The phenotypic and genetic effects of drought-induced stress on apical growth, ring width, wood density and biomass in white spruce seedlings

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Abstract

Forest plantations play an important role in maintaining a supply of high-quality timber from managed forest. With an expected increase in the prevalence of drought in some forested areas, climate change increases concerns about future seedling growth. A promising approach to promote the suitability of plantation seedlings to current and future climate would be to use variation in growth and wood traits of trees under drought as selection criteria in tree breeding programs, especially at a young stage when they are most vulnerable to drought. We evaluated the genetic control of the growth and wood density response of white spruce clonal seedlings submitted to various drought conditions in a greenhouse experiment. By varying the watering treatment of 600 two year-old seedlings from 25 clones, we simulated three levels of drought-induced stress during two growing seasons. Apical and radial growth decreased markedly as the intensity of drought increased, whereas wood density tended to increase. We also developed a woody biomass index composed of wood density and ring area, which was observed to decrease slightly with increasing drought. There was important variation in all traits among clones and heritability tended to decrease with the intensity and duration of drought-induced stress, mainly for wood density and radial growth. However, the heritability of apical growth tended to increase under drought conditions. Our results show that the response of young white spruce clones to drought is highly variable, and together with the significant levels of heritability noted, the results indicate that multi-trait genetic selection for drought stress response at a young age could represent a promising approach to increase resilience to drought.

Keywords White spruce · Drought-induced stress · Heritability · Genetic variation and selection · Wood density

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Introduction

An increased frequency of heat and drought stress is projected to occur in North America's boreal forests (Shukla et al. 2019). The combined effects of lower precipitation and higher temperatures lead to drought-induced stress for drought-intolerant species, which have been shown to reduce the growth rate and vigor of tree species and forests ecosystems (Shafer et al. 2001; Shukla et al. 2019; Allen et al. 2010; Pederson et al. 2012; Price et al. 2013; Choat et al. 2018; Boucher et al. 2019; Depardieu et al. 2020). Forest managers should therefore consider this factor in the choice of best adapted seedlings used for plantations.

Planting seedlings with improved resistance to drought may offer a solution to increase survival and improve the resilience of forest plantations because seedlings are particularly vulnerable to drought during many years after plantation, given that they lack a well-developed root system. However, before implementing this strategy at the operational scale, the performance of the genetic material improved for current climatic conditions needs to be tested under conditions that will emulate future more adverse conditions. In this context, studies have been initiated on the growth performance of improved spruce planting stock under predicted conditions of elevated CO_2 increased temperature, drought conditions and climate instability at the juvenile and more mature developmental stages (e.g. Wang et al. 1994; Carles et al. 2015; Ainsworth 2016; Benomar et al. 2022; Laverdière et al. 2022).

The response of trees to drought conditions can be complex. Drought stress directly or indirectly influences seedling growth by inhibiting cell growth, stomatal conductance and metabolic activity due to reduced photosynthesis and carbohydrate availability (Dreyer 1997). Maintaining leaf water potential above critical values is often considered an adaptation and resistance response to drought (Lüttge and Scarano 2004; Ditmarová et al. 2010). The results of Lüttge and Scarano (2004) show that the drought response of Norway spruce seedlings includes a number of physiological and biochemical changes that enhance the seedlings' ability to survive and thrive during drought periods. In addition to the expected reduction of growth rate due to drought-induced stress, trees growing under severe drought can undergo modifications of their xylem structure (Barber et al. 2000). For example, several studies reported an increase in wood density linked to a decrease in availability of soil water (D'Arrigo et al. 1992; Filipescu et al. 2014; Xiang et al. 2019). Such an increase in wood density is generally assumed to be a consequence of the negative correlation between radial stem growth and wood density. Unlike these studies, Balducci et al. (2015) observed a reduction of wood density as a result of drought stress. The authors suggested that this was attributable to the limited availability and allocation of resources due to the effects of drought on photosynthesis. Differences in drought severity, duration and seasonality may also explain such discrepancies between results (Franceschini et al. 2012; Xiang et al. 2019).

Wood density is one of the most widely used indicators of wood quality due to its positive correlation with other physico-mechanical characteristics of the material (Zobel 1989; Zobel & Van Buijtenen 1989; Saranpää 1994; Alteyrac et al. 2006). Given that wood density could be affected by drought and that it is correlated with other wood traits, it is important to predict and limit the impact of drought-induced stress not only on seedling growth but also on wood properties.

In addition to being used as an indicator of wood quality, wood density is also a key functional trait of trees through its link with both the structural and water transport functions of the xylem (Chave et al. 2009). For instance, due to the relatively constant

density of the woody cell wall, a high wood density is indicative of a low volumetric proportion of tracheid lumens in conifers. Studies have also reported negative correlations between wood density and lumen diameter in conifers (Hannrup et al. 2001; Rathgeber et al. 2006). Trees may thus respond to drought through changes in wood traits, which can help maintain a favorable water balance in the xylem (Tyree and Ewers 1991). However, Chen et al. (2017) also reported that growth climate relationships vary across populations and environmental gradients. Drought response may also vary with the age of the trees, for instance during the complex and well-described transition from juvenile to mature wood in spruces (e.g. Koubaa et al., 2000, 2005; Lenz et al. 2010, 2011; Soro et al. 2022). This variation offers the potential for genetic studies investigating strategies of adaptation and possibilities for selection.

White spruce wood is valued because of its desirable fiber characteristics, especially when compared to companion species such as balsam fir (*Abies balsamea* (L.) Mill.) (Zhang and Koubaa 2008; Hassegawa et al. 2020). Its high plasticity also makes it a highly reforested species in various silvicultural systems across the boreal forest of North America (Nienstaedt and John 1990). Thus, the importance of white spruce makes genetic improvement programs for this species among the most advanced in Canada (Mullin et al. 2011). Initially, genetic improvement programs focused on rapid tree growth, and therefore aimed to increase the volume growth and stem straightness of future plantations (Corriveau and Boudoux 1971; Li et al. 1993, 1997). Wood properties received little consideration in the early implementation of these programs (Zhang and Morgenstern 1995). More recently, quantitative genetics studies investigated the potential for wood properties such as wood density to be included in genetic selection programs (Lenz et al. 2010; McLean et al. 2016). Taylor et al. (1982) reported a negative correlation between wood density and growth rate in white spruce, and this correlation was later found to vary between families with the negative correlation being low in some families or individuals (Zhang and Morgenstern 1995). Since then, genetic correlations between growth and wood traits have been estimated over different cambial ages with the objective to optimize both growth and wood quality traits in genetic improvement programs (e.g. Lenz et al. 2010, 2011).

The heritability, or genetic control, of desired traits is a key parameter for selection of well performing trees and their propagation in tree breeding programs. Together with trait variation and selection intensity, the level of heritability will largely determine genetic gain and the superiority of next generation seedling stock. Consequently, if traits such as growth and wood density under intense drought-induced stress show sufficiently high heritability and variation, selection for those traits may be considered so to increase drought resilience in future plantations, especially those at the young age when seedlings are most sensitive to drought stress. Albeit recent studies on well established trees in long-term field experiments (Depardieu et al. 2020, 2021; Laverdière et al. 2022), it is also notable that relatively little is known about the role of genetic variation in resistance to drought in conifers, especially at the young age where trees are most vulnerable to drought conditions.

In this study, we used white spruce seedlings from various clones growing under controlled conditions, and tested their performance under different levels of drought-induced stress. Our objectives were to (1) assess the phenotypic and genetic variation in drought response among young white spruces in terms of growth and wood density and (2) evaluate the genetic control of wood and growth traits under long-lasting drought, which is an essential information for decisions regarding genetic selection and spruce breeding in the context of rapid climate change.

Materials and methods

Genetic material and seedling production

The Province of Québec has integrated multiclonal reproduction into their white spruce breeding and reforestation programs in the early 2000s in order to benefit from the genetic gain resulting from non-additive effects (Perron et al. 2018); accordingly, the Ministère des Forêts, de la Faune et des Parcs of Québec (MFFP) kindly provided the clonal seedlings for this research. The material originates from direct crosses of the first breeding cycle. Parents had previously been selected for superior growth from provenance trials and seed from well-performing crosses was multiplied by somatic embryogenesis (SE). For operational production, clonal SE emblings are grown into hedges to multiply the number of trees per clone in a cost-efficient way (Perron et al. 2018). Cuttings were then cultivated under an unheated polyethylene tunnel during their first growing season and outdoors during their second growing season under standard nursery practices at the MFFP forest tree nursery of Saint-Modeste, Quebec, Canada. More details relating to usual irrigation and fertilization practices during seedlings production in Québec provincial nurseries can be found in Lamhamedi et al. (2006) for example. Hence, the material used in this study represents a sample of genetic lines that are operationally deployed for reforestation. Clones are retained for good SE induction and reproduction capacity in the SE laboratory and cover a range of average to superior estimated genetic gain for height growth, in order to maintain genetic variation in multiclonal plantations.

Experiment design

For this experiment, we used 24 seedlings from 25 white spruce clones for a total of 600 seedlings. Trees were 2-years old at the beginning of the experiment, which lasted for two growing seasons and was conducted in a greenhouse at Université Laval, Québec Canada. The greenhouse was divided into eight blocks to control for potential micro-environmental variation. Blocks were of same size with 75 seedlings per block. Each block contained the three treatments (control, moderate and severe drought) with one seedling for each of the 25 clones assigned randomly to each treatment (one-tree plot), for a total of 75 clonal seedlings per block. The random assignment of seedlings was done using the random function of the R software.

The planting substrate was composed of a mixture of peat (3 units), perlite (1 unit) and vermiculite (1 unit). This mixture was made to obtain an aerated and not nutrient-rich substrate. We added fertilizer in the form of nitrate (N) 44%, phosphorus (P) 20% and potassium (K) 36%. Spread over 19 weeks, a total of 2.8 g of NPK per plant was provided. The same amount of fertilizer was used for all seedlings regardless of the treatment, to avoid any effect related to fertilization. Wood produced during the first years of a tree's life contains so-called "flexure wood" (Telewski 1989), which has similar properties to compression wood. To ensure the production of normal wood even at an early age, the seedlings were planted at an angle of 45° following a similar strategy to that used by Apiolaza et al. (2011a, 2011b). Using this strategy, compression wood was produced on the lee side of the stem while normal wood was available for our analyses on the opposite side. The experiment consisted of three treatments. To determine optimal watering levels, we first determined the field capacity of the substrate by comparing saturation mass and dry mass.

From the dry mass of the substrate, we then determined the volume of water to be added to reach the desired humidity level for each of the treatments. Previous studies showed that the optimum content of soil water for spruce growth ranges between 60 and 80% of maximum capillary capacity (Kutílek and Nielsn 1994; Tužinský 2002). A similar study carried out on Norway spruce seedlings submitted to drought stress used 60–80% of maximum capillary capacity for control treatment, 40–59% of maximum capillary capacity for mild drought stress and 20–39% of maximum capillary capacity for severe drought stress (Ditmarová et al. 2010). So, we watered the first treatment (control) (80–100% of the maximum capillary capacity) to avoid drought-induced stress while the other two treatments were subjected to moderate and severe drought stress. For the moderate drought stress treatment, the substrate was maintained at an intermediate humidity i.e. between 40 and 50% of the substrate maximum capillary capacity. For the severe drought stress treatment, it was decreased to between 20 and 30% of the maximum capillary capacity of the substrate. The decrease in soil water potential is usually established by progressive decline or immediate interruption of the watering of the seedlings. However, the difficulty in controlling the water potential of the substrate represents an essential limitation of this approach. Indeed, in our experimental set-up, the severity of water stress was determined by the rates of water evaporation at the soil surface and consumption by the seedlings. Thus, during the first two weeks of the experiment, 10-plant containers of each treatment were weighed every two days to determine the amount of water since the dry weight of the substrate was known. After two weeks, we managed to implement a watering method, which consisted of watering the seedlings of the control treatment every three days, those of the moderate treatment every six days and those of the withdrawal treatment every nine days. Each plant container had small holes at the bottom so that excess irrigation water or fertilizer solution could drain freely out of the system. Treatments were applied throughout the 2018 and 2019 growing seasons. The seedlings spent autumn, winter and early spring outdoors. During this period, the pots containing the seedlings were placed on the ground and were not covered. During the two growing seasons, the light time per day was set to 16 h in the greenhouse while temperature was set to 23 °C during the day and 19 °C at night. Three seedlings of clones 208 submitted to the severe drought stress treatment died during the second growing season (2019).

Apical growth measurement and microscopic dendrochronology

Apical growth was measured at the end of both growing seasons using a graduated ruler. The unit of measurement was the centimeter and measurements were made to the nearest millimeter. Only the current year increment was measured. At the end of the experiment, all seedlings were cut at the level of the collar using pruning shears to extract a sample of 2 cm from the largest part of the stem. The samples were sanded to facilitate the measurement of rings. Ring width was measured to the nearest hundredth of a millimeter for both growing seasons using an optical microscope. Ring width measurements were made in the direction of the normal wood i.e. opposite to the compression wood.

Anatomical sections and wood density measurements

For wood density measurements, we made 30-μm thick sections of the stems using a microtome. Sections were first saturated with water by successive cycles of vacuum and pressure. Once saturated, samples remained in water for at least 48 h before performing the

microtome cuts. Sections were bleached, then colored with safranin and mounted on strips. Images were taken using a camera connected to a microscope at 400×magnification. A picture was taken of each ring and then analyzed using the WinCell software (Regent Instruments®) to estimate the proportion of the cell wall per unit area. The analysis of images in the WinCell software was based on the colors and contrasts between the lumen and the cell wall. Assuming a 1500 kg m^{-3} cell wall density (Schniewind 1989; Unger et al. 2001), the software could estimate wood density from anatomical sections. From the estimated wood density and ring area, we produced a woody biomass index, that is, wood density times ring area. Ring area was measured from half over the entire surface of the ring opposite to wood compression, i.e. half of the stem disc.

Drought stress response index

The measurements described above allowed us to determine the mean response of clones to each treatment in terms of apical growth, radial growth (ring width), wood density, and woody biomass index. We then ranked the clones in order of performance for each trait and treatment. As the performance varied between traits, we developed a response index for clones considering all traits and all treatments combined. This procedure allowed to identify the clones that had best ranks for each of the treatments (control, moderate and severe drought stress) and that for all traits. In the calculation of the index, twice the weight of trait responses to control and moderate drought was given to trait responses to severe drought in order to identify clones that seem best adapted to intense drought conditions. The clone with an ideal drought stress response would rank first for the control treatment as well as under moderate and severe drought-induced stress treatments for all traits (apical growth, radial growth, wood density and woody biomass index). The response index was calculated as follows:

$$P = \sqrt{\sum_t \left(R_{t,C}^2 + R_{t,MD}^2 + 2R_{t,SD}^2 \right)} \qquad (1)$$

where P is the drought response index, R is the clone rank-order and t is the trait; C represents the control, MD the moderate drought-induced stress response and SD the severe drought-induced stress response.

Statistical analysis

All statistical analyses, graphs and charts were produced using the R open-source software (R Core Team 2020). We used linear mixed-effect models to assess the impact of treatment and year of apical growth, radial growth, wood density and biomass index using treatments as fixed effect, and block and clone as random effects, with the lme4 package (Bates et al. 2015). Tukey's HSD tests were used to determine which treatments were significantly different from each other, with $P < 0.05$ as the statistical significance threshold). The correlation between traits was evaluated using Pearson correlations in R.

Genetic analysis

Variance components for the estimation of heritability as well as breeding and genetic values (BLUP, Best Linear Unbiased Prediction) were estimated for each trait with

mixed-effects models using the ASReml-R v.4.0 (Butler et al. 2017). Considering that several clones shared parents, we decided to use an animal model framework to separate as much as possible the additive genetic variance from the reminder non-additive genetic variance. For analyses of individual growing seasons, models were of the form:

$$y = X\beta + Z_1a + Z_2b + Z_3c + e \tag{2}$$

where y is the phenotype that represents the different analyzed traits, i.e. apical growth, radial growth, wood density and biomass index; β represents the vector of fixed treatment effects and the overall mean, a is the random additive genetic effect nested in each treatment, with $a \sim N(0, V_A \otimes A)$; b is the random block effect $b \sim N\left(0, \sigma_b^2 I_b\right)$; c is the random clone effect nested in each treatment, which is combining the non-additive genetic effects including dominance and epistasis, with $c \sim N(0, V_C \otimes I_C)$; and e is the residual term, with $e \sim N(0, R)$, where R is a block diagonal matrix specifying a heterogeneous error variance structure for the three treatments:

$$R = \begin{array}{ccc} I_{e1}\sigma_{e1}^2 & 0 & 0 \\ 0 & I_{e2}\sigma_{e2}^2 & 0 \\ 0 & 0 & I_{e3}\sigma_{e3}^2 \end{array}$$

where I_{e1}, I_{e1} and I_{e3} are identity matrices corresponding to the number of individuals in each treatment, and σ_{e1}^2, σ_{e2}^2 and σ_{e3}^2 are the residual variances associated with each treatment. A is the pedigree-based relationship matrix quantifying relatedness between clones from sharing common parents. I_b and I_c are identity matrices of their proper dimension. V_A and V_C are 3×3 variance–covariance matrices defined by the additive genetic and clonal correlations between treatments and unique additive and clonal variances respectively for each treatment (i.e. CORGH in ASReml-R). The symbol $\otimes$ refers to the Kronecker product. The matrices X, Z_1, Z_2 and Z_3 are incidence matrices of their corresponding effects.

For each year, individual broad-sense heritability that estimates the proportion of the total genetic variance in the phenotypic variance was calculated as:

$$H_{ind}^2 = \frac{\left(\sigma_a^2 + \sigma_c^2\right)}{\left(\sigma_a^2 + \sigma_c^2 + \sigma_e^2\right)} \tag{3}$$

where H_{ind}^2 is the individual broad-sense heritability, σ_a^2 is the additive genetic variance within treatment, σ_c^2 is the non-additive genetic variance, and σ_e^2 is the residual variance within treatment. Standard errors of heritability estimates were obtained using the delta method (vpredict function, 4.0, Wolak 2012).

To estimate genetic correlations between traits, bivariate models were fit for all pairs of traits in ASReml-R using the following model:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = X\beta + Z_1a(t) + Z_2b + Z_3c(t) + e \tag{4}$$

where y_1 and y_2 are the stacked vectors of observations for traits 1 and trait 2; β represents the vector of fixed effects, including an overall mean for each trait; a is the random additive genetic effect within trait, with $a \sim N(0, A \otimes V_A)$; b is the random block effect for each trait and c is the random clonal effect within trait, with $c \sim N(0, I_c \otimes V_C)$; and e is the error term, with $e \sim N(0, I_e \otimes V_R)$. A is the additive relationship matrix and I_c and I_e are identity matrices of their proper dimension. V_A, V_C and V_R are 2×2 variance–covariance matrices

as defined by the correlation of effects between traits (r_a, r_c and r_e, respectively) and unique variances for each trait. The matrices X, Z_1, Z_2, and Z_3 are incidence matrices of their corresponding effects. Genotypic (genetic) correlations were calculated for the combined additive and non-additive genetic variance.

Spearman's rank correlations (Spearman's ρ)

To assess the stability of clone rankings between treatments, or conversely the amplitude of genotype-by-treatment interactions commonly called genotype-by-environment interactions (GxE), we calculated Spearman's rank correlation coefficients based on clonal mean trait values. The cor.test function in R was used to calculate Spearman's ρ.

Results

Comparisons between treatments

Figure 1 shows the response of seedlings to different levels of drought-induced stress over the two consecutive growing seasons. We observed reductions of values for all traits related to growth (apical and radial growth, biomass index) as both the intensity and exposure time of the drought stress treatments increased. Conversely, wood density tended to increase with the intensity of the drought stress treatment, although a significant effect was only detected after the second growing season. This effect was more significant for the severe drought stress treatment (control vs severe drought, $P < 0.001$) than for the moderate drought stress treatment (control vs moderate drought,
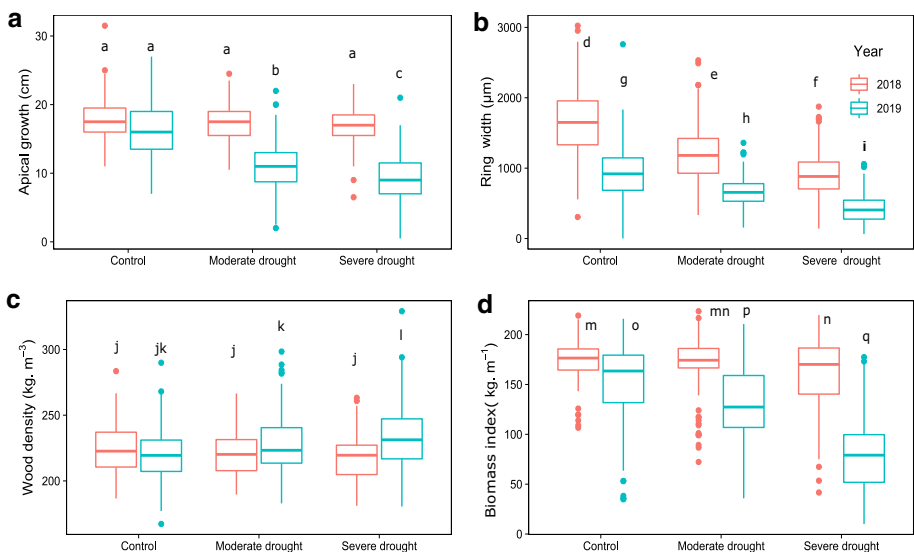

Fig. 1 The effects of drought-induced stress treatments during two consecutive growing seasons (2018 and 2019) on the different growth and wood traits. The color represents the different growing seasons, i.e. 2018 in red and 2019 in blue

$P < 0.01$). The effect of drought-induced stress on most traits between the two drought stress treatments was also significant (moderate drought vs severe drought, $P < 0.01$ for all traits). For apical growth and the biomass index, a significant effect was only measured after the second growing season for both moderate drought and severe drought stress treatments ($P < 0.001$) whilst ring width decreased significantly with increased drought stress in both years ($P < 0.001$).

Overall, phenotypic correlations between traits (Fig. 2) were weaker compared with their genetic counterparts (Fig. 3). The phenotypic correlations between traits as well as their genetic counterparts were very similar between the two consecutive growing seasons, which indicates that the drought exposure time had little effect on the relationships between traits. However, there was a decrease in genetic correlations between traits for the second growing season for the severe drought treatment, which represented the most intense drought effects afflicting the seedlings. Low to moderate positive phenotypic correlations were observed between wood density and radial (ring width) and apical growth (Fig. 2), while the corresponding genetic correlations were also positive but much higher (Fig. 3). The genetic correlations ranged from 0.31 ± 0.14 to -0.95 ± 0.21 from 2018 to 2019 between apical and radial growth, indicating a reversing of the trend with the second growing season including for the control treatment (Fig. 3 and Supplementary Table S2). This trend could not be noted for phenotypic correlations (Fig. 2 and Supplementary Table S1). As expected, the biomass index was positively correlated to wood density and growth traits but correlations were generally higher at the genetic level, with decreasing values of genetic correlations for the severe drought stress after two growing seasons as mentioned above (Figs. 2 and 3).

Because the mean rankings of clones by treatment were very similar for the two consecutive growing seasons, we only present here results obtained after the second growing season (Fig. 4). Although all clones were sensitive to drought-induced stress, responses varied largely among them. The three best performing clones as identified by the drought response index P (see Formula #1 in Materials and Methods) followed different patterns with each having a distinctively better performance for one or two traits. Clone 150 was among the top performers in terms of wood density and biomass index. Clone 11 was among top performers for apical growth, especially under drought conditions. Clone 85 also performed well in terms of apical growth, but also ranked well for all variables without standing out. In general, the apical growth of the three best performing clones seemed to be less affected by drought than for most other clones.

Genetic control

Given the large inter-clonal differences noted above, we estimated the heritability of traits to evaluate the level of genetic control in trait expression and the potential of selection for improving performance under drought stress. Individual broad-sense heritability estimates (H^2) varied among traits (Fig. 5 and Supplementary Table S3). The heritability for growth traits, whether radial (0.12 ± 0.07–0.57 ± 0.24) or apical (0.15 ± 0.10–0.45 ± 0.17), was generally not as high as that detected for wood density (0.24 ± 0.17–0.72 ± 0.26) or for the biomass index (0.04 ± 0.02–0.58 ± 0.24). Drought conditions also appeared to either result in slight decrease or increase in genetic control depending on the trait. Under drought-stress conditions, there was a reduction in heritability for ring width, wood density and biomass index, while there was a slight increase for apical growth under moderate drought
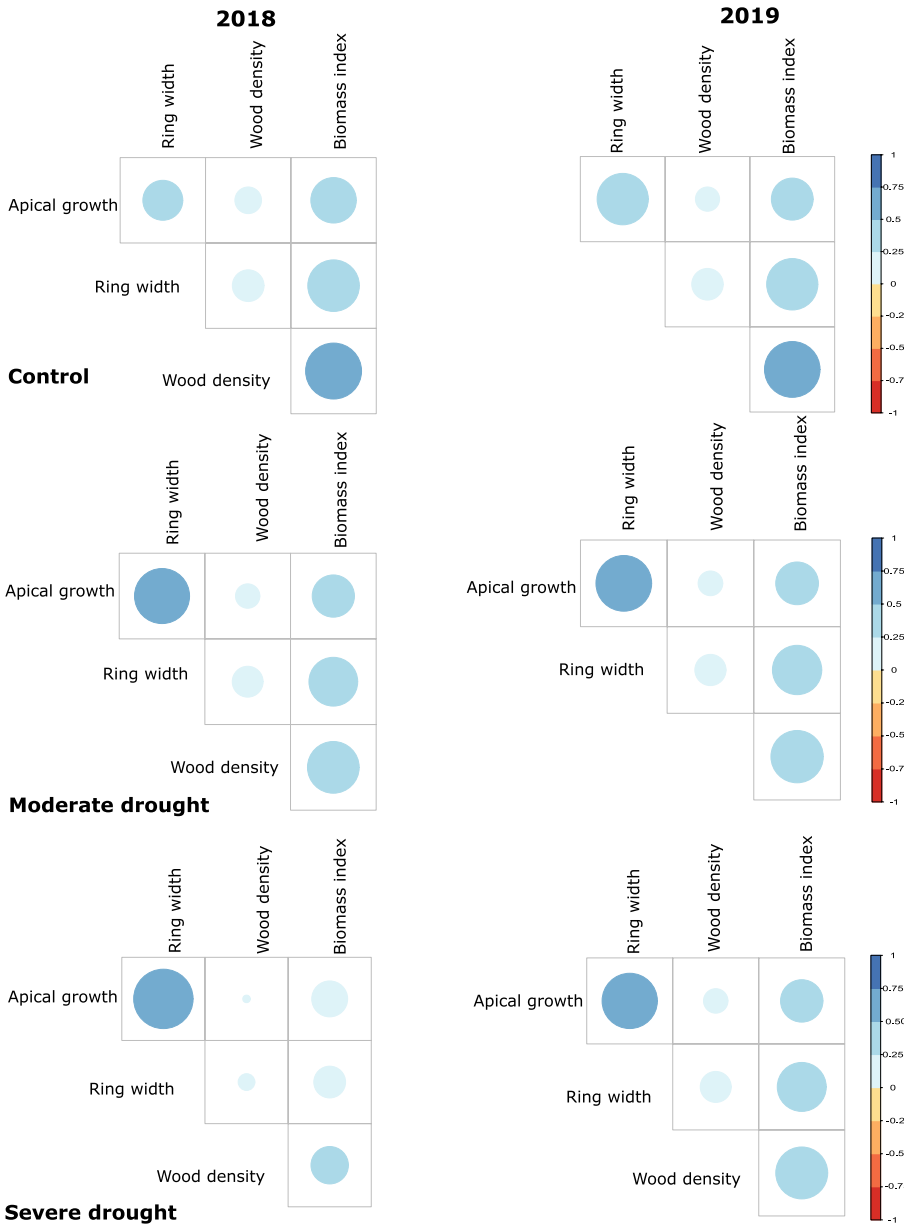
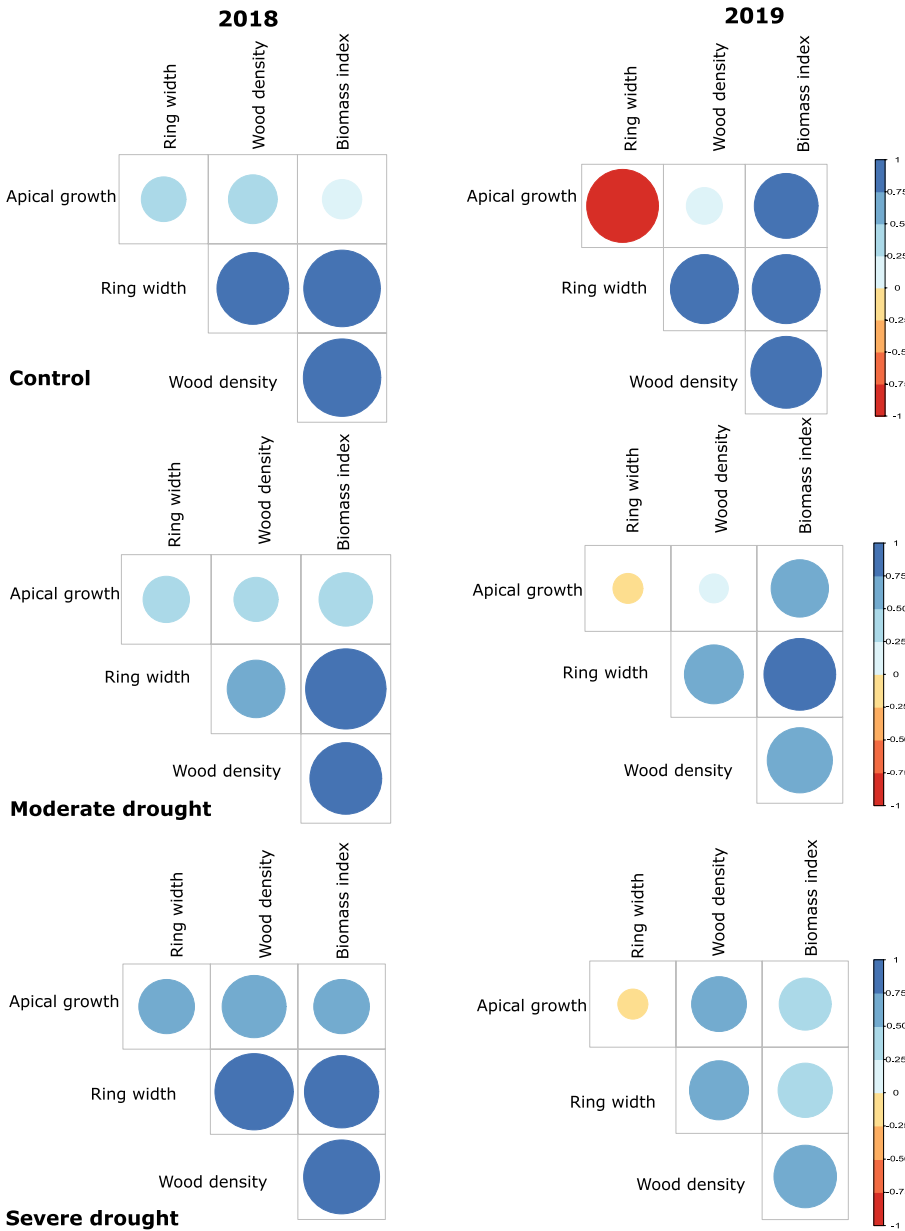**Fig. 2** Phenotypic correlation matrices between the different wood and growth traits for each growing season and treatment, i.e. the control, moderate and severe drought stress treatments. The higher the correlation, the larger the size of the dot and the intensity of the color. The color gradients indicate the direction and level of correlations (blue for positive correlations and red for negative correlations). Corresponding values and their standard errors can be found in Suppl. Table 1

Fig. 3 Genetic correlation matrices between the different wood and growth traits for each growing season and treatment, i.e. the control, moderate and severe drought stress treatments. The higher the correlation, the larger the size of the dot and the intensity of the color. The color gradients indicate the direction and level of correlations (blue for positive and red for negative correlations)

conditions. Broad-sense heritability estimates were higher than narrow-sense heritability estimates, especially for apical growth, indicating that a sizeable portion of genetics effects were of non-additive nature (Supplementary Table S3).
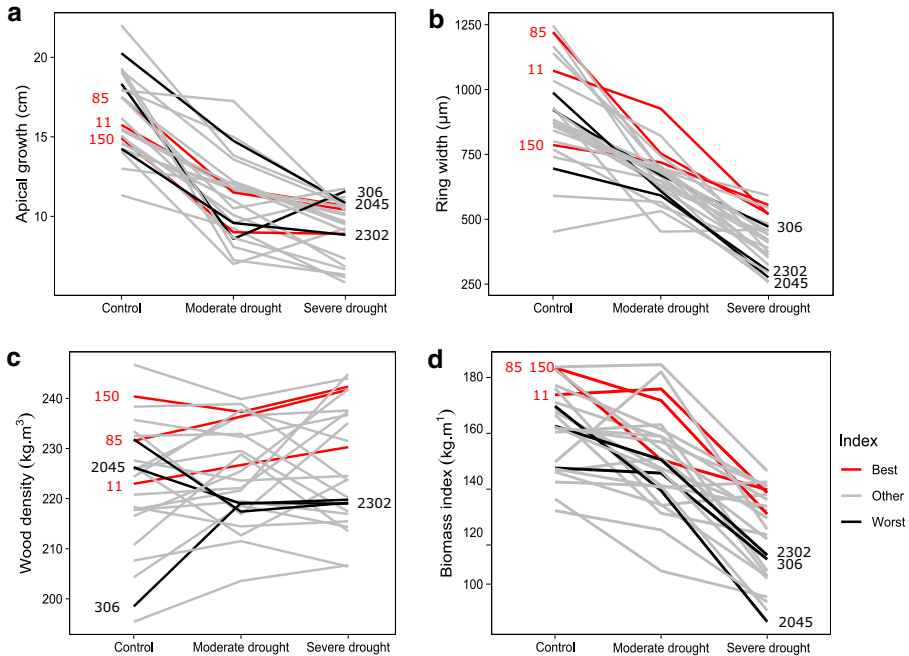
Fig. 4 Mean response of the 25 clones for each drought stress treatment after two growing seasons for the different wood and growth traits. The red line shows the three best clones based on the multi-trait response index *P* whereas the black lines represent the worst three clones. The grey lines represent all other clones

Spearman's rank correlations of clonal values between the different treatments considered both additive and non-additive genetic effects and showed little or no difference in clone ranks between the two growing seasons except for apical growth between the control and moderate drought treatments. (Fig. 6). Correlation coefficients were high (> 0.85) for clone ranks obtained between the control and moderate drought stress treatments for all traits, except a moderate correlation (0.50) for apical growth after the second year, indicative of stronger genotype-by-treatment effects (GxE). Correlation coefficients between the control and the severe drought stress treatment were high (0.73–0.99) for all traits, indicative of reduced GxE effects. Correlation coefficients between the two stress treatments were high (0.82–0.99) for all traits, again indicative of small GxE effects.

Discussion

Treatment effects and correlations between traits

As expected, the drought-induced stress treatments led to a decrease in biomass index, radial and apical growth of seedlings (Fig. 1). Many studies have shown that tree growth is usually limited by the availability of soil water and that any drought-induced stress affects physiology (Hogg and Schwarz 1997; Escós et al. 2000; Shafer et al. 2001; Shukla et al. 2019; Allen et al. 2010; Pederson et al. 2012; Price et al. 2013; Chen et al. 2017). For instance, stomatal closure is the first reaction to drought stress in most plants, and it
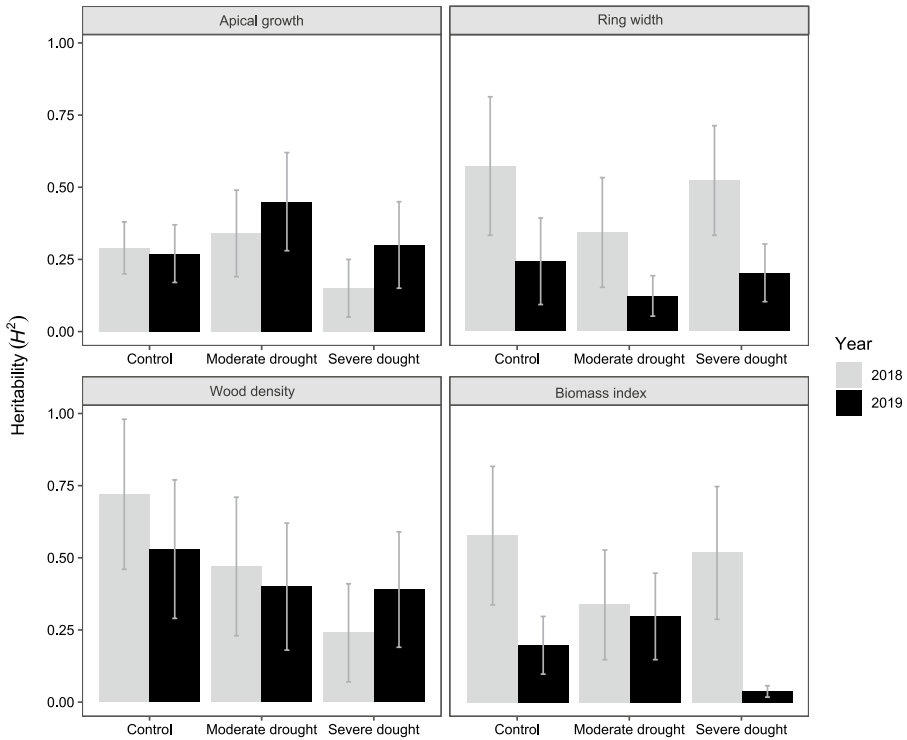
Fig. 5 Individual tree-level broad sense heritability (H^2) for apical growth, ring width, wood density and biomass index. After one (in gray) and two (in black) growing seasons. Error bars represent the standard errors. Provisional genetic gain estimated when selecting the top 5% of trees can be found in Supplementary Table S3

prevents water loss from transpirational pathways (Pirasteh-Anosheh et al. 2016). Several studies showed that the drought response of spruce seedlings includes several concurrent physiological and biochemical changes: these changes usually improve the ability of seedlings to survive and grow during drought periods, but only up to a certain extent (Kutílek and Nielsn 1994; Ditmarová et al. 2010).

Unlike apical and radial growth as well as biomass index, we noted that wood density increased slightly with a long-term exposure to drought-induced stress, as noted after the second growing season of drought-induced stress (Fig. 1). In a drought-stress situation, it is likely that seedlings mobilize more resources for cell wall formation despite having limited resources for growth. These results are similar to several studies showing a negative correlation between wood density and ring width (Fritts 2001; Bouriaud et al. 2005; Jyske et al. 2009; Gardiner et al. 2011). Other studies indicated that strategies investing in cell walls appear to limit the risk of embolism, because a stem with thicker cell walls and reduced lumen diameter would have greater mechanical strength and lower vulnerability to embolism (Pittermann et al. 2006; Hacke and Jansen 2009). The observation that the effect of drought-induced stress on wood density mostly materialized after a longer exposure duration time of two growing seasons is also in line with previous studies that showed that wood density in a given year is influenced by the ecophysiological and environmental conditions of the previous year (Bouriaud et al.
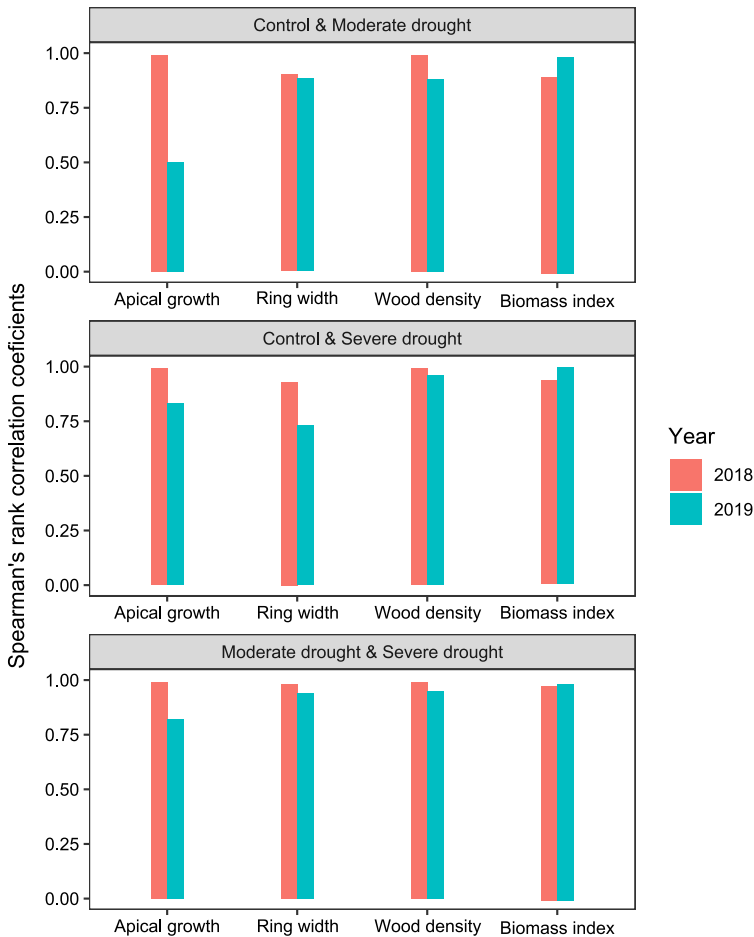
Fig. 6 Spearman's rank correlation coefficients of clonal values for the studied wood and growth traits between the various drought-induced treatments tested in a pairwise fashion, and illustrating the relative consistency of clonal response among treatments. Correlations for 2018 in red and for 2019 in blue

2005; Xiang et al. 2019). Besides, previous studies indicated that prolonged periods of drought-induced stress can alter xylem resource allocation (Martínez-Vilalta et al. 2012; Hereş et al. 2014).

Significant differences were observed for apical growth, ring width, and biomass index between the first and second growing seasons for the two drought-induced treatments, in line with expectations of reduced growth due to cumulative detrimental effects. However, a similar though much less obvious trend was noted for the control treatment, with ring width being the most negatively affected after two growing seasons (Fig. 1). This is likely explained by the fact that N, P, and K were added to the substrate in 2018 at the start of the experiment without being renewed at the start of the second growing season. Nevertheless, the observed phenotypic correlations between traits remained rather similar after the first or the second growing season, with apical growth, ring width and biomass index all being positively related (Fig. 2).

Large differences could be noted between correlations at the phenotypic level (Fig. 2) and the corresponding ones at the genetic level (Fig. 3). Such different patterns indicate that it was highly useful in this study to disentangle the genetic effects from the rest of the total variation observed under the various treatments and years of observations. While correlations between wood density and growth traits were marginally positive at the phenotypic level (Fig. 2), the corresponding genetic correlations were quite all highly positive, especially between wood density and ring width and biomass index after the first growing season of drought-induced stress, and also to a lesser extent after the second growing season (Fig. 3). This trend indicates that genetically, at the seedling stage, elements controlling for growth traits and those for wood formation are coordinated to some extent, even under conditions of drought stress, in contrast to the negative relationship usually observed between growth and wood density traits under drought stress at a later age, or at the cumulative lifespan level (Depardieu et al. 2021; Laverdière et al. 2022). Reductions in radial growth (Barber et al. 2000; Mood et al. 2021) and apical growth (Swidrak et al. 2013) have been previously reported under drought stress conditions but genetic effects could not be disentangled from environmental effects. Regarding the balance between apical and radial growth, we observed a reversing of trend between phenotypic and genetic correlations: while phenotypic correlations were positive, genetic correlations were negative after the second growing season of drought-induced treatment, even for the control treatment. This trend indicates that, under limited growth conditions including water stress but also lack of fertilizing treatment at the onset of the second growing season, resource allocation was altered with reduced radial growth compared to apical growth. The study of wood anatomical traits such as lumen diameter and tracheid shape should help to better understand changes in growth allocation that occurred after the two growing seasons under normal and water stress conditions.

Drought stress response index

The drought stress response index (P) that we developed based on the four growth and wood traits that we assessed (see Formula #1, Materials and Methods) may be used to classify and select clones or other types of genetic materials that are likely to maintain good growth and wood density under normal but also drought stress conditions. As the response of clones to treatments was not uniform among traits, the three best clones identified based on the drought stress response index were not optimal for all measured traits. In the context of operational tree breeding, genetic selection for multiple traits generally results in lower genetic gain for each trait compared with single-trait selection, because correlations between traits can be weak or negative. However, these clones would remain good candidates for selection when considering the multiple traits assessed in this study.

In the context of operational tree improvement of tree response to drought stress at the juvenile stage, a much larger number of clones, families or other genetic material would need to be screened in order to maintain genetic diversity in reforestation stock, than that screened for this present proof of concept study. The fact that each of these better clones performed well for one trait than another one suggests that different strategies may allow clones to endure drought stress. Similar results observed in previous studies on drought stress response in white spruce (Bigras 2000, 2005; Depardieu et al. 2020; Laverdière et al. 2022) also revealed different responses to drought among families and among widely distributed seed sources (provenances).

In addition, the apical growth response of white spruce clones to severe drought stress was highly variable. In general, Spearman's rank correlations of clonal values between the control and the drought-stress treatments were high for most traits (Fig. 6), indicating that good performance of clones in normal conditions would correspond to relatively good performance under water stress conditions. A similar trend was observed in comparative field plantation experiments with more mature white spruce material where good response to drought conditions was genetically correlated positively with lifespan tree vigor such as measured by cumulative growth (Depardieu et al. 2021; Laverdière et al. 2022). However, two of the three worst clones based on the drought stress response index had a very good apical growth in the control treatment but weaker growth under drought stress (Fig. 4), which translated in a weaker Spearman's rank correlation of clonal values between the control and moderate drought stress treatment for this trait (Fig. 6). Therefore, selecting for only one trait in normal conditions might lead to less than optimal choice of material for future reforestation and survival under more drought conditions.

Among coping mechanisms in conditions of water limitation or drought stress, trees may close their stomata to reduce evapotranspiration, change the anatomy of xylem cells to produce thicker and denser cell walls, or produce cell walls with a lower and therefore more rigid microfibril angle (Martínez-Sancho et al. 2017). Each of these strategies may come with potential trade-offs. For instance, stomatal closure reduces photosynthesis and can increase leaf temperature (Pirasteh-Anosheh et al. 2016; Urban et al. 2017) to a point that can be lethal. A denser cell wall implies a higher photosynthate investment, which may come at the expense of growth even if, at the genetic nor phenotypic level, we did not observe a negative relationship between growth parameters and wood density, even in drought stress conditions. Although our drought stress response index may allow to assess seedling performance in a more comprehensive manner than a trait-by-trait assessment, a current limitation of this study is that it provided little information about the likelihood of survival of seedlings under drought stress. The few seedlings that died during the course of this experiment belonged to clones 239 (3 seedlings) and 2302 (2 seedlings). Out of 25 white spruce clones assessed, these clones ranked 19th and 25th based on the drought stress response index and they ranked 23rd and 25th for radial growth, suggesting that seedlings with too little radial growth may have higher risk of mortality under severe drought stress conditions. Future work should thus aim to identify clones and other genetic material that are most likely to survive more extreme drought stress conditions than those tested in this study. Also, studying anatomical wood traits in relation to growth parameters in the present juvenile material exposed to drought stress would help understand resource allocation and the mechanisms implicated in juvenile stress response.

Trait heritability

Broad-sense trait heritability estimates were always higher than narrow-sense heritability estimates, especially for apical growth whether under control or drought-induced stress conditions, indicating the added efficiency of clonal selection over family selection for genetic improvement, particularly for this trait. Broad-sense heritability estimates for the different traits ranged from low to high depending on the trait. By low, we refer to H^2 below 0.30 and by high, equal of above 0.50 (Namkoong 1970). The significantly higher heritability estimates observed for wood density compared with growth traits had been reported earlier from studies at the more mature stage, and heritability estimates were consistent with values reported for similar traits in the literature for tree species from temperate and

boreal regions (Corriveau et al. 1991; Ivkovich et al. 2002; Beaulieu et al. 2006; Beaulieu and Bousquet 2010). Heritability for wood density was reported to be low (narrows-sense heritability $h^2 = 0.15$ for earlywood) in very juvenile white spruce growth rings (Lenz et al. 2010). However, our experimental approach made it possible to limit the effect of juvenility and obtain heritability estimates similar to estimates obtained in more adult wood. Our approach was inspired by the work of Apiolaza et al. (2011a, b) who obtained similar results when analyzing separately compression wood and opposite wood from systematically tilted radiata pines. The authors concluded that their approach reduces noise from the random presence of compression wood and opposing wood in juvenile stems, a type of wood referred to as flexure wood (Telewski 1989).

We observed a general reduction in heritability estimates with the intensity and duration (after one or two growing seasons) of the drought-induced stress for all traits except for apical growth to some extent (Fig. 5). This result suggests that the genetic control decreases with increasing stress intensity and duration of exposure to drought stress. Kannenberg et al. (2020) reported a decrease in heritability linked to higher intensity and longer duration of drought while Jiao et al. (2021) observed like us an amplification of the drought stress effects when stress was high in intensity and prolonged. Heritability estimates were notably higher for apical growth after the second year of drought-induced treatments (Fig. 5), but the Spearman's rank correlations among clones for this trait were lower after the second year of treatments (Fig. 6). This trend is likely indicating the presence of GxE under the form of genotype-by-treatment interaction, and implicating different allocation strategies among clones that would be under quite strong genetic control, which represents a positive outlook in the context of breeding for resilience to severe drought effects. It is also quite well known in forest genetics that differences in environmental conditions from one test site to another one do not have the same exact effects on various genotypes when comparing their growth (Beaulieu et al. 2009). Such GxE interaction has been reported to be more important for growth traits and is rather low for wood properties such as wood density (Beaulieu and Bousquet 2010; Lenz et al. 2020a, 2020b), as we observed in the present study at the seedling stage. In order to consider GxE interaction in white spruce, breeding and deployment zones have long been established that subdivide the area of reforestation into relatively homogeneous environmental subunits (Li et al. 1997; Andalo et al. 2005), so to ensure that the recommended plantation stocks retain their growth superiority and can be used without risk of maladaptation.

In a recent study, Laverdière et al. (2022) also reported a notable different response of white spruce families tested on two sites affected by two different drought episodes occurring at different ages and of different intensity. Thus, in spite of the fact that lifetime tree vigor seems to remain the best proxy to evaluate resilience to drought in absence of any data (Laverdière et al. 2022), our results confirm that the response of trees to the occurrence and intensity of drought stress need ideally to be tested before breeding in the context of climate change, so to select the most appropriate reforestation stock, particularly for regions more afflicted by drought episodes. In addition, if survival after plantation is one of the main goals, this response must be assessed at the very juvenile stage so to minimize losses by selecting optimal stock with multi-trait approaches. Besides extending the present analytical approach to screen much larger numbers of candidate clones, families or other genetic material, one other current challenge remains to pursue these assessments on older trees and also, to consider the future climatic conditions predicted in situ in the different regions prioritized for reforestation, with climate models better integrating the predicted increased frequency and severity of drought episodes in the future (Depardieu et al 2020, 2021).

Our results showed that the response to drought-induced stress was highly variable among white spruce clones and signatures of different adaptation strategies to drought were detected. Thus, the approach developed and tested in this study represents an interesting component that could be potentially added to the genetic improvement programs of white spruce and likely for other temperate and boreal spruce species used in reforestation across the northern hemisphere, in order to maintain adaptation, growth and wood quality in the face of more frequent and intense drought episodes. The use of mixed multiclonal and multifamilial deployment of plantation stock together with monitoring of genetic diversity (Namroud et al. 2012; Godbout et al. 2017) have been shown to represent an efficient approach to increase growth productivity in white spruce genetically diverse plantations (Lamhamedi et al. 2000; Wahid et al. 2012; Park et al. 2016). Our findings will thus inform the Québec white spruce breeding program and enable to retain specific clones that are actively used for reforestation in the province, together with the future testing of additional clonal lines at an early age using the approach developed in this study. Also, using genomic selection models to predict trait values from genomic profiles of thousands of candidates would represent a key strategy to reduce phenotyping efforts (Bousquet et al. 2021), given that genomic profiles are already available for thousands of related clones and candidate trees in the Québec white spruce advanced-breeding program (Perron et al. 2018).

Conclusions

This study was designed as a proof of concept to monitor spruce clonal response to different intensities and duration of drought at the young seedling stage where drougth effects can be most critical. It was also designed to estimate the part of genetic variation and control in the total phenotypic variation, which has been rarely monitored in studies of drought stress response in trees, especially at a young age. Additional studies implicating larger samplings of candidates will be needed before assembling white spruce varieties genetically diverse and presenting an improved juvenile response to drought stress. This study also provided a better understanding of the impact of different levels of drought-induced stress on juvenile seedling growth and wood properties responses in an ecologically widespread and widely reforested conifer. We notably observed different adaptation strategies among clones in drought-induced stress conditions.

The monitoring of the effects of drought-induced stress on wood density and growth responses at the juvenile stage indicated that the large-scale selection of better performing clones for breeding and reforestation purposes would be possible, based on the traits of interest and a newly developed multi-trait drought response index. Our study showed a decrease in trait heritability with increasing intensity and duration of drought-induced stress except for apical growth. This can be viewed as a challenge for tree breeders, given that lower heritability leads to lesser genetic gains in selection. However, regarding apical growth, which did not experience much of a decline in heritability under drought-induced treatments, it represents a key trait at the juvenile stage given the early competition in tree plantations. It could thus be improved quite efficiently at an early age for good response to drought stress conditions, especially when using clonal selection, because of the much higher broad-sense than narrow-sense heritability for this trait. The different clonal responses and the noted genotype-by-treatment interactions in relation to the intensity or

duration of drought stress should also be considered in deployment of selection strategies by tree breeders.

With drought episodes likely becoming more prevalent with climate change, the combination of key juvenile growth traits as well as wood density and biomass should make the proposed drought stress response index a valuable tool for choosing the best adapted seedling stock for survival and productivity, and to foster future reforestation success. More than ever, tree genetic improvement programs will have to consider future local climatic predictions and the likelihood of frequent drought episodes to select the best adapted material for reforestation.

Data availability Data will be shared upon request to the corresponding author.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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