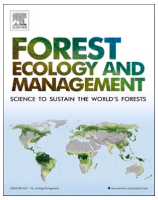
Forest Ecology and Management 597 (2025) 123129

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



# Black spruce growth under climate extremes: Genetic insights for managing a key resource production species

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## ARTICLE INFO

*Keywords:*
Stress events
Boreal forest
Common garden
Dendroecology
Genomic
Local adaptation

## ABSTRACT

Understanding the influence of intraspecific genetic variation on the response of tree species to stress events—like heatwaves, droughts, and growing season frost—is crucial. This genetic variation is linked to species adaptive potential and plays a pivotal role in shaping the resilience and long-term adaptability of species to climate change. Furthermore, genetic variation can affect populations' responses to stress events, thereby influencing forest productivity and carbon sequestration potential. We combined dendroecological and genomic approaches to analyze the growth response of 61 black spruce (*Picea mariana*) populations, grown for over 40 years in four common gardens, to daily extreme vapor pressure, soil moisture deficits, and growing season frosts. Our objectives were to 1) assess the effects of stress events defined from physiological thresholds on annual biomass production and 2) explore the potential influence of standing genetic variation on trees' responses to stress events at the population scale. The growth response of black spruce to those events was site-specific but with an important influence of soil or atmospheric drought at most sites. This response was also nonlinear, with a negative effect on growth occurring only after several stress events a year. Additionally, an interaction between this response and the geographic origin of the population indicated an influence of standing genetic variation, notably linked to local adaptation. These results may provide insight into tree resilience to stress events and help estimate the adaptive potential of the Canadian boreal forest. Moreover, this knowledge can help guiding forest management, for example assisted gene flow.

## 1. Introduction

The frequency and severity of climate extremes, including short-term events such as heatwaves and droughts, is increasing due to ongoing climate change, and this trend is expected to accelerate in the near future (Intergovernmental Panel On Climate Change, 2023). Concurrently, long-term warming—particularly in spring—is altering tree phenology, potentially increasing the risk of damage from late spring frosts due to earlier onset of the growing season (Marquis et al., 2020a, 2020b). These stress-inducing events are anticipated to negatively impact tree growth (e.g., Butt et al., 2014; Chamberlain and Wolkovich, 2021; Huang et al., 2018), with cascading consequences for forest resilience (e.g., D'Andrea et al., 2021; Thompson et al., 2009; Marchand et al., in press), productivity (e.g., Shekhar et al., 2024), and carbon sequestration potential (e.g., Wang et al., 2025). The climate crisis is closely linked to the current biodiversity crisis (Pörtner et al., 2023), particularly through its role in amplifying extreme climate conditions. Biodiversity, including intraspecific genetic variation, enhances ecosystem resilience by increasing the ability of ecosystems to buffer against disturbances. However, biodiversity itself is under threat from these same climate-related stressors. Understanding the role of different levels of biodiversity—genetic, species, functional, and landscape diversity—in shaping plant responses to climate extremes is therefore critical (Mahecha et al., 2024).

Intraspecific genetic diversity influences how populations respond to climate extremes and plays a key role in species' adaptation to future conditions (Isaac-Renton et al., 2018; Montwé et al., 2016; Robert et al., 2024; Zas et al., 2020). The ability of a population to persist in a given

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https://doi.org/10.1016/j.foreco.2025.123129
Received 24 April 2025; Received in revised form 26 June 2025; Accepted 25 August 2025

location depends on both its phenotypic plasticity—its capacity to tolerate environmental change in the short term—and its evolutionary potential, which is determined by the standing genetic variation available for natural selection to act upon (Aubin et al., 2016). Greater genetic variation, both within and among populations, increases the likelihood of the presence of pre-adapted alleles conferring adaptive advantages in changing environments (Barrett and Schluter, 2008; Li et al., 2022). Phenotypic plasticity, which varies among traits and populations, is itself genetically determined (Schneider, 2022), meaning that higher genetic diversity may enhance a population's ability to exhibit adaptive plasticity (for a review see Kremer et al., 2025). A deeper understanding of how intraspecific genetic diversity influences the response of tree populations to stress-inducing events—including heatwaves, drought, and frost—could provide valuable insights for climate change adaptation. This knowledge could inform forest management strategies aimed at enhancing resilience, such as assisted gene flow to enhance local genetic diversity (Aitken and Bemmels, 2016).

Black spruce (*Picea mariana* (Mill.) B.S.P.) is a keystone and resource production species of the Canadian boreal forest, playing a critical role in shaping forest structure, carbon storage, and ecosystem dynamics (Girona et al., 2023). It is widely distributed across North America, from the northern United States through Canada and into Alaska, thriving in diverse boreal environments (Burns and Honkala, 1990). Well adapted to cold climates and nutrient-poor soils, black spruce is commonly found in peatlands, muskegs, and poorly drained lowlands, though it can also establish on upland sites with better drainage. These forests form extensive stands characterized by slow growth rates and long-lived individuals, making significant contributions to boreal carbon sequestration. However, despite its resilience to many environmental stressors, black spruce is increasingly vulnerable to climate change (Burrell et al., 2024; Mirabel et al., 2023; Robert et al., 2024). Rising temperatures, shifting precipitation patterns, and more frequent climatically-induced stress events—including those from heatwaves, droughts, and growing-season frosts—pose significant risks to its growth and survival, with impacts expected to be most severe in vulnerable areas (Boulanger et al., 2022; Marquis et al., 2020a, 2020b). While climate-driven shifts in black spruce growth rates have been widely studied, less attention has been given to the role of intraspecific genetic variation and local adaptation in determining the species' sensitivity to these environmental changes (Girardin et al., 2021). This is particularly important given that black spruce exhibits high genetic diversity across its range (Isabel et al., 1995; Prunier et al., 2013). This genetic diversity is partly shaped by the species' phylogeographic structure, which reflects historical patterns of isolation in multiple glacial refugia during the late Quaternary. During glacial periods, populations became geographically and genetically isolated in distinct refugia, where they accumulated genetic differences (DNA polymorphisms) that may have contributed to adaptive divergence (e.g. Mayol et al., 2015). Following glacial retreat, the species recolonized its range, forming three main genetic lineages (Gérardi et al., 2010; Jaramillo-Correa et al., 2004) bearing both shared and lineage-specific polymorphisms (De Lafontaine et al., 2018; Prunier et al., 2012). During this recolonization phase, local adaptation and demographic processes, such as founder effects and range expansion, further contributed to the BS standing genetic variation, shaping the evolutionary potential of present-day populations. Understanding these historical and genetic factors is essential for predicting future boreal forest dynamics and informing adaptive management strategies, particularly under ongoing climate change (for a review see Kremer et al., 2025).

Among the climatic factors affecting tree growth, atmospheric dryness plays a crucial role. Vapor pressure deficit (VPD) is a widely used metric of atmospheric dryness, representing the difference between the actual water vapor content of the air and its saturation point (Grossiord et al., 2020; Mirabel et al., 2023). Higher temperatures increase the air's capacity to hold moisture, thus raising its saturation point, and increasing VPD if the vapor content of the air stays constant (Grossiord et al., 2020). Climate projections indicate a global rise in VPD due to increasing $CO_2$ concentrations, though the magnitude of this increase is expected to be less pronounced at higher latitudes (Chen et al., 2024). Additionally, extreme VPD events are projected to become more frequent worldwide (Hermann et al., 2024). High VPD typically triggers stomatal closure in plants, reducing transpiration, photosynthesis, and overall productivity (Grossiord et al., 2020). Conifers, including black spruce, are particularly sensitive to VPD fluctuations, as they rely on stomatal regulation to maintain water balance (Marshall and Waring, 1984). Prolonged exposure to elevated VPD can lead to carbon starvation and impaired photosynthetic efficiency due to the downregulation of Rubisco activity (Grossiord et al., 2020; López et al., 2021; Novick et al., 2016; Reich et al., 2018).

In addition to atmospheric dryness, soil moisture availability is a key determinant of tree growth. Future trends in soil moisture across Canada remain uncertain. Some studies suggest that higher precipitation could lead to increased annual soil moisture (Chen et al., 2024), while others predict more frequent and intense hydrological drought events (Zhao et al., 2020). The spatial distribution of these changes is expected to be heterogeneous, with drying trends in the southern central plains, whereas most of Canada may experience increased precipitation (Bonsal et al., 2013; Yang et al., 2021). Soil moisture regulates plant water uptake and influences stomatal conductance through the production of abscisic acid, a key phytohormone involved in drought responses (Davies and Zhang, 1991). Low soil moisture can reduce xylem hydraulic conductivity (Sperry et al., 2016), constrain transpiration (Lagergren and Lindroth, 2002), and lower carbon assimilation and productivity (Mensah et al., 2021), ultimately leading to reduced growth (Alavi, 2002). In extreme cases, severe soil moisture deficits can induce xylem embolism, resulting in tree mortality (Anderegg et al., 2012, 2016).

The phenological responses of black spruce, particularly the timing of bud burst, are strongly regulated by environmental cues, with temperature playing a dominant role (Rossi and Isabel, 2017). Different populations exhibit distinct temperature thresholds for bud burst, an adaptive trait that maximizes the growing season while minimizing frost risk (Guo et al., 2022; Marquis et al., 2020b; Perrin et al., 2017). Climate change is advancing bud break timing, increasing the likelihood of exposure to late spring frosts, which can severely damage developing tissues (Liu et al., 2018; Ma et al., 2019; Marquis et al., 2020b). The bud break process in spruces is associated with dehardening, a phase during which trees become highly sensitive to frost (Bigras and Hébert, 1996; Glerum, 1973). If frost occurs during this period, it can damage the apical meristem within buds (Clements et al., 1972) as well as the cambium (Marquis et al., 2020a; Montwé et al., 2018). Severe frost events throughout the growing season can also injure newly formed needles and kill developing shoots, leading to architectural deformities and reduced branch elongation (Dy and Payette, 2007).

In this study, we assessed the impact of extreme vapor pressure deficit (VPD), soil dryness, and recurring growing season frost (hereafter GSF) events on black spruce growth while exploring the potential influence of standing genetic variation on the difference among population sensitivities. These objectives are formalized into two main research questions. First, we examined whether the physiological thresholds described in the literature for the selected variables are associated with a decrease in the trees' annual biomass production. Second, we investigated whether this influence varies among populations depending on local adaptation or the phylogeographic structure of the species. To address these questions, we relied on dendroecological and genomic data obtained from a series of four common gardens established across Canada and employed a machine learning approach to assess the impact of these stress-inducing events on annual biomass increment (ABI) at the population scale. We accounted for standing genetic variation by considering local adaptation and the phylogeographic structure of the species.

## 2. Materials and methods

### 2.1. Common gardens, sample collection and processing

The data used in our study were obtained from four common gardens located across contrasted climatic and environmental conditions and distributed along a wide latitudinal and longitudinal range: Peace-River (PR, province of Alberta, 56.30° N, 117.30° W), Mont-Laurier (ML, province of Quebec, 46.60° N, 75.80° W), Chibougamau (CH, province of Quebec, 50.20° N, 74.20° W) and Acadia Research Forest (AC, province of New Brunswick, 46.00° N, 66.30° W). Over the last decades (1980–2019), the sites presented mean annual temperatures of 1.61°C, 3.74°C, −0.34°C and 5.46°C and relative % soil volumetric water contents of 50 %, 95 %, 98 % and 94 %, respectively (see details in supplementary Table ST1). These common gardens were established as part of the Range-Wide Provenance Study initiated in 1967 by the Petawawa National Forestry Institute of the Canadian Forest Service (Morgenstern, 1978). They were established in 1974 and 1975 following a complete randomized block design (see Robert et al., 2024 for more details). The provenances chosen for this study were representative of the whole species range, both in terms of climate of origin and phylogeographic structure (Supplementary Figure S1). The use of common gardens allowed us to explore the persistence of the species at the population scale using growth as a proxy for fitness, in a semi-natural setting. The relatively low mortality rates in the garden let us control for survival bias and include the growth response of individuals that would likely not have survived in a natural setting.

To obtain the tree-ring widths and densities that were used in the ABI calculation (See Supplementary Material SM1 for details of the calculation of ABI), more than 2600 trees from 61 provenances (352 in PR, 752 in ML, 806 in CH, and 717 in Acadia, see Supplementary Table ST2 for the number of trees sampled by provenance) were sampled from those gardens between 2014 and 2019. The provenances were chosen to be representative of the species range, from Alaska to Newfoundland and covering more than 20° of latitude, from 44° N to 65° N. However, not all provenances are present in all the gardens (see supplementary Table ST3 for a list of the provenances established in each garden). Following the method described in Robert et al. (2024), one wood increment core was collected and processed per tree. The growth rings were visually dated, and the dating was statistically validated via CDendro and COFECHA software (Holmes, 1983; Larsson, 2013). Their width was measured using the Coo-Recorder software (Larsson, 2013), and their density was measured with a Quintek X-ray system at Université Laval and the Laurentian Forestry Center (Québec, Canada) at a 20 µm resolution.

Needle tissue was also collected from 1628 trees, representing 61 provenances included in the wood core increment study, along with six additional provenances added to improve the geographic coverage for delineating genetic groups (refer to supplementary Table ST4). Following the methods outlined in Girardin et al. (2021) and Robert et al. (2024), DNA was extracted from those samples, and 229 SNPs were used to genotype the trees and to determine the genetic structure of the populations using Q-values. K= 3 was optimal and allowed to define three genetic clusters, which correspond to the three main glacial lineages of the species (Supplementary Figure S1a; Jaramillo-Correa et al., 2004). The genetic admixture proportions (Q-values) were averaged for trees of the same population to allow generalization.

### 2.2. Weather data (BioSIM)

The daily climates of the chosen variables over the study period (1980–2019) were obtained for each of the four common gardens using the BioSIM software (V.11.6; Régnière and Bolstad, 1994). The software produced daily mean temperatures and precipitation using Environment and Climate Change Canada's historical daily weather observations. Interpolation of daily data was achieved using the four closest weather stations to each of the gardens, adjusting them for elevation and location differentials with regional gradients and averaging values using a $1/d^2$ weight, where d is distance. Daily VPD and Soil Moisture Index (SMI) were then calculated from these data. VPD (in kPa) was calculated as the difference between actual atmospheric water vapour amount and the maximum amount at saturation for a given temperature. For that BioSIM followed the approach described in Allen et al. (1998) and used both minimum and maximum temperature to calculate the vapour pressure at saturation and the temperature at dewpoint to calculate actual vapour pressure. The dewpoint temperature was estimated from minimum temperature and precipitation using the method presented in Kimball et al. (1997). A high VPD indicates that the air is dry, while a low VPD indicates that the air is close to being saturated with water vapour. SMI (%), as defined by Hogg et al. (2013), represents the relative soil water content. It is based on the quantity of available soil water in the tree rooting zone, in mm, modeled using the quadratic-plus-linear (QL) formulation procedure (Régnière et al., 2014). This approach is based on the balance between evapotranspiration estimated using a simplified Penman–Monteith equation and precipitation. This quantity is expressed as a ratio over the maximum available soil water, which is calculated as the difference between the wilting point and field capacity assuming no difference between sites. As such, this index is an estimation reflecting the meteorological influence of weather on soil moisture. A SMI value of 100 % means soil moisture is at saturation while a value of 0 % means soil moisture is at the wilting point.

The average climate at the provenance (geographic origin) was used to assess the role of local adaptation. Three variables related to either temperature or precipitation gradients were considered: the mean annual temperature (MAT) of the provenance, the mean daily precipitation (MDP) of the provenance, and the average growing degree day above 5°C (GDD) of the provenance (see Supplementary Figure 1). BioSIM was used to produce daily temperature and precipitation data for the 30 years before the seeds of the trees were collected (1930–1969). We then calculated GDD from these data before averaging all the variables.

### 2.3. Stress events

Short-duration climate extremes—often driven by weather processes—are considered extreme when they are rare relative to the typical conditions of a specific location and time of year (Mahecha et al., 2024). However, the definition of "rare" varies widely depending on the context (IPCC, 2023). One common approach is to define thresholds near the extremes of observed variable ranges (Sanginés De Cárcer et al., 2018). However, this approach will not define short-duration climate extremes consistently in time, as in the future, the range of the variables will change. Moreover, it lacks biological and ecological meaning (Gutschick and BassiriRad, 2003). As an alternative, we propose to examine the impact of what we term stress events, rather than extreme events. We define these stress events by fixing a climatic threshold corresponding to the limit beyond which tree physiology and growth are affected (Sanginés De Cárcer et al., 2018, Niinemets, 2010). To determine these thresholds, we drew on published studies describing the effects of VPD, SMI, and GSF on black spruce growth at the physiological level, where such information was available. Those physiological effects on growth were usually determined in a controlled setting and represent the short-term internal response of trees. As such they provide important prior knowledge for exploring the effect of stress events on annual growth (ABI) at the population scale.

For VPD, we chose a threshold associated with stomatal closure, as this process is directly linked to growth reduction (Grossiord et al., 2020). In black spruce, stomatal closure starts when the absolute humidity deficit (difference in absolute humidity between needles and air) is greater than 12–14 $g.m^{-3}$ (Lamhamedi and Bernier, 1994). Several VPD values corresponding to stomatal closure have been proposed, such as 0.7 kPa in Fan et al. (1995) and 1.5 kPa in Grant et al. (2009). The results of Pepin et al. (2002), in contrast with those of Dang et al. (1991), (1997), suggest that most of the decrease in stomatal conductance, approximately 50 %, occurs when the VPD increases from 0.1 to 1.4 kPa. It does not decrease much above that as the total decrease is of 60 % when the VPD reaches 4.0 kPa. In the more widely studied Norway spruce, stomata have also been shown to close at approximately 1.5 kPa (Kurjak et al., 2012; Sanginés De Cárcer et al., 2018; Zweifel et al., 2002). Relying on those studies, we considered 1.5 kPa to be the threshold above which VPD is high enough for trees be experiencing a stress event.

For SMI, the point where soil moisture depletion induces a decrease in transpiration would have been a suitable threshold for defining a stress event. However, to our knowledge, no study has proposed a SMI value where this point is reached for black spruce. For other species, such as Norway spruce, the proposed thresholds below which soil moisture has a negative impact on growth are highly variable across studies, trees and sites. For example, Lagergren and Lindroth (2002) reported that a reduction in transpiration began when SMI decreased to around 20 %, with a high variability between trees. On the other end of the spectrum, Karlsson et al. (2023) reported that days under 95 % SMI were associated with a decrease in growth. These discrepancies may be due in part to soil properties, as soil moisture may not necessarily be available to trees in the same way in every soil and therefore drought may not influence growth the same way (e.g., Alavi, 2002; Rehschuh et al., 2017). Owing to the difficulty in comparing the influence of soil moisture values across sites with varying soil properties—and considering the high heterogeneity in soil moisture ranges among our sites, with PR being significantly drier than the others—we defined stress events relative to site-specific thresholds. We considered days with SMI values within the lower 10 % of the monthly range over the studied period (see supplementary Table ST5) to be a stress event, as a low SMI corresponds to a high level of moisture depletion. By using a composite approach to define the different thresholds we can capture the fact that some stress factors are linked to universal physiological thresholds, for instance VPD or GSF, when others are context-dependent, like SMI.

Finally, for GSF, the temperature below which frost damages a tree's vegetative tissue, notably buds and cambium, and impairs growth is a relevant threshold. Laboratory studies suggest that the hardiness of black spruce in winter is under −40°C but increases to approximately −11°C at the bud swelling phase (beginning of bud break) and stabilizes at approximately −5°C after bud break, with temperatures under those thresholds damaging buds and needles (Bigras and Hébert, 1996; Glerum, 1973). In parallel, field experiments have shown that temperatures under −4°C during the growing season kill growing shoots and cause reductions in net photosynthesis and stomatal conductance in 1-year-old needles, whereas no significant impact is observed at −3°C (Dang et al., 1992; Lamhamedi and Bernier, 1994). A temperature of –5°C will damage both the cambium (Bigras and Hébert, 1996; Dy and Payette, 2007; Marquis et al., 2021) and buds (Bigras and Hébert, 1996; Glerum, 1973); therefore, we chose to use this value as a threshold.

We defined the number of stress event occurrences as the number of days during which VPD, SMI, or GSF exceeded their respective thresholds. For VPD and SMI, this was assessed over the growing season (April to November), while for GSF, it was limited to the period from the onset of the snow-free season to the end of August. The growth of black spruce is also influenced by climate from the previous growing season because black spruce, an overwintering species, contains stem units that are preformed in the terminal bud (Kayal et al., 2011), and early-season development relies on stored non-structural carbohydrates (Tixier et al., 2019). For this reason, stress events during the previous growing season were also considered. The chosen thresholds make the probability of the occurrence of stress events high enough so it usually occurs several times a year, but not too high so years with no events are still possible (the distribution ranges from 0 to a few dozen or hundreds of events a year, depending on the variable; Supplementary Figure S2). Having a daily threshold as a variable should allow us to capture both short stress events (e.g., frost events) and longer-lasting events such as dry spells. It should also integrate stress frequencies and capture the effect of repeated stresses. As a downside, it does not allow us to consider the effects of the duration or intensity of the stress events separately. It is important to note that VPD influences soil moisture by increasing the atmospheric demand for water from the land surface, thus increasing evaporation (Lu et al., 2022). The correlation between SMI and VPD can constitute a confounding factor that is often overlooked when assessing their respective effects on growth (L. Liu et al., 2020; Mirabel et al., 2023). In our case, the correlation coefficient between the two types of stress events was less than 0.5 at all the sites except ML, where it was approximately 0.7. Since it has been shown that in boreal forests, the SMI and VPD, although in interaction, had a different effect on tree growth (L. Liu et al., 2020; Mirabel et al., 2023), this was deemed reasonable.

### 2.4. *Modeling*

For each site separately, a random forest algorithm (Breiman, 2001) was used to model the ABI of the population as a function of stress events while accounting for the climate at the provenances of the populations and the admixture proportion of the populations. The random forest model is capable of accounting for confounding factors such as tree age and size effects on growth, simply by the addition of those factors as independent variables. However, we chose not to do so here to force the algorithm to focus only on our factors of interest. The rationale behind this decision is that independent variables with strong effects may be favored during tree construction, which may partially conceal the effects of variables with more moderate effects. This is normally addressed by adjusting the number of variables in the subset of variables considered at each split but at the expense of reducing the strength of each individual tree (Probst et al., 2019). Here, we chose to avoid this issue by removing from the models the age and tree size, which are generally the factors that have the greatest influence on growth but are secondary to the present study. Instead, the ABI was detrended via a generalized negative exponential approach (Girardin et al., 2012) to remove low-frequency trends in the ring series due to age and tree size. As a side effect, the trend associated with climate change and rising CO2 was also removed (Ols et al., 2023). Therefore, we also detrended the stress event occurrences, with a simple spline using Python (V3.11.2, Van Rossum and Drake, 2009) and the package dplpy (Bunn et al., 2022), to maintain the correlation between growth and climate. From the three variables representing the genetic clusters, only two (proportion of the western cluster and proportion of the eastern cluster) were included in the model. This is because those variables are relative proportion of the total genome and their sum is equal to one, which make the inclusion of only two of them sufficient and can even induce a bias if all three variables are included in the model.

Modeling was performed via R statistical software (V4.3.2, R Core Team, 2023) and the randomForest package (Liaw and Wiener, 2002). It was done according to the following steps. The dataset was divided into training and testing sets (90 % and 10 % of the data, respectively). We first tuned the hyperparameters of the algorithm via a grid search on a subsample of the training dataset (20 %). The model was then retrained using the full training set, and both the mean squared error (MSE) and R2 were obtained using the testing dataset that was previously set aside. Variable importance was calculated via permutation using MSE increase as a metric of importance. ALE (accumulated local effects) plots were generated to show the effect of each variable via the ALEplot package (Apley, 2018). As second-order ALE are, by design, only accounting for the interaction between variables (Molnar, 2022), the mean absolute second-order ALE was calculated as a metric for the variable interaction strength for every combination of provenance and stress events variables, and two-way ALE plots were generated for the variables with the strongest interactions.

This approach allowed us to test two key hypotheses to answer our research questions:

i) Relevance of established thresholds: the thresholds described in the literature significantly influence growth in a semi-natural setting. This is evidenced by the significant importance of these variables in our model, suggesting that the algorithm detects a meaningful effect of the variables. The number of days passing this threshold is negatively and linearly correlated with the ABI. The 1D ALE plots allow us to visualize this effect.

ii) Variation in sensitivity: Populations exhibit variations in sensitivity to stress events linked to local adaptation or genetic clusters. This is supported by 2D ALE plots showing interactions between climate variables and provenance, indicating that growth responses to stress events vary across populations on the basis of their genetic or climatic origin.

## 3. Results

### 3.1. Modeling

In this study, we trained a series of random forest models to explain the effects of stress events—defined as days with VPD above 1.5 kPa, days within the lowest 10 % of the SMI, and days below –5 °C during the growing season—on black spruce ABI. The models also accounted for the effects of local adaptation and the species' phylogeographic structure (hereafter referred to as provenance variables). These models scored differently for each site (Table 1). The highest variance was explained at the Peace-River site (37 %), followed by the Acadia site (30 %), the Mont-Laurier site (28 %), and the Chibougamau site (15 %).

### 3.2. Variable importance

The importance of the variables in the models was assessed through permutation with the increase in MSE as a metric. At all the sites, stress event variables had greater importance than provenance variables, i.e., they resulted in a greater increase in the MSE when permuted (Fig. 1). At Peace-River (Fig. 1A), the ABI was influenced mostly by high-VPD days from the previous year (MSE increased more than 50 % when this variable was permuted, see Table 1 for MSE values) and, to a lesser extent, by high-VPD days from the same year (MSE increased more than 20 %). GSF days and low-SMI days also had some influence (over a 10 % increase in MSE). At the Mont-Laurier site (Fig. 1B), GSF days were the most influential (over a 12 % increase), as were previous-year high-VPD days (over a 10 % increase). The increase in MSE for other stress event variables was approximately 8 %. At the Chibougamau site (Fig. 1C), the most influential variable was the number of low-SMI days in the previous year (over a 7 % increase). The permutation of other variables increased the MSE less than 5 %. Finally, at the Acadia site (Fig. 1D), the most important variable was also the number of low-SMI days from the previous year, which caused an increase in the MSE of over 20 %, whereas other stress event variables had a more moderate effect, increasing the MSE by 9–15 % when permuted.

### 3.3. Effect of individual factors on the ABI

ALE plots were used to visualize the modeled effects of the two most important variables at each site (Fig. 2; see Supplementary Figures 3, 4, 5 and 6 for the other variables). At the PR site, the number of high-VPD days in both the previous and current year had a similar effect on tree growth (Fig. 2A and B). When there were fewer than 5 high-VPD days in a year, tree growth (detrended ABI) was above average—about 0.35 kg above average for the previous year and 0.2 kg for the current year. However, once the number of high-VPD days exceeded 5, the effect on growth dropped sharply and stabilized below average, around −0.2 kg and −0.1 kg for the previous and current year, respectively.

At the ML site, when the number of GSF days per year was low (less than 4), tree growth was approximately 0.1 kg above average, and this effect stayed fairly stable (Fig. 2C). However, when there were more than 4 GSF days per year, the effect on growth turned negative, and tree growth stayed about 0.1 kg below average. Similarly, when the previous year had fewer than 8 high-VPD days, the effect on tree growth was stable, ranging between 0.1 kg and 0 kg (Fig. 2D). As the number of high-VPD days increased to 20, the effect on growth became more negative, ranging from 0 kg to −0.1 kg. When the number of high-VPD days exceeded 20, tree growth dropped sharply, reaching −0.4 kg at 26 days.

At the CH site, the number of previous-year low-SMI days had a slightly positive effect on tree growth, increasing ABI from −0.05 kg to 0.05 kg as the number of days increased from 0 to 135 (Fig. 2E). ABI showed some fluctuations along the way. In years with fewer than 4 GSF days, tree growth was close to average, but in years with more than 4 GSF days, ABI was about 0.05 kg above average (Fig. 2F).

At the AC site, fewer than 40 low-SMI days in the previous year were associated with growth up to about 0.1 kg above average (Fig. 2G). However, when the number of low-SMI days exceeded 40, the effect turned strongly negative, with ABI dropping 0.4 kg below average at 90 days. For high-VPD days in the previous year, 7–10 days increased ABI to 0.2 kg above average, while 10–15 days decreased it to about 0.1 kg below average. When there were more than 15 high-VPD days, ABI stayed slightly above average, ranging from 0 kg to 0.05 kg (Fig. 2H).

### 3.4. Interactions between factors

Table 2 shows the four combinations of event variables and provenance variables having the highest mean absolute second-order ALE and therefore the strongest interactions. Two are from the PR site, and two are from the ML site (see supplementary Table ST6 for the other variables and sites). Fig. 3 shows the ALE plots of those variable combinations (see supplementary Figure S7 for the 12 combinations with the highest interaction after those). Interestingly, the range of values of the interactions (from approximately −0.06–0.06 Kg) is one order of magnitude smaller than the range of values of the ALE of the stress event variables (from approximately −0.3–0.3 Kg). At ML, the range of values of the ALE of the provenance variables (from approximately −0.005–0.005 Kg) is also one order of magnitude smaller than the values of the interactions, whereas at PR, they are the same order of magnitude (from approximately −0.01–0.02 Kg).

The second order ALE is showing by design the effect of the

**Table 1**
Goodness of fit ($R^2$) and mean square error (MSE) of the final model at each site and the corresponding hyperparameters retained from the grid search.

| Site | Hyperparameters retained | | | | $R^2$ | MSE |
|---|---|---|---|---|---|---|
| | number of decision trees in the random forest | number of variables considered at each split | minimum node size | maximum number of nodes | | |
| Peace-River | 100 | 6 | 10 | 50 | 0.371 | 0.204 |
| Chibougamau | 400 | 2 | 10 | 50 | 0.149 | 0.073 |
| Mont-Laurier | 1000 | 2 | 100 | 400 | 0.282 | 0.231 |
| Acadia | 1000 | 2 | 100 | 400 | 0.305 | 0.122 |

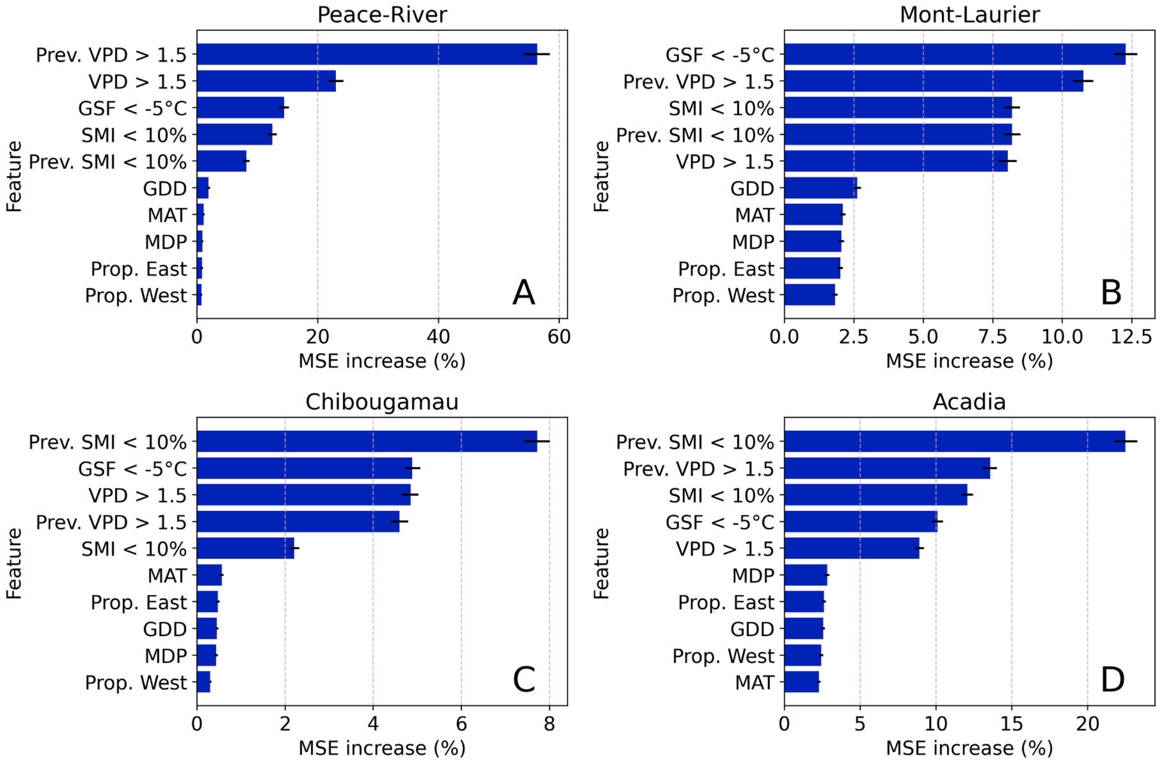

**Fig. 1.** Importance of the variables within the model at each site determined by the increase in the mean square error (MSE) when a given variable is randomized (permuted; averaged over 1000 repetitions). Black bars represent the 5 % and 95 % quantile of importance values from 1000 repetitions. VPD> 1.5 and Prev. VPD > 1.5 stand for the number of days when the vapor pressure deficit is above 1.5 kPa during the year of the growth season and the year preceding it, respectively. SMI< 10 % and Prev. SMI< 10 % stand for the number of days when the soil moisture index is within the lower 10 % of its monthly range during the year of the growth season and the year previous to it, respectively. GSF stands for the number of days when the temperature is under −5°C during the growth season. GDD, MAT and MDP represent the average growing degree days above 5°C, the mean annual temperature and the mean daily temperature at the provenance, respectively. Prop. east and Prop. west represent the proportion of the eastern and western clusters in the genome of the population, respectively.

interaction of the two variables on the dependent variable without their main effect. In the present case they can be interpreted as an increase or decrease of the main effect of the stress event on ABI (shown in Fig. 3A, D, G and J) for the different provenances ordered along the climate at their origin (MDP or GDD, main effect shown in Fig. 3C, F, I and L). At the PR site, the two most important interactions were between high-VPD days of the previous year and either GDD (Fig. 3B) or MDP (Fig. 3E). Overall, the effect of previous-year high-VPD days (i.e., strong negative effect above 5 days, Fig. 3A) is exacerbated; that is, the positive effect is greater (up to 0.065Kg higher), and the negative effect is lower (up to 0.065Kg more negative) for populations from provenances with higher GDDs, whereas it is attenuated for provenances with lower GDDs (up to 0.03Kg closer to zero for both the positive and negative effect), with a sharp delineation at a GDD of 1277 (see Fig. 3C). Similarly, the pattern of interaction with the MDP shows that for dry provenances (under 1.25 mm of average daily precipitation, see Fig. 3F), the effect of high VPD days (Fig. 3D) is attenuated (up to 0.05Kg closer to zero), whereas it is exacerbated for wetter provenances (up to 0.05Kg more extreme).

At the ML site, the two most significant interactions involved GDD and high-VPD days from either the previous year or the current year. In the former case (Fig. 3G-I), provenances with a GDD less than 1434 are less positively affected (up to 0.04Kg less) when there are fewer than 5 high-VPD days a year, whereas they experience a less negative impact (around 0.03Kg higher) with a greater number of high-VPD days. Conversely, for provenances over 1434 GDD, the opposite trend was observed. Interestingly, the pattern was completely reversed for high-VPD days in the current year (Fig. 3J-L). Provenances with lower GDDs are stimulated (around +0.02Kg) by fewer days with high VPDs and are negatively impacted (around −0.02Kg) by a greater number of high-VPD days, and conversely for provenance with higher GDDs.

## 4. Discussion

### 4.1. Nonlinear effect of repeated stress on growth

We hypothesized that when stress events had a significant effect on growth, the effect would generally be negative, which was confirmed by our results. However, contrary to our expectation, the relationship was not linear, as shown by the ALE plots. For most variables, the effect followed a similar pattern, with a first plateau corresponding to a constant positive effect on growth, followed by a sudden negative effect after a threshold was passed (Fig. 2). This pattern needs to be investigated in greater depth, as it may be important for understanding tree responses to repeated stress events. One possible interpretation is that it may be linked to a balance between a priming or acclimation effect and a cumulative effect of the stress. Trees often acclimate to stress, and an initial stress event can have a priming effect, enabling them to maintain growth during subsequent events (Mitchell et al., 2015; Niinemets, 2010). On the other hand, tolerance to stress could be dependent on carbon reserves and non-structural carbon remobilization (D'Andrea et al., 2021; Sala et al., 2012; Zhang et al., 2020). If the time between repeated stress events is too short to replenish the carbon reserves, the tolerance of the trees decreases. These two opposing effects may interact to produce the sharp threshold observed in response to an increasing number of stress days. The priming effect allows the trees to maintain their growth as the number of events increases, up to a point where the time period between stresses is not sufficient to allow trees to replenish their carbon reserves, canceling the beneficial effect of acclimatization and simultaneously decreasing their tolerance capacity (Niinemets, 2010).

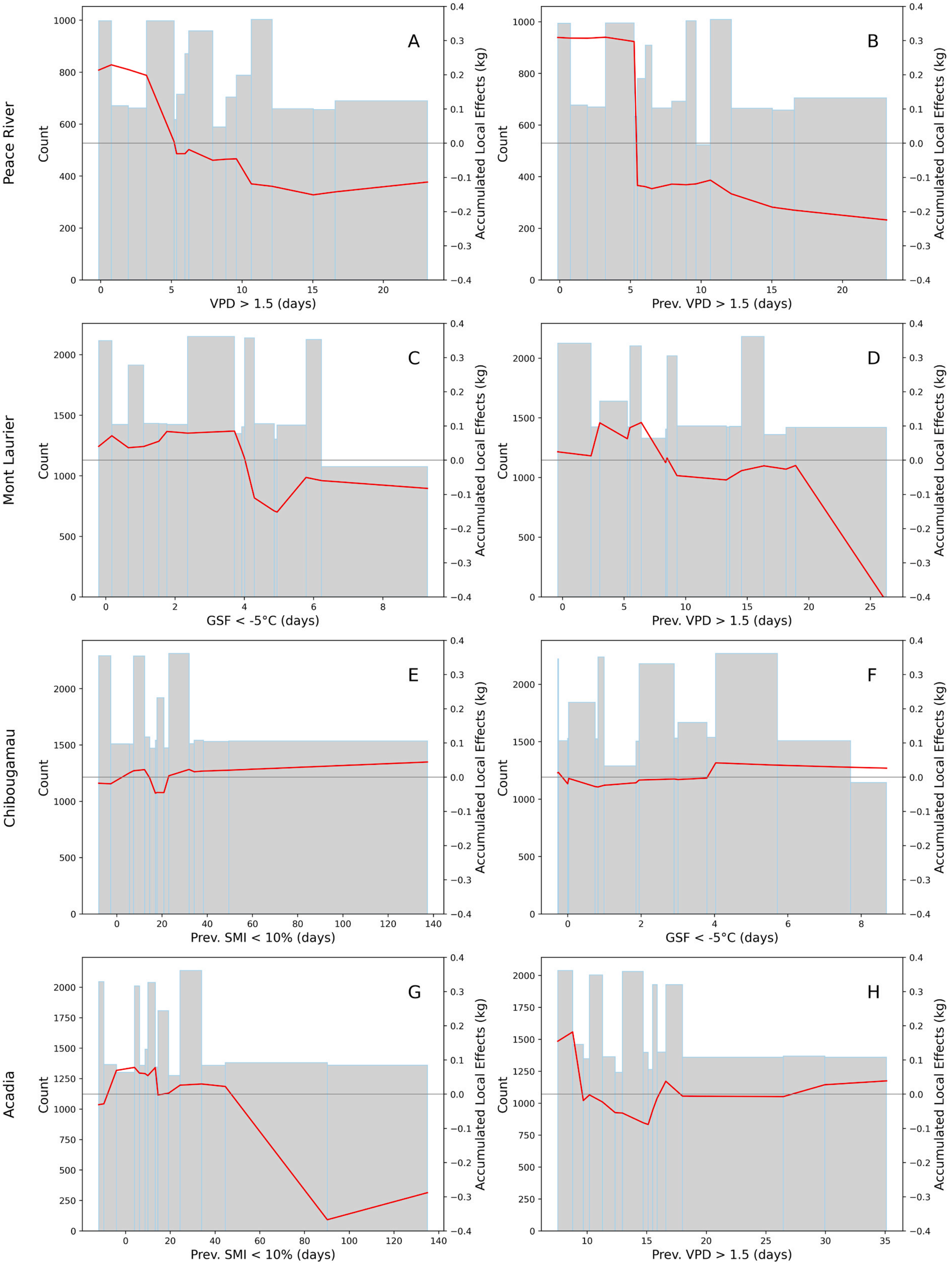

**Fig. 2.** Plots of the accumulated local effects (ALE) in terms of ABI of the two most important variables for each site (red lines). The plots are centered on the average (gray horizontal line). The gray histogram shows the limits of the bins on which the ALE was calculated as well as the count of data instances in each bin (height of the bar). VPD> 1.5 and Prev. VPD > 1.5 stand for the number of days when the vapor pressure deficit is above 1.5 kPa during the year of the growth season and the year previous to it, respectively. Prev. SMI< 10 % stands for the number of days when the soil moisture index is within the lower 10 % of its monthly range during the year preceding the growth season. GSF stands for the number of days when the temperature is under −5°C during the growth season.

**Table 2**

The four combinations of stress event and provenance variables with the highest mean absolute two-way accumulated local effects (ALE). VPD above 1.5 and Prev. VPD above 1.5 stand for the number of days when the vapor pressure deficit is above 1.5 kPa during the year of the growth season and the year preceding it, respectively. GDD and MDP represent the average growing degree days above 5°C and the mean daily temperature at the provenance, respectively.

| Site | stress event variable | Provenance variable | mean absolute ALE (Kg) |
|---|---|---|---|
| Peace-River | Prev. VPD above 1.5 kPa | GDD | 0.0218 |
| Peace-River | Prev. VPD above 1.5 kPa | MDP | 0.0129 |
| Mont-Laurier | Prev. VPD above 1.5 kPa | GDD | 0.0121 |
| Mont-Laurier | VPD above 1.5 kPa | GDD | 0.0085 |

### *4.2. Variation of the importance of the factors between sites*

All the models had some explanatory power, and all stress event variables had some importance in those models. These results confirm our hypothesis that the described physiological thresholds are indeed influential on growth. However, the influence of stress events on ABI is not uniform across sites but instead varies based on local climatic and environmental conditions. This variability is consistent with previous studies (e.g., McLane et al., 2011; Suvanto et al., 2016; Taeger et al., 2013), which suggest that differences in microenvironmental factors can shape tree responses to stressors. Even among sites with similar broad-scale conditions, factors such as soil properties (including soil microbiome), water availability, and stand density can introduce variability in how trees respond to drought, frost, and other stress events (Zas et al., 2020). Our results underscore the importance of considering site-specific conditions when assessing the impacts of climate extremes on tree growth, as even subtle environmental differences can influence physiological responses. These findings also suggest that as climate change alters the frequency and intensity of stress events, the primary limiting factors for black spruce growth may shift depending on regional conditions.

Overall, the amount of variance explained varied between sites in a manner consistent with their local climate and the relative importance of the variables included in the models. At PR, the highest proportion of variance was explained, highlighting the strong relevance of the tested variables in accounting for ABI variation at this site. The most influential variable by far was the high-VPD days in the year before growth, whereas high-VPD days in the year of the growth ranked second. Being situated in the central plains of Canada, the PR site is the driest of all in

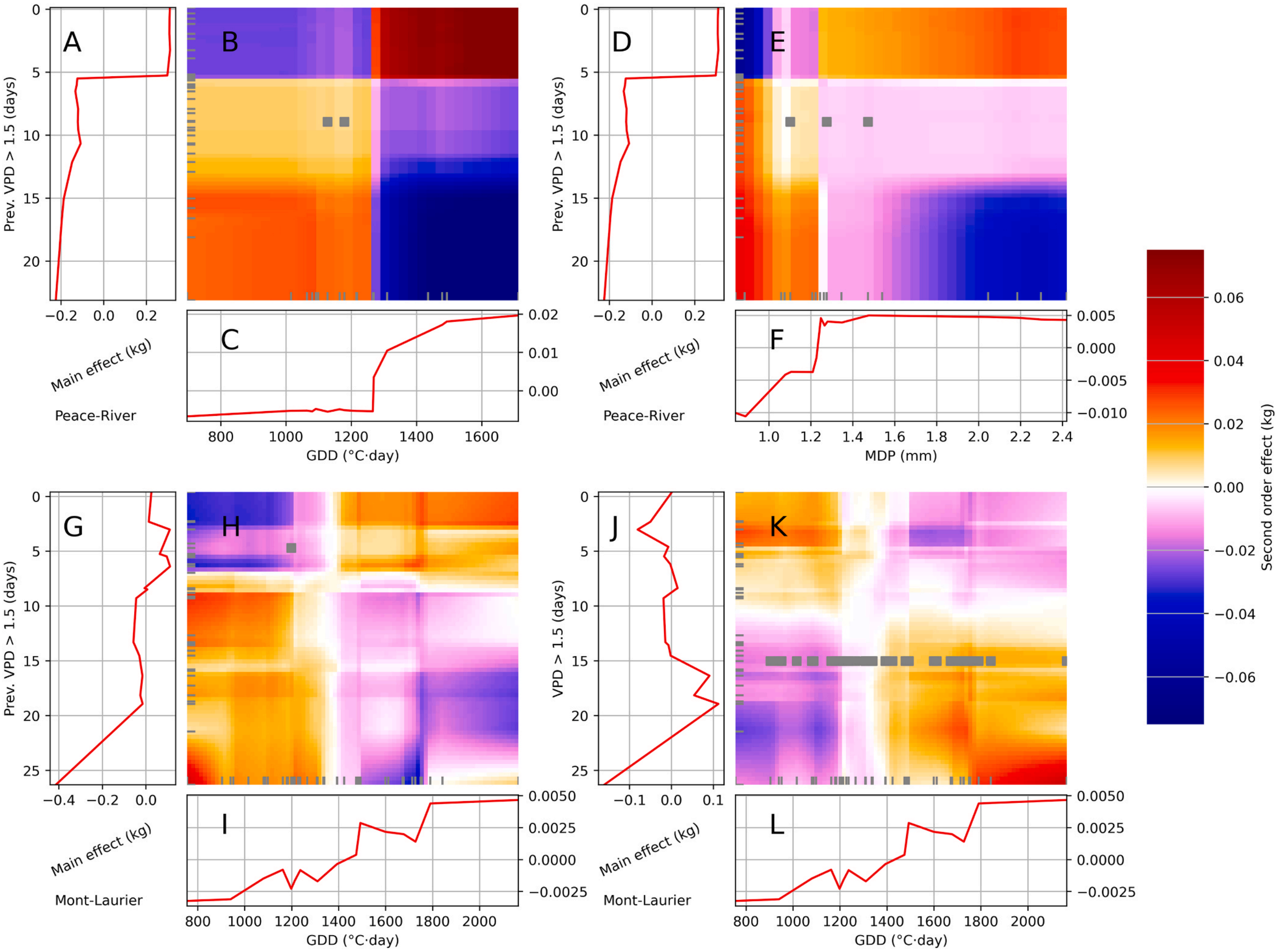

**Fig. 3.** B, E, H, K: Two-way accumulated local effects (ALE) plots showing interactions between the variables selected in Table 2. A, C, D, F, G, I, J, L: ALE plots of individual variables corresponding to their first-order effects shown as a reference. The gray ticks represent the limits of the bins over which the ALE was calculated. The values within those bins were linearly interpolated using Python and the package Scipy. The gray squares indicate empty bins. VPD > 1.5 and Prev. VPD > 1.5 stand for the number of days when the vapor pressure deficit is above 1.5 kPa during the year of the growth season and the year previous to it, respectively. GDD and MDP represent the average growing degree days above 5°C and the mean daily temperature at the provenance, respectively.

terms of SMI and it has been shown that this could accentuate the effect of VPD on growth (Mirabel et al., 2023). This would be linked to a more conservative stomatal behavior induced by an acclimation of the tree to the lower SMI (Stefanski et al., 2023). Tree plantation density is also slightly greater at this site, which is a known factor influencing tree response to drought (e.g., Li et al., 2020; Zas et al., 2020), as it could increase competition for water, accentuating drought effects (Castagneri et al., 2022).

At AC and ML the variance explained was similar, and lower than at PR for both. Stress event variables were closer in relative importance, with drought-related variables—high VPD and low SMI days—among the most influential in explaining ABI variation. However, the relative importance of atmospheric versus soil drought differed by site, suggesting that site characteristics mediate tree sensitivity to these stressors. For instance, at AC, the warmest site, days with low SMI had the most significant impact, whereas at ML, days characterized by high VPD were among the most influential factors. It makes intuitive sense as those two sites are the warmest. One being more sensitive to atmospheric drought (VPD), and the other to soil drought (SMI) may be related to differences in soil characteristics (e.g., Alavi, 2002; Rehschuh et al., 2017), including soil microbiology (Allsup et al., 2023). At ML, the number of GSF days was the most influential factor. This site is the second warmest site and seems to be more exposed to GSF (Supplementary Figure S8), i.e., it is warm enough to have an early beginning of the growing season but cold enough to still be exposed to low temperatures in spring. This contrasts with previous findings showing that black spruce growth is generally less affected by frost than that of other spruce species (Marquis et al., 2020a, 2020b), and that black spruce foliage sustains minimal damage from growing-season frosts (Marquis et al., 2021). As the climate warms, sites north of ML may experience a similar climate, and GSF may become more of an issue for black spruce in the future.

Finally, CH was the site with the least variance explained. The model's poor predictive performance at this site suggests that the selected variables do not fully capture the underlying dynamics or are not sufficiently representative of the site-specific conditions. This is the northernmost and coldest site, and low-SMI days during the year before growth was the most influential variable. However, it has been shown that SMI is negatively correlated with growth in black spruce at colder sites (Pau et al., 2022) and at CH in particular (Girardin et al., 2021). Although the mechanism behind this relationship is not completely clear, it could be linked to frost (Moyes et al., 2015) or waterlogging (Krause and Lemay, 2022; Lamhamedi and Bernier, 1994; C. Liu et al., 2022). In fact, the ALE plot of low-SMI days at the CH site seems to display a slight positive trend, indicating a positive effect of a low SMI on growth. However, this effect is not strong nor obvious. This is probably because our variable was designed to identify the negative impact of stress events.

### *4.3. Influence of standing genetic variation*

Our results revealed a relatively small, but notable, influence of standing genetic variation on biomass compared with the effect of stress events. This influence was notably expressed through interactions with stress event variables. This confirms our second hypothesis that the species exhibits variations in sensitivity to extreme climatic events linked to local adaptation and genetic clusters. Even though the effects of provenance variables and their interactions are small, they are likely to be constant over the lifespan of the trees and ultimately have a significant effect on growth in the long term (as shown in Robert et al., 2024). The four strongest interactions across sites and provenance variables were with GDD and MDP (variables linked with the phylogeographic structure ranking considerably lower, Supplementary Table ST6), suggesting an adaptive origin to this influence.

The patterns of interactions between stress event variables and provenance variables inform us about the influence of local adaptation and phylogeographic structure on the effects of stress events on growth. For example, at the PR site, the growth of trees from provenances with a high GDD, i.e. warmer provenances mostly from the south-east of the range (Supplementary figure SF1), was more affected by high-VPD days. This greater sensitivity may be interpreted as an adaptive strategy to avoid xylem cavitation via a faster stomatal response (Grossiord et al., 2020; Jamnická et al., 2019). In this case, growth is sacrificed to ensure survival (Zhang et al., 2020). Interestingly, if this pattern of interaction with GDD is the same for high-VPD days in the previous year at the ML site, it is inverted for high-VPD days in the current year. Provenances with high GDDs are growing better when the number of high-VPD days increases. This could be because, even though adapted trees close their stomata, they manage to continue growing using their carbon reserves. As a result, the effect of high-VPD days is only visible the next year (Cabon et al., 2022; Teets et al., 2022). This type of lag in growth response to high VPD has been previously shown for various boreal species (Mirabel et al., 2023). At the PR site, the pattern of interaction between MDP and VPD shows that drier provenances are better at maintaining their growth with a greater number of high-VPD days. This could be an adaptation linked to a more anisohydric behavior (Sade et al., 2012). Interestingly, the adaptation to a dry climate seems to be opposite to the adaptation to warm climatic conditions described above, i.e., a more important decrease in growth in the case of a greater number of high-VPD days.

This difference between provenances may be related to a trade-off between growth and survival linked with the "fast-slow" growth spectrum (Reich, 2014). The theory behind this spectrum suggests that species or provenances from more extreme environments tend to have more conservative strategies, sacrificing growth to ensure survival, while provenances from milder environments will have traits and strategies oriented toward resource acquisition and sustained growth (Volaire, 2018). This could be reflected in a variety of traits linked with either survival, for instance stomatal sensitivity, or growth, like the use of non structural carbon resources, during and after stress events. To explore further this variation in adaptive strategy it would be interesting to look at the resilience of trees, i.e. their capacity to resume growth after a stress event, to see if the same kind of intraspecific variation can be observed.

Interestingly, there seems to be a sharp delineation between provenances with different strategies, notably for the response to high-VPD days (see Fig. 3B and E). This is unexpected as variation between populations for several traits like growth, height, or timing of bud flush and bud set is rather clinal (i.e. continuous) in BS (Beaulieu et al., 2004; Prunier et al., 2011; Silvestro et al., 2023). Additionally, changes in adaptive strategies within a species, like for instance between isohydric and anisohydric response to drought, is now thought to be continuous through a progressive change in traits along environmental gradients (Klein, 2014). It could be interesting to explore the genomic basis of this pattern of intraspecific variation in adaptive strategies. This could be done, for example, through a genome wide association study (e.g. Chhetri et al., 2020; Depardieu et al., 2021), and would help increase our understanding of the adaptive potential of the species.

### *4.4. Buffering capacity of diversity and implications for forest management*

These results illustrate how standing genetic variation is an important component of the buffering capacity of the ecosystems. We showed that within a species, the influence of different types of stress events on growth varies on a site-specific basis and that the response of populations to those events varies with intraspecific genetic variation. As a result, different populations may be more adapted at different sites. In the context of an increase in the frequency and intensity of stress events, local populations may not necessarily stay adapted in the future, especially if the most influential stress event at the population's site changes. Forest management may play a role in sustaining the adaptive capacity of forests by ensuring that adaptive genes are available for selection in populations under future climates. This could be through the introduction of adaptive alleles by maintaining high diversity in planted populations using assisted gene flow, thus increasing the chance of the right alleles being present (Aitken and Bemmels, 2016). However, in their recent review, Kremer et al. (2025) found that the interplay of local adaptation and high gene flow generally allows the maintenance of genetic diversity at the species level for widespread tree species. Management practices promoting natural selection could therefore be sufficient to facilitate adaptation. This could be done for example by increasing the density of seedlings during natural seeding, as natural selection is stronger at this stage (Kremer et al., 2025). However, our results show that the effects of the stress events are still one order of magnitude greater than the potential mitigation effect due to local adaptation. This could indicate a limit to the capacity of forest management to mitigate the effects of this type of events, especially as their frequency and intensity increase in the future.

Our results also imply that selecting populations using the ability to maintain growth during stress events as a criterion (i.e., resistance), e.g., in tree improvement programs or for assisted gene flow, may be selecting for populations that are less adapted to those extreme climate events in some cases. Indeed, there seems to be a trade-off between resilience and resistance, with populations with higher resistance being less resilient (Castagneri et al., 2022). This may be linked to a difference in strategies for plants to protect themselves from stress events (Li et al., 2020). Populations adapted to stress events may be sacrificing their growth faster, i.e., at a more conservative threshold (low resistance), to ensure survival on the one hand, and conserve resources that will authorize them to resume growth more rapidly after the event (high resilience) on the other hand. As shown for instance with populations from hotter provenances being more sensitive to drought in this study. When populations are adapted to a climate with a lower risk of stress events, it may be a better bet for them to maintain growth, even when they are exposed to high fluctuations in environmental conditions (high resistance) and therefore remain competitive in terms of fitness.

In this study, we explored how the frequency of stress events affected black spruce annual biomass production at the population scale. The effect of the stress induced by those events and the response of trees to it are complex. The increasing frequency of stress events may be one of the main challenges posed by climate change, making it essential to improve our understanding of their impacts on forests—particularly on black spruce. Some important aspects of this question still need to be explored in greater depth in future studies. Notably, exploring how several stress events may interact and produce compounded stresses on trees is relevant (Mitchell et al., 2015), e.g., frost has a greater effect when soil is dry (Clements et al., 1972; Dy and Payette, 2007; Niinemets, 2010). Additionally, our approach focused on physiological thresholds but could not directly address other aspects, such as stress intensity or duration, which may influence tree response. In this study, we focused on living trees; however tree mortality is an important component of the impact of stress events on forest with wide implications, notably in terms of forest resilience (Wang et al., 2012) and mitigation potential (Anderegg et al., 2020), but also in relation to adaptation and adaptive potential of tree populations. The influence of mortality on the adaptive potential of species is complex, for instance mortality may eliminate maladapted trees, thereby promoting the adaptation of a population (Kuparinen et al., 2010), but may also eliminate genetic diversity making populations less likely to adapt to future climates and potentially warranting assisted gene flow (Aitken and Whitlock, 2013). Finally, when studying the adaptive potential of tree species, phenotypic plasticity needs to be considered. This factor is implicitly accounted for in our model as part of the tree's response, but future studies may attempt to isolate its effect on trees growth response to explore its potential role in terms of adaptation to future climates in combination with standing genetic variation (Aubin et al., 2016; Walter et al., 2023). However, to reliably assert the adaptive nature of plasticity, it needs to be carefully assessed and interpreted, and several traits should be considered, as plasticity can vary between traits (Schneider, 2022). For example, low plasticity in terms of growth (i.e., populations tend to maintain their growth across climates) may be a sign of high adaptive plasticity for physiological traits allowing the maintenance of growth.

## 5. Conclusion

The results presented here outline the non-linear nature of trees' responses to stress-inducing climate events, as well as the influence of standing genetic variation on these responses, with an emphasis on local adaptation. In a context of future climatic changes, GSF may become an important factor impacting the growth of black spruce, as warming of northern sites expose trees to an earlier beginning of the growth season. But since GSF was not the most influential factor at the warmest sites, this phenomenon could be only transitory and eventually drought may be the dominant factor impacting tree growth in the long run. We believe that the results of this study may provide insights for seed sourcing and improvement programs as well as for assisted gene flow programs in selecting provenances that are more adapted to stress events. The high variability in the importance of stress events between sites, however, implies that there is no one-size-fits-all solution and that simply compensating for climate range shift is not sufficient. Provenance selection must be made on a case-by-case basis, and the best strategy overall might be to maintain a high genetic diversity and promote natural selection (Kremer et al., 2025). Finally, since the effect of local adaptation did not allow trees to fully compensate for the impact of stress events, it may be necessary to look for complementary strategies to maintain forest health and growth, for example, by selecting provenances, families, or genotypes with a high capacity for growth recovery after drought (Depardieu et al., 2020; Laverdière et al., 2022) rather than relying only on resistance to drought impact.

## Funding sources

This work was made possible by the financial and in-kind support provided by the Canadian Forest Service of Natural Resources Canada (NRCan) for the T-REX project (Tree Rings in common garden Experiments), the Sustainable Fibre Solution program of the Canadian Wood Fibre Centre and the Genomics R&D Initiative. Further financial support was provided by the NSERC Discovery Grant program (RGPIN--2019--06672). Funding sources were not involved in the study design, collection, analysis and interpretation of data, writing of the report and decision to submit the article for publication.

## Author Contributions

All the authors participated in the conceptualization of the study. Etienne Robert performed the formal analysis and wrote the original draft of the manuscript. All authors participated in reviewing and editing the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## CRediT authorship contribution statement

**Girardin Martin:** Writing – review & editing, Conceptualization. **Yves Bergeron:** Writing – review & editing, Conceptualization. **Patrick Lenz:** Writing – review & editing, Conceptualization. **Etienne Robert:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Nathalie Isabel:** Writing – review & editing, Conceptualization.

## Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Martin P. Girardin reports financial support was provided by NSERC. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledgements

We thank David Gervais, Christine Simard, Marie-Claude Gros-Louis, Manuel Lamothe, Xiao Jing Guo, Esther Pouliot, Simon Nadeau, Marie Deslauriers, Philippe Labrie, Jean-François Légaré, Eric Dussault, Daniel Plourde, Jamie Farrell, Jeanne Portier, and Johann Housset, all from NRCan, for field and laboratory work, help with data and planning, and technical advice. Thanks to Deogratias Rweyongeza and colleagues from the Alberta Ministry of Forestry and Parks for providing access to the Peace River site and to Jim Stewart and Jared Salvail from NRCan, for support with fieldwork at this site. Thanks to Dale Simpson and John McMullen for access to and metadata from the Acadia site. We also thank Jean Bousquet from Canada Research in Chair Forest Genomics (Université Laval) for sharing their black spruce SNP resources. We acknowledge all the people who were involved in seed collection, curation, and plantation establishment during the 1960s and 1970s, as well as colleagues involved in the maintenance of sites and data collection and who hence helped to create and foster this important resource over the decades.

## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2025.123129.

## Data availability

The data and code that support the findings of this study are available on figshare at (https://doi.org/10.6084/m9.figshare.25772784.v1).

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