, warming generated taller trees with higher $\delta^{13}C$ and increased the evolutionary potential of height growth and $\delta^{13}C$ across populations. We found, however, no pronounced gradient in defences and their evolutionary potential along populations or test sites. Response to selection was weak in defences across test sites, but high for height growth particularly at warm test sites. Response to the selection of $\delta^{13}C$ varied depending on its selective strength relative to height growth. We conclude that warming could promote the adaptability and evolvability of growth response and drought avoidance with a limited evolutionary influence from pest (biotic) pressures.

1. Introduction

Forests of boreal and temperate regions are dominated by gymnosperm trees in which conifers are a key component and comprise greater than 39% of the global forests [1]. In this era of unprecedented climate change, numerous studies have documented maladaptation of some tree species to environments due to adaptive constraints (e.g. long lifespans and slow migration rates) [2–4]. Coniferous trees show strong resiliency even to extreme climates [5], implying a high degree of...
adaptable to heterogeneous environments. However, global warming has lowered such resiliency by increasing the duration and frequency of natural disturbances including drought and insect outbreaks [6–11]. Drought could limit tree growth, which could further adversely affect resource allocation to tree defences against biotic agents [12–15]. The interacting effects of drought and insect attacks promote tree death possibly through depletion of carbohydrates and carbon-dependent defence metabolites [14,16–18].

Pines are considered drought-tolerant species and have well-defined defences against a broad range of ecologically and economically important insect herbivores and pathogens [7,11,19–21]. Frequent climatic events under ongoing global change such as protracted drought can impose an additional selective pressure on or directly affect functional traits that enable local adaptation to dry conditions [17]. To withstand drought stress, plants have evolved a drought avoidance strategy [22,23] involving reduced water loss through changes in hydraulic conductance to enhance water-use efficiency, and maintain cellular homeostasis during drought. Measurements of ecophysiological status can be used for determining water-use efficiency, such as carbon isotope discrimination δ13C [24]. High water-use efficiency inferred from δ13C indicates the potential to maximize survival under drought and thus has a synergistic effect on plant growth (fitness). On the other hand, effects of biotic interactions are, however, less predictable due in part to the specificity, conditionality and complexity of their relationship with many other factors [7]. For example, pest outbreaks have been promoted by direct effects of warmer temperatures on pest life cycles [25] and indirect effects of drought on improving host susceptibility by reducing the efficiency of tree defences [14,26–29]. Variable factors affecting host susceptibility to pests prompt its equivocal relationship with growth or drought avoidance. Currently, the interactions between multiple traits in pine populations are poorly understood.

Range edge plant populations take on urgency for research, given that they are a more sensitive harbinger of climate change than central populations and may be trailing, suffering from declining population sizes and low genetic diversity, and thus at greater risk of mortality or extirpation [30]. In this study, we selected autochthonous populations of lodgepole pine (Pinus contorta Dougl. ex. Loud. var latifolia Englm.) located along the eastern edge of the species distribution range and relocated to four proveny trials (figure 1a–c) as analogues for future climate change scenarios (e.g. +1–2 °C). Our goal was to examine the adaptability and evolvability of several phenotypic traits in a multi-variante context, including height growth, δ13C indicating the ability to evade drought-caused physiological stress (i.e. drought avoidance), and host suitability to two most abundant pest species. Western gall rust (WGR; Endocronartium harknessii Hirats.) is an important fungal disease on lodgepole pine and widespread across the study region; the second pest is mountain pine beetle (MPB; Dendroctonus ponderosae Hopkins), which is one of the most important agents of lodgepole pine mortality in western North America (e.g. [7,25]). We expected that warming likely promotes both adaptive capacity and evolutionary potential for populations from a high latitude growing in proximal locations. To that end, we sought specifically to test for the following three hypotheses:

H1: Warming promotes tree growth and δ13C increase. Warm-origin populations growing in a warm test site have greater height and higher δ13C than cold populations in any test site; warm test sites create a higher evolutionary potential for height growth and δ13C than cold test sites.

H2: There is an indeterministic association between warm population and high pest susceptibility; evolutionary potential of pest susceptibility in warm versus cold test sites is not pronounced either.

H3: If H1 and H2 hold, then in a multi-dimensional trait space, a warm climate still generates higher evolutionary response to the selection of tree growth and δ13C, whereas response to selection in pest susceptibility remains weak and varies greatly within warm test sites.

2. Methods

(a) Plant material and experimental design

We selected five lodgepole pine provenances (populations hereafter), representing a total of 224 maternal half-sib families, grown in four proveny test sites (greater than 35 years) arrayed along various climatic gradients in central Alberta, Canada (53–59 families from each test site used for this study; figure 1b,c; electronic supplementary material, table S1). All 224 families were divided into 21 sets, each consisted of about 12 families (electronic supplementary material, figure S1). At each site, the field design was sets nested in five replicates with 21 sets per replicate, and families within each set were planted in four-tree row plots at a 2.5 m × 2.5 m spacing. All sites were fenced and each trial had a border row of trees around the outside. Across the four proveny test sites, we chose a total of 1490 trees for phenotyping.

(b) Phenotypic measurements

Detailed phenotypic trait measurement procedures were described in the electronic supplementary material, methods S1. Concisely, height growth (m) was measured at age 35 years with a clinometer. Carbon isotope ratio (δ13C, in ‰) analysis was performed at Alberta Innovates in Victoria, using outside slabs cut and ground from the 5 mm increment cores taken from the north side of each tree at approximately breast height (1.3 m) at age 35. Samples were analysed using an established method on a MAT253 Mass Spectrometer with Conflco IV interface (Thermo Fisher Scientific, Waltham, MA, USA) and a Fisons NA1500 EA (Fisons Instruments, Milan, Italy). We assessed the severity of WGR infection in the test sites by a qualitative scoring system with discrete categories ranging from no gall symptoms to deceased (four tiers) for all trees sampled at age 36. We also investigated these trees’ suitability to MPB. Host tree suitability to MPB was evaluated by quantifying defence chemicals (mainly monoterpenes) using a gas chromatography/flame ionization detector (Agilent Tech., Santa Clara, CA, USA) based on cambial tissues collected by a hole punch when trees were actively growing, coinciding with MPB flight in western Canada. Then, chemical profiling was performed to test against MPB performance based on laboratory bioassays reported by Ullah et al. [31]. We used a cutoff of four categories to classify trees with different MPB suitability levels (see electronic supplementary material, methods S1 for details).

(c) Data analysis

(i) Detrending phenotype

Based on raw phenotypic data, we detrended phenotypic traits caused by environmental variation within test site. We analysed each trait in each test site using a mixed model with a spatial
autocorrelation. In the model, population was a fixed effect, and the random-effect terms consisted of replicate, set and genetic effects derived from pedigree information (details in electronic supplementary material, methods S2). The residuals included spatially dependent and independent components with a first-order autoregressive (co)variance structure (AR1 × AR1). The detrended phenotypic traits were obtained for each tree at each site by removing the estimated design effects and autoregressive residual effects. The detrended traits were used for all subsequent analyses unless otherwise indicated.

(ii) Phenotypic selection, evolutionary potential and response to selection

We performed selection analysis, as previously described [32], to estimate how natural selection operates on $\delta^{13}C$ and pest suitability after adjusting for trait correlations. Succinctly, we used $\delta^{13}C$, which equalled range limits between ‘cold’ test sites; and (ii) Judy Creek and Virginia Hills are ‘warm’ populations, and Deer Mtn, Inverness River and Swan Hills are ‘cold’ populations. In addition, four capital letters were used for test sites, and full site names denoted populations throughout the paper.

Figure 1. Map of the distribution range of *Pinus contorta* (a), five study populations (b) and four progeny trial test sites (c). The *Pinus contorta* distribution range is shaded in green on the map with our study region marked by a red rectangle. MAT: mean annual temperature; MAP: mean annual precipitation (monthly average). The study region is boreal forests, characteristic of a dry continental climate with cold winters and warm summers. Based on MAT, we defined: (i) JUDY and VIRG are ‘warm’ test sites, and TIME and SWAN are ‘cold’ test sites; and (ii) Judy Creek and Virginia Hills are ‘warm’ populations, and Deer Mtn, Inverness River and Swan Hills are ‘cold’ populations. In addition, four capital letters were used for test sites, and full site names denoted populations throughout the paper.

3. Results

(a) Correlative patterns in traits and trait-climate

Correlation analysis revealed relationships between focal traits and climatic characteristics. There was an intermediate, positive correlation between height and $\delta^{13}C$ (Pearson’s $r = 0.302$, $p < 0.05$; electronic supplementary material, figure S2), whereas correlations between pest suitability versus height or pest suitability versus $\delta^{13}C$ were low and not significant (all $|r| < 0.05$, $p > 0.05$; electronic supplementary material, figure S2). Height and $\delta^{13}C$ exhibited a high relationship with mean annual temperature (MAT) of population origin ($r = 0.81$ and 0.95, respectively; significance for...
Table 1. Linear and quadratic selection gradients (β and γ) and selection differentials (s and C) for each focal trait in each or all progeny test sites of *Pinus contorta*. Height was used as a proxy for fitness and thus it was not possible to perform selection analysis for it. The signs and magnitudes indicate the direction and strength of linear (selection gradient β or selection differential s) or quadratic selection (selection gradient γ or selection differential C) on each trait in each or all test sites combined. Linear (directional) selection includes positive (i.e. genetic hitchhiking) and negative (i.e. background selection) selection. For quadratic selection, a negative significant selection value of γ or C indicates stabilizing selection, whereas a positive significant value is evidence for disruptive selection. Mean (s.e.) values were estimated and significance was determined by performing 5000 bootstrap samples. Significance: ***p < 0.0001, **p < 0.01, *p < 0.05.

| trait                     | test site | linear selection (negative or positive) | quadratic selection (stabilizing or divergent) |
|---------------------------|-----------|------------------------------------------|-----------------------------------------------|
|                           |           | β        | s                  | γ    | C          |
| drought avoidance (δ¹³C)  | TIME      | 0.020 (0.004)*** | 0.021 (0.004)*** | −0.006 (0.006) | −0.006 (0.006) |
|                           | SWAN      | 0.023 (0.004)*** | 0.023 (0.004)*** | −0.002 (0.006) | −0.002 (0.006) |
|                           | VIRG      | 0.002 (0.005)   | 0.002 (0.005)   | −0.008 (0.007) | −0.008 (0.007) |
|                           | JUDY      | 0.010 (0.006)*  | 0.009 (0.006)   | −0.016 (0.008)* | −0.015 (0.007)* |
|                           | all sites | 0.029 (0.003)*** | 0.029 (0.002)*** | −0.006 (0.004) | −0.005 (0.004) |
| severity of WGR           | TIME      | −0.009 (0.005)*  | −0.009 (0.005)* | −0.008 (0.007) | −0.008 (0.006) |
|                           | SWAN      | −0.004 (0.004)   | −0.002 (0.004)   | −0.009 (0.005)* | −0.008 (0.005) |
|                           | VIRG      | −0.003 (0.005)   | −0.003 (0.005)   | −0.003 (0.006) | −0.003 (0.006) |
|                           | JUDY      | −0.003 (0.005)   | −0.003 (0.005)   | −0.002 (0.005) | −0.003 (0.005) |
|                           | all sites | −0.002 (0.003)   | −0.002 (0.002)   | −0.003 (0.003) | −0.003 (0.003) |
| suitability to MPB        | TIME      | −0.002 (0.004)   | −0.001 (0.004)   | −0.001 (0.004) | 0 (0.004) |
|                           | SWAN      | −0.005 (0.004)   | −0.004 (0.004)   | −0.008 (0.004)* | −0.007 (0.004)* |
|                           | VIRG      | −0.003 (0.005)   | −0.003 (0.005)   | −0.003 (0.005) | −0.002 (0.005) |
|                           | JUDY      | −0.006 (0.005)   | −0.005 (0.005)   | −0.007 (0.004)* | −0.005 (0.004) |
|                           | all sites | −0.004 (0.002)*  | −0.003 (0.002)   | −0.004 (0.002)* | −0.004 (0.002) |

is noteworthy that all test sites were relatively warmer and drier than most of the population-origin sites (figure 2b horizontal axis range and figure 1 legend).

(b) Evolutionary potential measures
We compared evolutionary potential of focal traits using two genetic measures, h² and CVₐ. Estimates of h² of each trait did not differ substantially between test sites (figure 3a). Average point estimates of h² were about 0.5 for these traits (figure 3a), indicating significant additive genetic variation and that these traits are under strong genetic control. Metrics of CVₐ in height and δ¹³C were remarkably higher in JUDY and VIRG (figure 3b). By contrast, CVₐ had no noticeable difference in WGR or MPB between test sites, and CVₐ was close to zero (10 × 10⁻⁴) for MPB compared to about −1 for WGR (scaled for showing in figure 3b).

(c) Estimation for phenotypic selection and response to selection
By performing selection analysis via height as a fitness proxy in a univariate manner, we identified selection patterns for each trait in each test site. The form of selection in δ¹³C and pest suitability differed depending on test sites (table 1). The δ¹³C trait was under directional selection (p < 0.0001) in the two cold sites, TIME and SWAN (table 1), and under both directional and diversifying selection (p < 0.05) in a
that relatively low correlations between height and each test site. Population mean across common gardens and common-garden mean across populations are portrayed by different shapes. Quadratic regression is plotted on the graph with adjusted pseudo-

noted in figure 1. Quadratic regression is plotted on the graph with adjusted pseudo-

Figure 2. Population trait means as a function of MAT at site-of-origin, population differentiation for focal traits as a function of MAT transfer distance and mean trait values for each combination of the source population and test site groups. (a) Black lines depict a linear model-predicted relationship with 95% CI on a population basis. Significant relationships suggest local adaptation. The relative density of underlying data points is represented by contour lines. The trait values averaged by population are shown in coloured triangles. WGR and MPB denote western gall rust (Endocronartium harknessii) and mountain pine beetle (Dendroctonus ponderosae), respectively; both traits were scaled and high/low values are indicative of high/low pest symptoms, respectively. Less negative δ13C values suggest higher water-use efficiency and thus higher drought avoidance capability. Significant: ∗∗∗p < 0.001, ∗∗p < 0.01, ∗p < 0.05, n.s. not significant. (b) The MAT transfer distance (ΔMAT) was calculated as the difference in MAT between a test site and a population-origin location. Positive (negative) values indicate MAT(garden) > MAT(population) (MAT(garden) < MAT(population)), respectively. Filled black circles with 95% CIs were plotted for each population in each test site. Population mean across common gardens and common-garden mean across populations are portrayed by different shapes. Quadratic regression is plotted on the graph with adjusted pseudo-R² estimated. (c) We, respectively, classified source populations and test sites by MAT to cold versus warm groups, as noted in figure 1.

The two cold test sites had relatively high δ13C in warm environments after assuming that the selection gradient in height was lower than that in δ13C (figure 3d). However, given a higher selection gradient in height relative to δ13C, response to selection for δ13C was lower in warm than cold sites, whereas height remained more selected for in warm sites with less selective intensity compared with the previous scenario (r = 0.62 versus 0.85, p < 0.0001; figure 3d). With regard to pest suitability, the overall response to selection was lower than height or δ13C by one order of magnitude (figure 3d). The two cold test sites had relatively high responses to selection for both WGR and MPB, whereas a warm, more rainfall climate (e.g. VIRG) led to the highest (lowest) response to selection for WGR (MPB), respectively (figure 3d). Similarly, a warm, less rainfall climate
(e.g. JUDY) resulted in the lowest response to selection for WGR but a relative high response to selection for MPB (figure 3d). Moreover, we observed only one positive response to selection for a pest suitability—WGR at JUDY (figure 3d). These patterns in warm climate were in line with a negative correlation between WGR and MPB at VIRG and JUDY (figure 3c). Furthermore, the efficacy of selection based on G-matrices indicated that VIRG and JUDY had a smaller correlation between height and \( \delta^{13}C \) (0.01–0.03) than SWAN and TIME (0.09–0.11) (electronic supplementary material, figure S5). Meanwhile, autocorrelation for these two traits was higher in VIRG and JUDY than in SWAN and TIME (0.51–0.59 versus 0.3–0.38 and 0.43–0.44 versus 0.34–0.38 for these two traits, respectively) (electronic supplementary material, figure S5).

4. Discussion

We showed how warming affects the evolution of height growth versus resistance traits in a uni- and multi-dimensional trait space by planting seed-source populations of lodgepole pine in four test sites, mimicking future *in situ* climate change scenarios over time. The selected populations were based in the species range edge, possibly under the greatest exposure to climatic change. These common-garden studies revealed that warming would promote evolutionary response to the selection of both height and \( \delta^{13}C \), and affect host suitability to pests depending on precipitation. Due to fluctuating weak response to the selection of pest suitability, there was a limited evolutionary influence of pest suitability on height and \( \delta^{13}C \) response. The significance of the work accentuates weak selection with high variability in pest suitability, according with subtle ecological association between warm climate (warm origin or test site) and high pest attacks; moreover, biotic pressures from pests have a limited impact on the evolution of height growth and \( \delta^{13}C \).

(a) Do height growth and drought avoidance always possess a synergistic relationship and high evolutionary potential under warming?

It has been widely accepted for the use of \( \delta^{13}C \) as an indicator of the intensity of drought exposure in plants (e.g. [37,38]). This study showed that fast-growing populations had greater xylem hydraulic conductance (i.e. high \( \delta^{13}C \)) in warm test site, indicating the importance of maintaining water conductance to growth in warmer conditions. While \( \delta^{13}C \) indicates drought avoidance by measuring reduced water loss—a water-saving strategy, drought avoidance also involves enhanced water uptake from roots—a water-spending strategy [39]. Trees could rely on resource investment in rooting depth to increase access to deep soil water to withstand drought stress [40,41]. Our investigation of drought avoidance strategies inferred from \( \delta^{13}C \) could be improved by the further investigation into the below-ground determinants of plant water relations using combinations of hydraulic traits such as \( P_{50} \) (i.e. the water potential at which 50% of hydraulic conductivity is lost) and water potential at stomatal closure or turgor loss (e.g. [42,43]). Combining multiple interlinked, yet distinct, aspects of plant water relations can better quantify...
water-use strategies based on interactions between plant traits and environmental conditions. Moreover, considering other drought adaptive strategies including drought escape (e.g. flowering or pollination time), tolerance (e.g. osmotic potential) and resilience (e.g. dendrochronological measure indicating recovery capacity after drought) [22] allows for a better understanding whole-plant drought strategies and their relationship with plant growth and pest resistance.

We observed that height and δ13C differed in populations and test sites. Higher positive sensitivity to temperature in both traits at relatively warmer sites today tells us that trees at relatively cooler sites may anticipate more rapid growth and greater δ13C in a warmer future. Moreover, high additive genetic variation or heritability suggests that directional selection could increase adaptability to novel climatic scenarios. Consistently, we found that both height and δ13C had greater evolutionary potential under a warmer exposure based on CVk. It is worthwhile to note that the other metric used—h2 may not reflect the true potential of adaptive evolution due to environmental variation under natural conditions greatly affecting phenotypic traits and fitness, leading to a possibility of small or no significant change in h2 even when Vk is high or greatly alters [44,45]. An instance in P. sylvestris also showed that progeny derived from warmer climates outperformed local seed sources in ‘cold’ locations, and local seeds grew best locally only in very warm source locations [46]. In addition to adaptive evolution, lodgepole pine hybridization with jack pine (P. banksiana) at our study region has been found to enable an expansion of range limits eastward [47], providing another evolutionary avenue for these pine range-margin populations to enhance genetic variation and adapt to changing climates.

(b) Selection and evolution of host suitability to pests under warming

We found a positive or negative trend along a thermal cline for two constitutive defences against a phytopathogen and an insect herbivore, respectively. Populations from warm versus cold environments had an inverse pattern of these defence traits in test sites. This indicates that tree suitability to different species of pests varies under different environmental conditions. Nonetheless, this study used height growth as a proxy for fitness, which might limit our inference about the evolution of traits including pest suitability under climate change. There are three main components of plant fitness including growth, reproduction and survival [48]. Central to these components is metabolism, providing the carbon necessary for allocation to various structures and functions. However, natural selection that operates on pest suitability and functional traits is likely more by directly affecting tree survival and reproduction than through their relationship with tree growth. Although trees with slower growth rates are found to be more likely to die than faster growing counterparts (e.g. [49]), a first-order constraint on plant growth is photosynthetic capacity in assimilating energy and matter.

Further, this study investigated trait patterns in association with two climatic drivers—MAT and MAP. Other than climate, edaphic conditions could be another important selective force driving the evolution of growth and resistance traits [50]. The test site JUDY had a more acidic brunisol soil with a pH of 3.9, compared to a luvisolic soil with a pH of 5.5 in the other test sites (electronic supplementary material, table S1). The difference in soil texture may contribute to the disparity observed in response to the selection of pest suitability in JUDY versus the other test sites.

Previous studies confirmed that pine populations grown in optimal growing conditions had higher susceptibility to pests than in less favourable conditions [51]. This study demonstrated that selection in pest suitability was much weaker than δ13C and varied greatly in two warm sites with different rainfall, suggesting fluctuating weak selection in pest suitability. This selection pattern in pest suitability could be interpreted by pine life-history characteristics. Pinus contorta commences reproduction at around 10 ± 5 years old [52,53], whereas MPB doesn’t typically attack trees until they are much older, that is, greater than 60 years [54,55]. P. contorta produces serotinous cones with viability for up to 10–15 years after the tree has been killed [56,57]. This chronological discrepancy provides an extended period during which trees that will be ultimately killed by MPB can still grow and reproduce. Furthermore, the thickness and constituents (e.g. nutrients and toxic secondary compounds) of phloem, which are usually positively correlated with tree age and size, are main direct factors affecting host suitability to bark beetles or other phloem-feeding insects [7,58]. In addition, conifer defences against bark beetles are strongly mediated by environmental stress [16,59], which increases uncertainties in defence selection.

(c) Evolutionary interactions of height growth, drought avoidance and pest suitability

This study revealed that climate strongly influenced the pattern of selection in δ13C and host suitability to pests, albeit overall weak for pest suitability. As opposed to selection on isolated traits, multi-variate analysis assumes that selection acting on one trait will produce an evolutionary response in other genetically correlated traits, even though selection does not act directly on them. Prediction of evolutionary changes in multiple traits relies on the form and magnitude of selection in height growth and δ13C, and on historical influences from pest attacks (e.g. [60]). We found that evolutionary response to selection was strongest for height in warmer sites, in accordance with its high adaptability and evolutionary potential. Warming could also promote response to selection in δ13C if it was under stronger selection than height growth. If selection is stronger in height than δ13C, then we could expect that a great extent of warming would likely select against high δ13C. These particular results suggest that height growth is always selected for to maintain a direct performance gain, but its strength of selection affects evolutionary changes in δ13C. Furthermore, higher response to selection of height and δ13C in warm sites may be modulated by populations responding differently to warm conditions (i.e. a strong selective pressure) and higher selective efficiency under warming.

In addition, we demonstrated that under warming conditions, precipitation significantly affected response to selection in pest suitability, indicating that selection is likely to be affected by warm temperature and rainfall interactions. As such, we could expect different patterns of selection under dry versus humid hot or through temperature and precipitation interactions. Pest outbreaks are highly contingent on climate with contrasting impacts for dry hot versus humid
droughts and plant defences are highly variable across a gradient of the environment [61], indicating possibly variable selection over space and time.

In conclusion, this study provides evidence that rising temperatures are beneficial to adaptive evolution in height growth and \( \delta^{13} \text{C} \) (drought avoidance), resulting in taller and more drought-tolerant trees, and that biotic pressures from pest attacks have a limited influence on evolutionary response to the selection of height growth and \( \delta^{13} \text{C} \). Nonetheless, as trees are sessile organisms with a long-life cycle of multiple decades or even centuries but most pest species have seasonal migration in an annual cycle [62], trees attacked by pests are determined largely by pest behaviour and tree–host–environment–pest interactions. As climate changes, we could expect shifts in evolutionary response to the selection of growth and drought avoidance towards high values without too much evolutionary constraints by pest suitability. Great impacts of pest suitability on growth or fitness would be generated primarily at the ecological level possibly by a sudden massive pest attack further exacerbated through an interaction with drought spells.

Data accessibility. Data and modelling code supporting this paper are available from Dryad Digital Repository [63].

Electronic supplementary material is available online [64].

Authors’ contributions. Y.L.: conceptualization, formal analysis, investigation, methodology, software, visualization, writing—original draft and writing—review and editing; N.E.: data curation, funding acquisition, resources and writing—review and editing; B.R.: data curation and resources; J.G.K.: data curation and resources; X.W.: data curation and resources; A.U.: data curation and resources; E.P.C.: resources; C.C.: funding acquisition and resources; B.R.T.: data curation, funding acquisition, resources and writing—review and editing; Y.A.E.: funding acquisition, resources, supervision and writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. The authors declare no competing interests.

Funding. We acknowledge funding for this work from University of Cambridge, and for this large-scale research project from Genome Canada, Genome Alberta through Alberta Economic Trade and Development, Genome British Columbia, the University of Alberta and the University of Calgary. Further funding has been provided by Alberta Innovates BioSolutions, Forest Resource Improvement Association of Alberta, the Forest Resource Improvement Program through West Fraser Ltd. (Blue Ridge Lumber and Hinton Wood Products) and Weyerhaeuser Timberlands (Grande Prairie and Pembina), Alberta Agriculture and Forestry, Blue Ridge Lumber West Fraser, Weyerhaeuser Timberlands Grande Prairie, and the Thomas, Wishart and Erblijgin laboratories in support of the Resilient Forests (RES-FOR): Climate, Pests & Policy—Genomic Applications project.

Acknowledgements. We are thankful to height trait contributors (B. R. Lumber and S. Sadowsky), S. Barot (Sorbonne Université) for helpful comments on an early version of this manuscript, and the UBC Advance Research Computing platform (ARC Sockeye) to undertake computational simulations. Finally, we thank the editor and two anonymous referees for their helpful suggestions and comments after critical reading.

References

1. Jin WT, Gernandt DS, Wehenkel C, Xia XM, Wei X, Wang XQ. 2021 Phylogenomic and ecological databases reveal the spatiotemporal evolution of global pines. Proc. Natl Acad. Sci. USA 118, e2022302118. (doi:10.1073/pnas.2022302118)

2. Kuparinen A, Savolainen O, Schurr FM. 2010 Increased mortality can promote evolutionary adaptation of forest trees to climate change. For. Ecol. Manage. 259, 1003–1008. (doi:10.1016/j.foreco.2009.12.006)

3. Atikin SN, Yeaman S, Holliday JA, Wang TL, Curtis-McLane S. 2008 Adaptation, migration or extirpation: climate change outcomes for tree populations. Ecol. Appl. 1, 95–111. (doi:10.1111/j.1572-4571.2007.00013.x)

4. Browne L, Wright JM, Fitz-Gibbon S, Gugger PF, Sork VL. 2019 Adapational lag to temperature in valley oak (Quercus lobata) can be mitigated by genome-informed assisted gene flow. Proc. Natl Acad. Sci. USA 116, 25 179–25 185. ((doi:10.1073/pnas.1908771116))

5. Savolainen O, Pyhäjärvi T, Knürr T. 2007 Gene flow and local adaptation in trees. Annu. Rev. Ecol. Evol. Syst. 38, 595–619. (doi:10.1146/annurev.ecolsys.38.091206.095646)

6. Anderegg WRL et al. 2015 Tree mortality from drought, insects, and their interactions in a changing climate. New Phytol. 208, 674–683. (doi:10.1111/nph.13477)

7. Erbilgin N. 2019 Phytochemicals as mediators for host range expansion of a native invasive forest insect herbivore. New Phytol. 221, 1268–1278. (doi:10.1111/nph.15467)

8. Hogg EH, Michaelian M, Hook TI, Undersultz ME. 2017 Recent climatic drying leads to age-dependent growth reductions of white spruce stands in western Canada. Glob. Change Biol. 23, 5297–5308. (doi:10.1111/gcb.13795)

9. Meddens AJH, Hicke JA, Macalady AK, Buote PC, Cowles TR, Allen CD. 2015 Patterns and causes of observed pines pine mortality in the southwestern United States. New Phytol. 206, 91–97. (doi:10.1111/nph.13193)

10. Young DJ, Stevens JT, Earles JM, Moore J, Ellis A, Jirka AL, Latimer AM. 2017 Long-term climate and competition explain forest mortality patterns under extreme drought. Ecol. Lett. 20, 78–86. (doi:10.1111/ele.12711)

11. Kidb TE, Fettig CJ, Ayres MP, Benz BJ, Hicke JA, Mathiasen R, Stewart JE, Weid AS. 2016 Observed and anticipated impacts of drought on forest insects and diseases in the United States. For. Ecol. Manage. 380, 321–334. (doi:10.1016/j.foreco.2016.04.051)

12. McDowell NG, Beerling DJ, Breshears DD, Fisher RA, Raffa KF, Stitt M. 2011 The interdependence of mechanisms underlying climate-driven vegetation mortality. Trends Ecol. Evol. 26, 523–532. (doi:10.1016/j.tree.2011.06.003)

13. Sala E, Woodruff DR, Meinzer FC. 2012 Carbon dynamics in trees: feast or famine? Tree Physiology. 32, 764–775. (doi:10.1093/treephys/tp2143)

14. Huang JB et al. 2020 Tree defence and bark beetles in a drying world: carbon partitioning, functioning and modelling. New Phytol. 225, 26–36. (doi:10.1111/nph.16173)

15. Hussain A, Classens G, Guerra-Razo S, Cale JA, Rajabzadeh R, Peters BR, Erbilgin N. 2020 Spatial variation in soil available water holding capacity alters carbon mobilization and allocation to chemical defenses along jack pine stems. Environ. Exp. Bot. 171, 1033902. (doi:10.1016/j.envexpbot.2019.103902)

16. Erbilgin N et al. 2021 Combined drought and bark beetle attacks deplete non-structural carbohydrates and promote death of mature pine trees. Plant Cell Environ. 44, 3636–3651. (doi:10.1111/pce.14197)

17. Chaot B, Brodribb TJ, Brodersen CR, Duursma RA, Lopez R, Medlyn BE. 2018 Triggers of tree mortality under drought. Nature 558, 531–539. (doi:10.1038/s41586-018-0240-x)

18. Mitchell PJ, O’Grady AP, Tissue DT, White DA, Ottenschlaeger ML, Pinkard EA. 2013 Drought response strategies define the relative contributions of hydraulic dysfunction and carbohydrate depletion during tree mortality. New Phytol. 197, 862–872. (doi:10.1111/nph.12064)

19. Mumm R, Hilker M. 2006 Direct and indirect chemical defence of pine against folivorous insects. Trends Plant Sci. 11, 351–358. (doi:10.1016/j.tplants.2006.05.007)

20. Raffa KF, Mason CJ, Bonello P, Cook S, Erbilgin N, Keefer-Ring K, Klutsch JG, Villari C, Townsend PA,
2017 Defence syndromes in lodgepole—whitebark pine ecosystems relate to degree of historical exposure to mountain pine beetles. Plant Cell Environ. 40, 1791–1806. (doi:10.1111/pce.12965)

21. Franceschi VR, Knoupe P, Christiansen E, Krekling T. 2005 Anatomical and chemical defences of conifer bark against bark beetles and other pests. New Phytol. 167, 353–376. (doi:10.1111/j.1469-8137.2005.01346.x)

22. Volaire F. 2018 A unified framework of plant adaptive strategies to drought: crossing scales and disciplines. Glob. Change Biol. 24, 2929–2938. (doi:10.1111/gcb.14062)

23. Levitt J. 1980 Responses of plants to environmental stresses. Volume II. Water, radiation, salt, and other stresses. Cambridge, MA: Academic Press.

24. Farquhar GD, Ehleringer JR, Hubick KT. 1989 Carbon isotope discrimination and photosynthesis. Annu. Rev. Plant Physiol. Plant Mol. Biol. 40, 503–537. (doi:10.1146/annurev.pp.40.060189.002443)

25. Ruffa KF, Aukema BH, Bents BJ, Carroll AL, Hicke JA, Turner MG, Romme WH. 2008 Cross-scale drivers of natural disturbances prone to anthropogenic amplification: the dynamics of bark beetle eruptions. Bioscience 58, 501–517. (doi:10.1641/B580067)

26. Huot B et al. 2017 Dual impact of elevated temperature on plant defence and bacterial virulence in Arabidopsis. Nat. Commun. 8, 1808. (doi:10.1038/s41467-017-00164-z)

27. Huberty AF, Denno RF. 2004 Plant water stress and its consequences for herbivorous insects: a new synthesis. Ecology 85, 1383–1398.

28. Jactel H, Petit J, Desprez-Loustau ML, Delzon S, Piou et al. 2018 Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 185, 562–566. (doi:10.1007/s00442-018-4370-8)

29. O'Leary M. 1995 Environmental effects on carbon fixation in terrestrial plants. In Stable isotopes in the biosphere (eds E Wada, T Yoneyama, M Minagawa, T Ando, B Fry), p. 78. Kyoto, Japan: Kyoto University Press.

30. Tardieu F, Simonneau T. 1998 Variability among species of stomatal control under fluctuating soil water status and evapotranspiration: modelling isohydric and anisohydric behaviours. J. Exp. Bot. 49, 419–432. (doi:10.1093/jxb/49.Special_Issue-419)

31. Volta F, Locatelli D, Chambel MR, Ferrio JP. 2015 Intraspecific variation in the use of water sources by the circum-Mediterranean conifer Pinus halepensis. New Phytol. 208, 1031–1041.

32. Liu Y, El-Kassaby YA. 2019 Phenotypic plasticity of provenances: evidence of genetic trade-offs between adaptation to optimal conditions and resistance to the maritime pine bark scale (Matsucoccus fayetaudi). For. Sci. 62, 553–563. (doi:10.3894/forsci.15-109)

33. Liu Y, El-Kassaby YA. 2020 Ecological drivers of plant life-history traits: assessment of seed mass and germination variation using climate cues and nitrogen resources in conifers. Ecol. Indic. 117, 106517. (doi:10.1016/j.ecolind.2020.106517)

34. Kotiaho JS, Evans JP. 2012 Comparing evolvabilities: weak selection exert a limited influence on the constitutive and herbivore-induced chemical defences in pine trees emerge only under low nutrient availability. J. Ecol. 99, 818–827.

35. Di Matteo G, Volta J. 2016 Multienvironment evaluation of Pinus pinaster provenances: evidence of genetic trade-offs between adaptation to optimal conditions and resistance to the maritime pine bark scale (Matsucoccus fayetaudi). For. Sci. 62, 553–563. (doi:10.3894/forsci.15-109)

36. Walsh B, Blows MW. 2009 Abundant genetic variation in strong selection—multivariate genetic constraints: a geometric view of adaptation. Annu. Rev. Ecol. Evol. Syst. 40, 41–59. (doi:10.1146/annurev.ecolsys.110308.120232)

37. Ehleringer JR, Cooper TA. 1998 Correlations between carbon isotope ratio and microhabitat in desert plants. Oecologia 76, 562–566. (doi:10.1007/BF00397870)

38. Shore TL, Safyanlik Y. 1992 Susceptibility and risk rating systems for the mountain pine beetle in lodgepole pine stands. Information report BC-X-336. Victoria, BC: Forestry Canada, Pacific Forestry Centre.

39. Leidy J. 1975 The role of cone senility in lodgepole pine forests. In Management of lodgepole pine ecosystems: symposium proceedings (ed. DM Baumgartner), pp. 471–495. Pullman, WA: Washington State University, Cooperative Extension Service.

40. Aoki CF, Romme WH, Rocha ME. 2011 Lodgepole pine seed germination following tree death from mountain pine beetle attack in Colorado, USA. Ann. Midl. Nat. 165, 446–451.

41. Hutchison IK, Reid ML. 2022 Phloem and defence traits in relation to tree size and age: implications for host selection by bark beetles. For. Ecol. Manage. 513, 120183. (doi:10.1016/j.foreco.2022.120183)

42. Klutsch JG, Bean RD, Jacobi WR, Negron JF. 2014 Bark beetles and dwarf mistletoe interact to alter dominance wooden material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. For. Ecol. Manage. 315, 63–71. (doi:10.1016/j.foreco.2013.12.024)

43. de la Mata R, Hood S, Sala A. 2017 Insect outbreak shifts the direction of selection from fast to slow growth rates in the long-lived conifer Pinus ponderosa. Proc. Natl Acad. Sci. USA 114, 7391–7396. (doi:10.1073/pnas.1700332114)

44. Weed AS, Ayres MP, Hicke JA. 2013 Consequences of climate change for biotic disturbances in North American forests. Ecol. Monogr. 83, 441–470. (doi:10.1890/13-0160.1)

45. Chapman JW, Reynolds DR, Wilson K. 2015 Long-range seasonal migration in insects: mechanisms, evolutionary drivers and ecological consequences. Ecol. Lett. 18, 287–302. (doi:10.1111/ele.12407)

46. Liu Y et al. 2022 Data from: Pest defences under weak selection: a limited influence on the evolution of height growth and drought avoidance in marginal pine populations. Dryad Digital Repository. (doi:10.5061/dryad.n2z34mzb)

47. Liu Y et al. 2022 Pest defences under weak selection: a limited influence on the evolution of height growth and drought avoidance in marginal pine populations. FigsShare. (doi:10.6084/m9.figshare.c.6125922)