Relating the Growth Phenology and Biomass Allocation in Seedlings of 13 Acadian Tree Species With Their Drought Tolerance

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Climate models predict an increase in the frequency and intensity of drought events in the Acadian Forest Region, with higher risk of tree growth decline and mortality. To accurately predict future species response, we need to better compare drought-coping traits between Acadian tree species, especially at early life stages as young trees tend to display increased sensitivity to small environmental changes than mature trees. Here, we compared the seasonal growth phenology and biomass allocation in seedlings of 13 Acadian tree species in a controlled environment to assess their ability to predict species drought tolerance rankings. We focused on two traits associated with drought tolerance, namely biomass allocation to root systems, which affects water uptake, and phenology of seasonal growth, where earlier growth can avoid the peak drought period in late summer. We find an earlier onset of height growth in drought-tolerant species ($P < 0.05$), supporting the late-summer drought avoidance hypothesis. The observed biomass allocation patterns did not support the hypothesis of a higher allocation to roots with drought tolerance. In fact, we report an initially higher shoot-to-root ratio in drought tolerant species ($P < 0.05$), which becomes non-significant as the season progresses. Our results highlight the complexity of drought response strategies, as the developmental traits reported here only account for a fraction of each species overall drought tolerance. Yet, the important differences in growth phenology observed here between species, and their linkage with drought tolerance indices, could help predict species response to future drought regime.

Keywords: Acadian forest, biomass allocation, drought tolerance, phenology, shoot-to-root ratio, root mass fraction

INTRODUCTION

Climate models predict an increase in frequency and intensity of drought events throughout large tracts of land across the globe, including North America (Dai, 2011; Xu et al., 2019). This climate shift could have severe impact on forest trees, as exemplified by the recent drought-driven widespread tree mortality reported in the southern Canadian boreal forest (Michaelian et al., 2011). Trees at the seedling stage are more vulnerable to differences in temperature and precipitation than mature trees, and demonstrate increased sensitivity to small environmental

changes (Gerhardt, 1996; Bell et al., 2014; Mathys et al., 2018). Additionally, the limited root systems of seedlings mean they do not have access to water stores located in lower soil layers (Engelbrecht et al., 2005; Niinemets, 2010) compounding their increased sensitivity to drought events. Therefore, species-specific variation in seedling establishment patterns and survival rates may be a crucial predictor of species responses to climate change compared to mature trees, especially those at their distributional limits (Mathys et al., 2018).

Physiological and environmental conditions have created varying levels of tolerance to drought in tree species, where some species display increased tolerance to drought events relative to others (Niinemets and Valladares, 2006). Tree species drought-coping strategies are often categorized as drought avoidance and drought resistance (Kramer and Boyer, 1995; Polle et al., 2019). Drought avoiding species have adopted mechanisms to reduce water loss and maximize their uptake of water, including completing their seasonal growth prior to regular seasonal drought, increased leaf thickness, and deep root systems (Kramer and Boyer, 1995; Nguyen et al., 2017; Polle et al., 2019). Drought-resistant species like oaks have maximized traits like hydraulic resistance to embolisms that insure maintenance of superior growth during drought, providing a competitive advantage over more conservative species (McDowell et al., 2008). Knowledge of each species drought-coping traits, including their co-variations and trade-offs, are required to enable accurate prediction of their functional responses to drought events and competitive fitness under a warmer, drier climate.

Under water stress, plants often alter their morphology to maximize their belowground surface area to maximize water uptake and conservation (Brouwer, 1963; Markesteijn and Poorter, 2009). The most substantial morphological difference linked with drought tolerance is root morphology (Møller and Jennions, 2002; Niinemets and Valladares, 2006; Markesteijn and Poorter, 2009). There is a general understanding that the allocation of carbon to root production demonstrates an initial flush before aboveground production takes place, then peaks in late spring into the summer (Burke and Raynal, 1994; Steinaker et al., 2010; McCormack et al., 2014). Tree species that are adapted to drought generally have deeper root systems and increased root-to-shoot ratios than those with lower drought tolerance (Kozlowski and Pallardy, 2002; Hartmann, 2011), and this growth response is influenced by the severity of stress (Poorter et al., 2012; Brunner et al., 2015). Drought tolerant species often reduce their leaf biomass to minimize water loss, and increase carbon allocation to their root systems to allow for additional water acquisition (Niinemets and Valladares, 2006; Markesteijn and Poorter, 2009). While there is increasing evidence that the growth and structure of root systems are impacted by drought (Kozlowski and Pallardy, 2002), there is little information that allows comparison of the magnitude of their response to drought between species, as well as the role they may play in the overall species drought tolerance (McDowell et al., 2008; Hamanishi and Campbell, 2011; Brunner et al., 2015).

Climate model predictions suggest an earlier start to the spring growing season, leading to increasing drought during the later part of summer, which could cause substantial declines in forest productivity, as already observed in some North American forests (Richardson et al., 2010; Buermann et al., 2018). Species that are actively growing late in the growing season may thus be more vulnerable to these late summer droughts (Houle et al., 2012; Buermann et al., 2013, 2018). Similarly, recent studies have reported that sensitivity of tree growth to drought varied significantly over the growing season, depending on the phenology of growth and its synchrony with drought (Foster et al., 2014; D'Orangeville et al., 2018; Kannenberg et al., 2019b; Vanhellemont et al., 2019). The timing of drought may even have a greater impact on tree functionality than the drought intensity (D'Orangeville et al., 2018; Forner et al., 2018). Most of the current knowledge on species phenology is related to differences between wood structure types in deciduous species, where ring-porous species complete most of their annual growth earlier in the growing season and in a shorter amount of time relative to diffuse-porous species (Waring, 1951; Ladefoged, 1952; Zimmermann and Brown, 1971; Panchen et al., 2014). Historically, evidence of the onset and duration of shoot and diameter growth in coniferous species has been unclear (Ladefoged, 1952; Hunter and Lechowicz, 1992; Zweifel et al., 2006), however, recent studies have found that while the onset and duration of wood growth in conifers are not correlated (Cuny et al., 2014), the timing of other phenological patterns and weather signals display some control over xylem phenology (Rossi et al., 2013, 2016). Coniferous species, therefore, have high plasticity and are able to adapt their phenological patterns to local conditions (Rossi et al., 2013, 2016). Therefore, a better understanding of species growth phenology is needed to predict impacts of future drought events.

Assessing drought stress responses in mature trees is often done retroactively through dendrochronological approaches, while seedling performance are often evaluated in controlled environments, such as common gardens (McDowell et al., 2013; Csilléry et al., 2020). Common garden experiments have a long history of use in forest genetics to assess local adaptation of traits, as they provide a unique ability to control for phenotypic plasticity that cannot be controlled *in situ* (Sork et al., 2013; de Villemereuil et al., 2016; Housset et al., 2018). In these experiments, traits are often used as a proxy for other fundamental characteristics, and help inform species vulnerabilities, conservation practices, and adaptive management approaches (McKay et al., 2001; de Villemereuil et al., 2016; Housset et al., 2018). Drought stress affects many functional traits in seedlings, including phenology patterns (Nguyen et al., 2017; D'Orangeville et al., 2018), wood anatomical traits (Crous et al., 2012; D'Orangeville et al., 2021), and biomass allocation (Møller and Jennions, 2002; Niinemets and Valladares, 2006; Markesteijn and Poorter, 2009), however, it is still unclear which traits are most important for understanding and predicting species drought tolerances (Moran et al., 2017).

Species growing in the Acadian forest region are likely more susceptible to future changes in climate and environmental conditions than those found in other forest regions. The Acadian forest region is part of the ecological transition zone between northern boreal coniferous and southern temperate deciduous forests (Loo and Ives, 2003; Taylor et al., 2017),

composed of species and communities living at the extreme edges of their range (Fisichelli et al., 2014; Taylor et al., 2017). As a result of ongoing rapid climate change, there will likely be a shift in the composition of the Acadian forest region toward more temperate species as conditions become less favourable for boreal conifers, reducing their ability to compete with temperate species (Bourque and Hassan, 2008; Taylor et al., 2017). In addition to this compositional shift, climate change throughout the 21st century will likely create a lagged growth effect; although temperate species are more competitive, still living mature boreal conifers block the ability of temperate species to colonize newly favorable environments, resulting in decreased overall growth of the Acadian forest (Zhu et al., 2012; Corlett and Westcott, 2013; Taylor et al., 2017). Previous studies on tree growth phenology and biomass allocation patterns are often limited to a small number of species mostly native to Europe (Panchen et al., 2014; Piper and Paula, 2020). Adequate knowledge comparing the drought-coping traits of the main Acadian tree species is critical to predict the species-specific impact of drought events in that ecosystem. In this study, we monitored the development of 13 Acadian tree species with different drought tolerances over one growing season to determine if their drought tolerance could be predicted from phenological and morphological growth traits. We focused on two traits associated with drought tolerance, namely biomass allocation and seasonal growth phenology, and tested the hypotheses that more drought-tolerant species would (i) complete their growth earlier in the season while conditions are more favorable, and (ii) allocate a higher fraction of their new biomass to their root system as the season progresses and risk of water stress increases.

MATERIALS AND METHODS

With the exception of Norway spruce, seeds of thirteen coniferous and deciduous species characteristic of the Acadian forest were collected from local populations in Atlantic Canada and provided by the National Tree Seed Center, the Canadian repository of tree seeds. While Norway spruce is not indigenous to the Acadian forest, this species is widely present in the region due to historical and current plantations. Most seed sources were in regions of New Brunswick, while eastern white pine and Norway spruce seeds were collected from Nova Scotia and Maine, respectively (**Table 1**). All seeds were collected from within the Acadian forest region, suggesting similar forest dynamics between source locations, and grown under controlled conditions for one to 2 years. A total of 403 trees were released from dormancy on June 7, 2019, transplanted into 7.6 liter pots with standard tree nursery growing medium and grown outside in full sun with regular watering until the final measurements were recorded on October 3, 2019. The temperature that summer (18.2°C over JJA) was representative of the long-term average (18.1°C over 1981–2010). Sixty-five of these seedlings were monitored weekly as part of our phenology measurements, and the remaining 338 seedlings were used to assess biomass accumulation patterns.

Height, diameter at root collar, and bud development stage were recorded for all individuals of each species when they were released from dormancy. Five seedlings of each species were randomly selected for repeated weekly measurements of height and root collar diameter.

Three additional seedlings of each species were randomly selected each week for destructive sampling and biomass measurements. These three seedlings were measured for height, root collar diameter, and bud development stage, and their oven-dried (70°C for 48 h) root, leaf, and aboveground wood biomass weight. The scaly foliage of eastern white cedar could not be weighed separately from wood.

Analysis of Data

Four individuals were excluded from the phenological analysis due to mortality or severe breakage during the experiment. We also excluded 12 individuals composed of balsam fir, white pine, jack pine, red maple, and red spruce species which displayed second flushes of growth as the data analysis was focused on a single flush of growth. Diameter growth was not determined for yellow birch as following the removal of trees experiencing mortality, only one sample tree of yellow birch remained.

A logistic growth model was fitted to the seasonal height and diameter growth of each tree separately:

$$Height_t = Height_{initial} + \frac{G}{1 + e^{Po - (r * t)}} + \varepsilon$$

where t is a given day of year during the growing season, G is the total height growth, Po is a scaling parameter for the Y axis, r is the growth rate, and ε is the residual error of the model. This approach is similar to that implemented by D'Orangeville et al. (2021), however, here the approach is applied to young trees to look at height as well as diameter growth, in a more controlled environment.

We derived three key variables associated with primary and secondary growth: the day of year (DOY) where each individual tree achieved 25, 50, and 75% of its cumulative annual growth of height and diameter. The period of rapid growth for each species was calculated from the difference between 25 and 75% DOY. Red maple and yellow birch were removed from diameter analysis because only two datapoints were available for red maple and one for yellow birch on a possibility of five.

Due to the increasing size and corresponding effort needed for biomass measurements, the number of individual samples per species was reduced from 3 to 2 from August 8, 2019 onward. The last two measurements of biomass data in September and October were excluded from the final analysis due to manipulation errors. Biomass ratios were then calculated for the foliage-to-belowground, wood-to-belowground, aboveground-to-belowground, and foliage-to-wood biomass allocation patterns of each species.

To test the hypothesis that measured traits reflected species drought tolerance, linear regression models were fitted to the resulting phenological indices as well as biomass values and ratios against species drought tolerance scores taken from Niinemets and Valladares (2006). Regression slope values and their significance were used to assess relationships between

TABLE 1 | Tree characteristics and seed provenance, including drought tolerance ranking from **Niinemets and Valladares (2006)** where 0 represents no tolerance and 5 represents maximal tolerance.

Common name	Latin name	Seed source	Native forest region	Wood structure	Drought tolerance
Balsam fir	*Abies balsamea*	New Brunswick	Boreal & temperate	Non-porous	1
Black spruce	*Picea mariana*	New Brunswick	Boreal & temperate	Non-porous	2
Eastern hemlock	*Tsuga canadensis*	New Brunswick	Temperate	Non-porous	1
Eastern white cedar	*Thuja occidentalis*	New Brunswick	Temperate	Non-porous	2.71 ± 0.38
Eastern white pine	*Pinus strobus*	Nova Scotia	Boreal & temperate	Non-porous	2.29 ± 0.38
Jack pine	*Pinus banksiana*	Unknown	Boreal & temperate	Non-porous	4
Norway spruce	*Picea abies*	Maine	Temperate	Non-porous	1.75 ± 0.41
Red spruce	*Picea rubens*	New Brunswick	Temperate	Non-porous	2.5
White spruce	*Picea glauca*	New Brunswick	Boreal & temperate	Non-porous	2.88 ± 0.12
Red maple	*Acer rubrum*	New Brunswick	Boreal & temperate	Diffuse-porous	1.84 ± 0.16
White birch	*Betula papyrifera*	Unknown	Boreal & temperate	Diffuse-porous	2.02 ± 0.3
Yellow birch	*Betula alleghaniensis*	New Brunswick	Boreal & temperate	Diffuse-porous	3
White ash	*Fraxinus americana*	New Brunswick	Temperate	Ring-porous	2.38 ± 0.38

drought tolerance rankings and observed morphological and phenological species traits. All analyses were performed using R software (version 4.1.0, 2021).

RESULTS

The seasonal growth models displayed a good overall fit for species height (normalized RMSE = 4.1%) and diameter growth (normalized RMSE = 5.4%), with the model demonstrating an insignificant fit ($P > 0.05$) for the height or diameter of less than 10% of sample trees. The onset of rapid height growth, defined here as the time when 25% of annual growth is completed, preceded the period of rapid diameter growth by 4–34 days across species (mean of 18 days; **Figures 1A,B**) apart from eastern hemlock, whose rapid diameter growth started 4 ± 3 days before rapid height growth.

While there was no clear trend of height and diameter growth phenology between coniferous and deciduous species (**Figures 1A,B**), within the conifers, temperate forest species displayed a later initiation of height growth which then extended further into the growing season. Among broadleaf species, the growth of ring-porous white ash was precocious relative to diffuse-porous species. White ash initiated its peak diameter growth period 21 ± 8 days earlier than white birch, and its peak height growth period at least 10 ± 3 days earlier than the three diffuse-porous species (**Figures 1A,B**). Among conifer species, the timing of rapid height growth onset was highly variable, ranging from June 17 ± 4 days for jack pine to July 18 ± 3 days for eastern hemlock (**Figure 1A**). With the exception of red spruce, which initiated rapid diameter growth in early August, the onset of the period of rapid diameter growth for the thirteen coniferous species occurred over a 2 week period in mid-July.

Onset and duration of height and diameter growth of seedlings varied according to wood structure types (ring-porous, diffuse porous, and non-porous). With the notable exception of eastern hemlock and eastern white cedar, coniferous species demonstrated the largest delay in diameter growth onset relative to height growth onset (**Figures 1A,B**). Ring-porous white ash
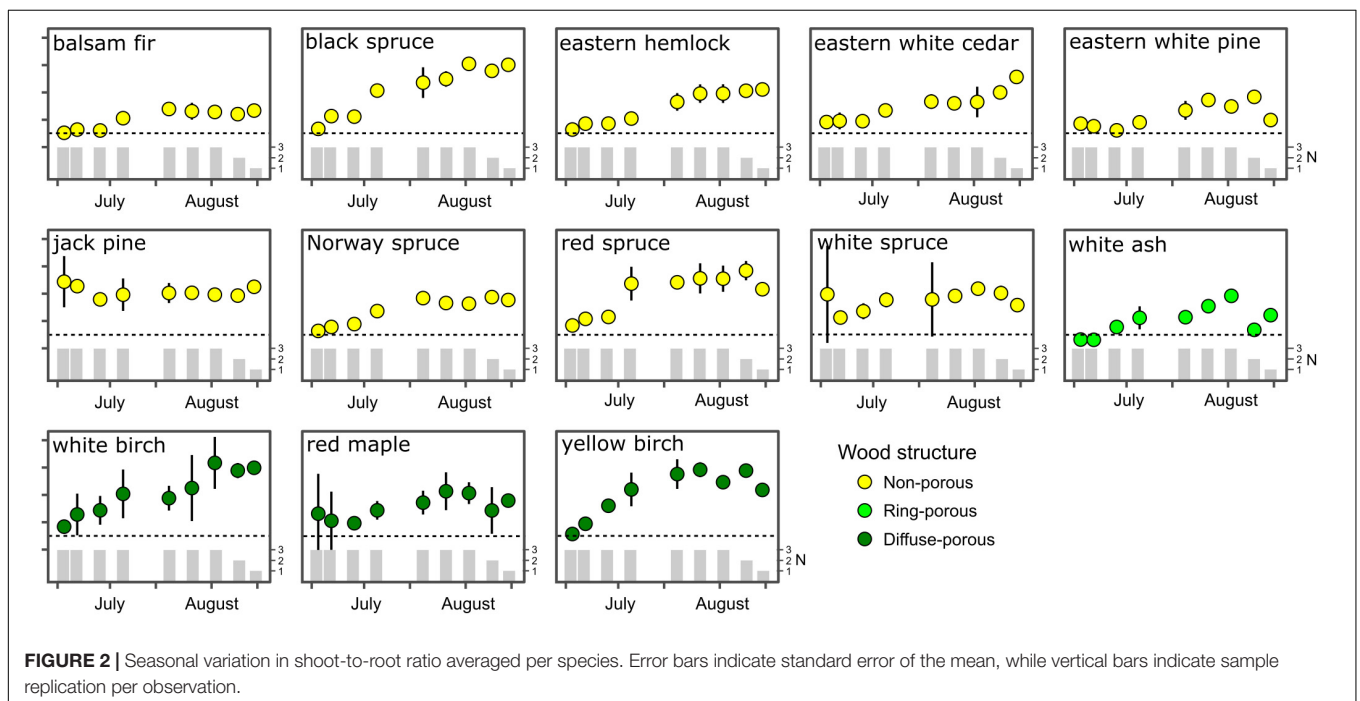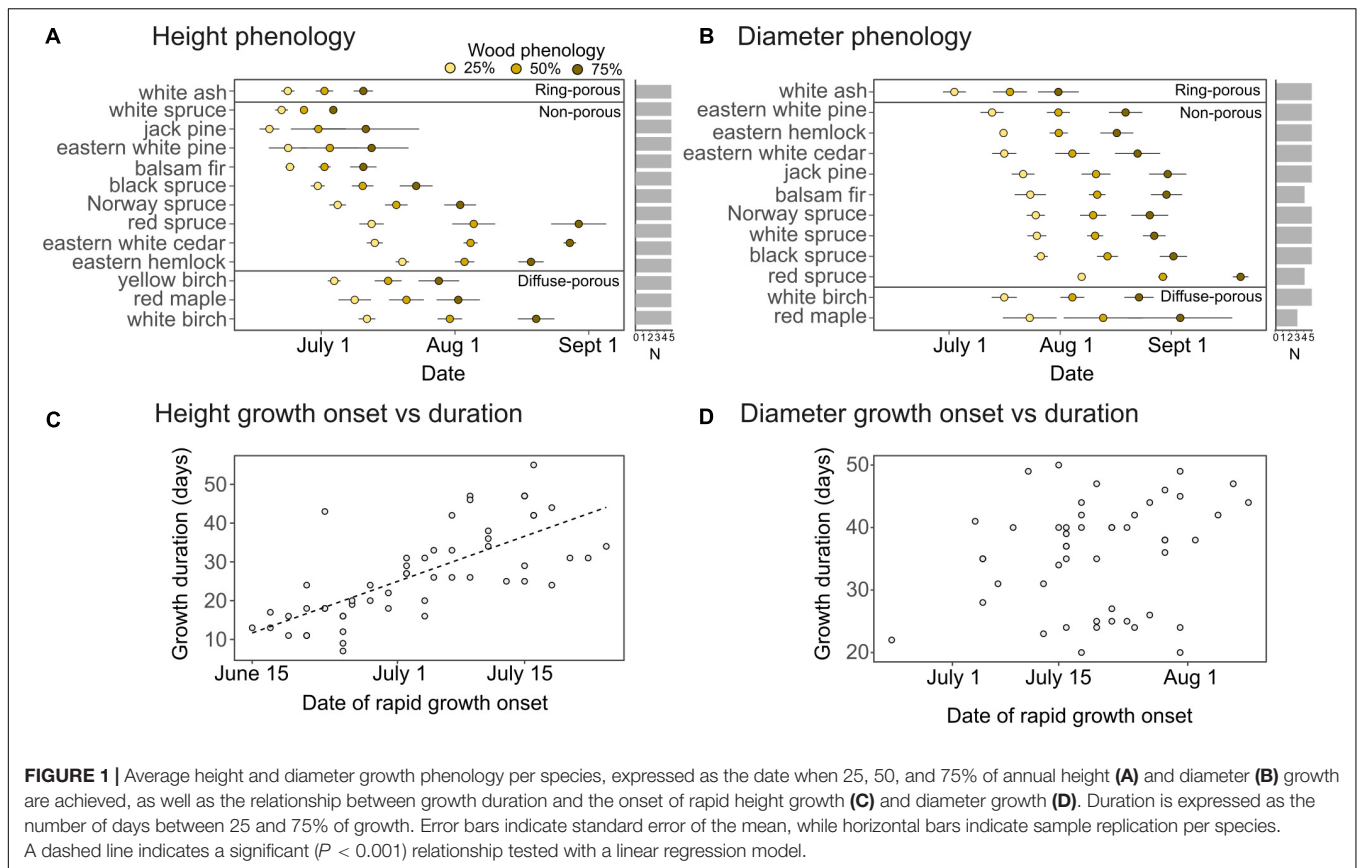
had an earlier (by up to 19 days) and shorter (by 11 days on average) period of rapid height growth than the diffuse-porous species (**Figures 1A,B**). While the time at which ring-porous species and diffuse-porous species were actively growing was different, there was no obvious difference in the length of time between the onsets of height and diameter growth. Species initiating height growth later in the season, including white birch, eastern white cedar, and red spruce, tended to display lower growth rates (**Supplementary Figure 1**), leading to an extended height growth period (**Figures 1A,C**). This relationship between onset and duration of height growth was not significant for diameter growth (**Figure 1D**).

Biomass Allocation Patterns

With the exception of jack pine and white spruce, all species displayed an initial shoot-to-root ratio (SRR) of approximately 1:1, and reached an asymptote by the first week of August where the ratio remained the same or declined (**Figure 2**), suggesting more investment in belowground biomass later in the growing season. Throughout the growing season, the SRR remained lowest in balsam fir suggesting balsam fir allocates biomass to both above and belowground stores, while species with higher SRR, such as black spruce, demonstrate a strong preferential allocation pattern to aboveground biomass. Diffuse-porous species allocated more growth to aboveground biomass than ring-porous species, with SRR for ring-porous white ash consistently lower than in diffuse-porous species throughout the growing season. Both white and yellow birch consistently favoured aboveground biomass allocation during their growth (**Figure 2**). We did not report any differences in biomass allocation patterns between boreal and temperate species.
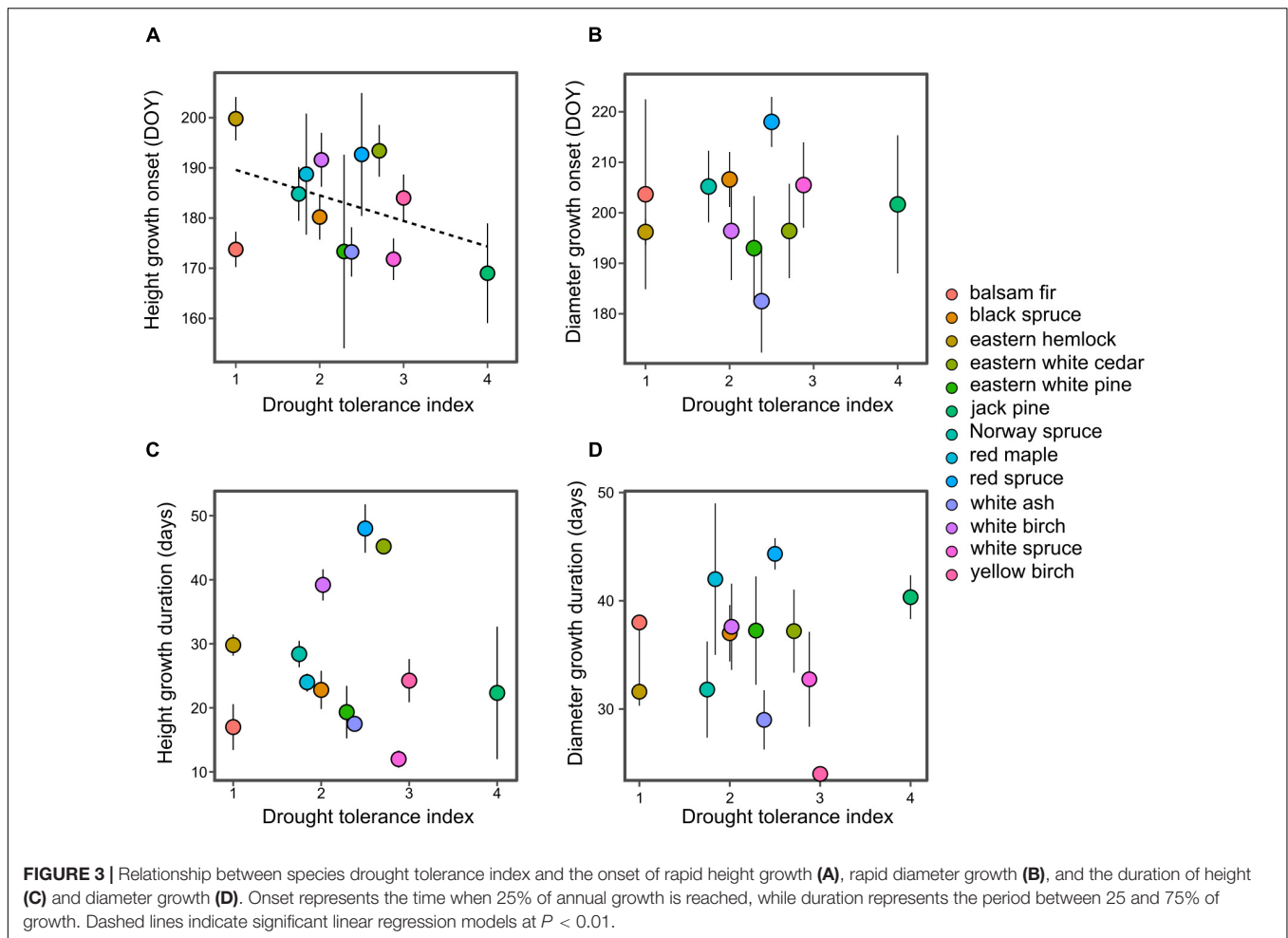
Growth Trade-Offs With Drought Tolerance

In support with hypothesis 1, we find that drought tolerant species tend to initiate their period of rapid height growth earlier than drought intolerant species ($P < 0.01$; **Figure 3A**), this result remains significant ($P < 0.01$) without eastern white pine which

FIGURE 1 | Average height and diameter growth phenology per species, expressed as the date when 25, 50, and 75% of annual height **(A)** and diameter **(B)** growth are achieved, as well as the relationship between growth duration and the onset of rapid height growth **(C)** and diameter growth **(D)**. Duration is expressed as the number of days between 25 and 75% of growth. Error bars indicate standard error of the mean, while horizontal bars indicate sample replication per species. A dashed line indicates a significant ($P < 0.001$) relationship tested with a linear regression model.

FIGURE 2 | Seasonal variation in shoot-to-root ratio averaged per species. Error bars indicate standard error of the mean, while vertical bars indicate sample replication per observation.

has the highest drought tolerance. This trend weakens as the season progresses, with a near-significant relationship at 50% height growth ($P = 0.06$) and non-significant at 75% height growth ($P > 0.1$). Drought tolerance displayed no significant relationship with the phenology of diameter growth or the duration of growth (**Figures 3B–D**).
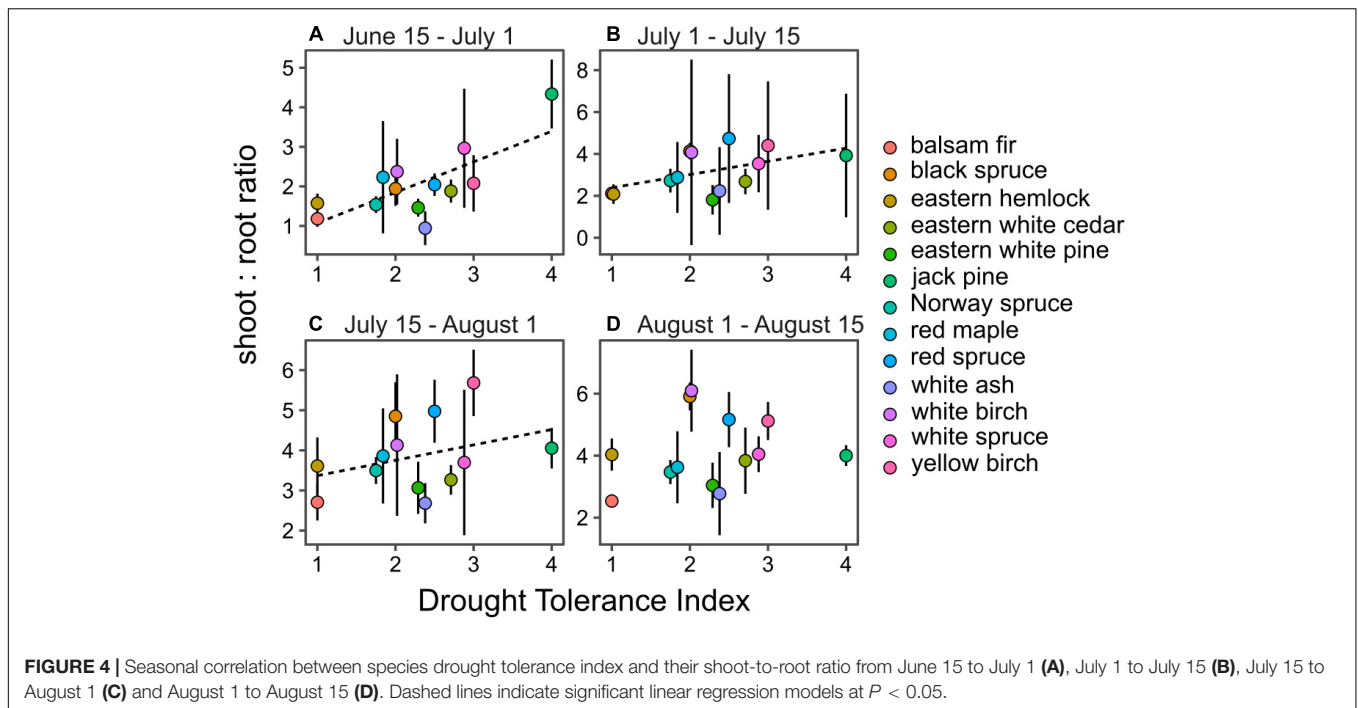
FIGURE 3 | Relationship between species drought tolerance index and the onset of rapid height growth **(A)**, rapid diameter growth **(B)**, and the duration of height **(C)** and diameter growth **(D)**. Onset represents the time when 25% of annual growth is reached, while duration represents the period between 25 and 75% of growth. Dashed lines indicate significant linear regression models at $P < 0.01$.

Contrary to our second hypothesis, drought tolerance was positively correlated with SRR during three out of four periods of the growing season ($P < 0.05$; **Figure 4**). A strong relationship was observed early in the season, which gradually declined as season progressed until no significant relationship was observed for the last period of growth in August. The gradual loss of significance was mostly due to the steady increase in SRR from drought intolerant species during the growing season, while SRR of drought tolerant species like jack pine remained stable, indicating even allocation of biomass to aboveground and belowground organs (**Figure 4**).

DISCUSSION

The ability of tree seedlings to withstand drought conditions is dependent on the sum of their physiological, morphological, and phenological traits (Tyree et al., 2003; Poorter and Markesteijn, 2008). Though there are principles that apply to both gymnosperms and angiosperms, there are also significant fundamental differences in their physiology and morphology (Moran et al., 2017). The vessel elements in deciduous species make them less resistant to drought induced embolism than

coniferous species, which only have tracheids, though deciduous species have much higher diversity in their anatomical responses to drought, allowing them to persist in harsh environments (Brodribb et al., 2012; Carnicer et al., 2013; Moran et al., 2017). Similarly, the differing climate and disturbance regimes between the northern, colder boreal forest and southern, warmer temperate forest create varying levels of drought tolerance (Bugmann, 1996; Carnicer et al., 2013), as those adapted to cooler environments are likely less capable of tolerating extreme heat, which was evidenced in the earlier onset of height growth in northern boreal forest conifers.

The extent of response to drought through biomass allocation is species specific (Zhang P. et al., 2020), and may also depend on individual drought coping strategies (Lloret et al., 2018; Zhang P. et al., 2020), where drought tolerant species demonstrate increased adaptation to drought through altered morphological patterns (Piper, 2011; Piper and Paula, 2020). Drought tolerant species, especially in drier forest regions, have been reported to display superior water uptake by increasing the biomass allocation to their root system, resulting in lower SRR (Poorter and Markesteijn, 2008; Wiley, 2020). Our results do not support these previous findings. Instead, we found that seedlings of Acadian tree species with higher drought tolerance maintained

FIGURE 4 | Seasonal correlation between species drought tolerance index and their shoot-to-root ratio from June 15 to July 1 **(A)**, July 1 to July 15 **(B)**, July 15 to August 1 **(C)** and August 1 to August 15 **(D)**. Dashed lines indicate significant linear regression models at $P < 0.05$.

a steady, even allocation of growth between their roots and shoots throughout the season, while those with lower drought tolerance displayed a lower allocation to their root system. There is not yet a clear trend of SRR in relation to drought tolerance in seedlings (Sack et al., 2003; Poorter et al., 2012; Olmo et al., 2014; Puglielli et al., 2020); some tolerant species increase allocation to root systems, while others maintain more equal allocation patterns. Species additionally may be maladapted for drier conditions, or biomass allocation to root systems may not play a significant role in determining drought tolerance of seedlings in the Acadian forest. Maintaining equal allocation to roots throughout the season, as was found here, could be a conservative growth strategy by seedlings to ensure the maintenance of higher water uptake capacity.

The phenological traits of species are increasingly recognized to play an important role in their relative drought tolerance levels through the maximization or completion of annual growth prior to the regular drought season during late summer (Zhang P. et al., 2020; D'Orangeville et al., 2021). The timing of drought affects drought vulnerability in trees, since the process of cambial cell division at the heart of primary and secondary growth is highly sensitive to water availability (Gruber et al., 2010; Foster et al., 2014; Lempereur et al., 2015), though the productivity of coniferous forests may be less sensitive to changing phenology patterns than deciduous forests (Richardson et al., 2010; Carnicer et al., 2013). Drought impacts on the diameter growth of mature trees in temperate Eastern North America were reported to peak in June (D'Orangeville et al., 2018; Kannenberg et al., 2019a) coinciding with the period of maximal cambial activity (Rossi et al., 2006; Deslauriers et al., 2007). Shifts in phenological patterns have already been observed in many species (Alberto et al., 2013), and these adaptations

can occur without the need for significant genetic evolution (Gienapp et al., 2008; Alberto et al., 2013). The significant observation of an earlier timing of height growth in seedlings with increasing drought tolerance provides additional evidence that height growth phenology could play an important role, along with many other physiological and morphological traits, in helping predict species drought tolerance. Impacts to height phenology patterns may additionally have increased importance in understanding vulnerabilities and survival of seedlings, given the role shoot extension plays in the competition for light resources. These findings are in line with previous works (Zapater et al., 2013; Vanhellemont et al., 2019; D'Orangeville et al., 2021), that demonstrate a drought avoidance strategy whereby species have altered growth phenology patterns, avoiding active growth during the drought season. In addition, the high level of interspecific variation in growth phenology reported here suggests that drought could have variable impacts.

While there is evidence that supports both the resilience of the Acadian forest (Zhang P. et al., 2020; Zhang Y.-L. et al., 2020), and the future demise of the region (Reyer et al., 2013; Taylor et al., 2017), lack of drought tolerance knowledge featuring a variety of species and geographic regions (Panchen et al., 2014; Piper and Paula, 2020) limit the accuracy of predictions. The complex drivers of species growth patterns (Pearse et al., 2017; Csilléry et al., 2020) additionally mean that the expected response to climate variables, such as drought, are often more complex than models are able to predict (Alberto et al., 2013). Photoperiod and temperature have significant control over phenology patterns (Körner and Basler, 2010), and these were consistent between species in this experiment, which likely resulted in a homogenizing effect of species' phenology patterns (Csilléry et al., 2020). Similarly, the limited resources available

to potted seedlings and relatively late release from dormancy compared to the natural start of the growing season mean species growth patterns may not reflect those in natural environments. Considerably more research into the drought tolerance and individual species adaptations is needed to better understand how the Acadian forest region will respond to the increased drought frequencies and intensities predicted for this region (Dai, 2013; Cook et al., 2015).

DATA AVAILABILITY STATEMENT

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

AUTHOR CONTRIBUTIONS

LD'O contributed to conception and design of the study and to data collection. EP performed the statistical analysis and wrote the first draft of the manuscript with contributions from LD'O. Both authors contributed to the interpretation of the results and to the manuscript revision, read, and approved the submitted version.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/ffgc.2022.784382/full#supplementary-material

Supplementary Figure 1 | The relative growth rate of seedlings of thirteen species throughout one growing season.

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