

**Moisture impacts on planted conifer seedling growth in boreal Québec: A water
manipulation study**

by

Detian Zhao

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Supervisor: Loïc D'Orangeville, PhD, FOREM

Examining Board: John A. Kershaw, PhD, FOREM
David A. MacLean, PhD, FOREM

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ABSTRACT

In order to study the impact of water limitations on boreal forest growth, a water manipulation experiment consisting of soil water content control during growing seasons was conducted for 4 consecutive years in a humid boreal forest of Québec, Canada. Impacts of moisture of the growth on seedlings of four different commonly planted conifer species was investigated. Jack pine (*Pinus banksiana* Lamb.) displayed the fastest growth, followed by black spruce (*Picea mariana* (Mill.) BSP.), balsam fir (*Abies balsamea* (L.) Mill.) and white spruce (*Picea glauca* (Monech) Voss). A linear mixed effects model was used to predict effects of soil water content (SWC) on growth. Increasing SWC in early growing season of the current year increased diameter growth for black spruce, jack pine and balsam fir and height growth for black spruce and white spruce. Higher SWC later in the growing season of the previous year increased the diameter growth for jack pine and balsam fir and height growth for black spruce and balsam fir. However, it decreased growth of small seedlings. As seedlings grow and mature, they have greater water demand but also develop water use-efficiency.

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Table of Contents

ABSTRACT.....	ii
ACKNOWLEDGEMENTS.....	iii
Table of Contents.....	iv
List of Tables.....	v
List of Figures.....	vi
List of Abbreviations.....	viii
Introduction.....	1
Methodology.....	6
Study site.....	6
Experimental design.....	6
Treatments.....	7
Data collection.....	11
Data analysis.....	12
Results.....	14
SWC.....	14
Growth.....	15
Mixed Effects Modeling.....	20
Discussion.....	26
Conclusions.....	32
References.....	33
Curriculum Vitae	

List of Tables

Table 1. Parameter estimates and associated standard errors (in parentheses) and regression summary statistics for the linear mixed effects model (Eq. 1) for diameter growth by species. Bold values indicate statistically significant ($p < .05$) parameter estimates..... 22

Table 2. Parameter estimates and associated standard errors (in parentheses) and regression summary statistics for the linear mixed effects model (Eq. 1) for height growth by species. Bold values indicate statistically significant parameter estimates ($p < .05$).23

List of Figures

Figure 1. A. Location of the study site. B. Schematic diagram of experimental design Values at the center of each plot correspond to the percentage of precipitation received. Treatments 100N and 100R correspond to control and procedural control, respectively. C. Example of the distribution of seedlings in each plot. Each color corresponds to one of the four species tested: white spruce, black spruce, jack pine, and balsam fir.	7
Figure 2. Aerial view of the experiment (left) and example of plot in spring before tarp installation (right). Photographs by Charles Massicotte (left) and Loïc D'Orangeville (right).	9
Figure 3. Distribution of the July-August (left) and the previous year's September- October (right) soil water content (SWC) by growing season year.....	14
Figure 4. Average diameter growth by year and species (vertical bars indicate $\pm 1sd$).17	
Figure 5. Average height growth by year and species (vertical bars indicate $\pm 1sd$). 17	
Figure 6. Annual diameter growth across the July-August and the previous year's September-October soil water content by species, using linear smoother.....	18
Figure 7. Annual height growth across the July-August and the previous year's September-October soil water content by species, using linear smoother.....	19
Figure 8. Fitted diameter growth by diameter, species, and soil water content based on estimates from equation 1 (Table 1).	24

Figure 9. Fitted height growth by height, species, and soil water content based on
estimates from equation 1 (Table 2). 25

List of Abbreviations

SWC soil water content

JA July and August

SO September and October

Introduction

Climate change is projected to increase the probability of severe impacts on humans and ecosystems as a result of higher temperatures and more frequent and prolonged droughts (IPCC 2014). The Earth's surface temperature increased by 0.6°C–0.9°C from 1905 to 2005, and depending on future greenhouse gas emissions, climate models predict further increases of approximately 2°C–6°C, by the end of the 21st century (Ahima 2020). Although warming is predicted to increase the length of the growing season, which could increase annual forest productivity, especially in boreal forests (Way and Oren 2010), co-occurring droughts could offset these benefits. Seedlings could benefit from a longer growing season, but water stress and competition from herbaceous species also could limit the growth and survival of seedlings (Benayas et al. 2002). Compared with mature trees, the small and superficial rooting of seedlings could make them more susceptible to water deficits because deeper soil water is not accessible (McDowell et al. 2008). Water deficits have triggered growth reductions (Beck et al. 2011) and increased tree mortality in boreal forests of Western North America (Peng et al. 2011). In Québec, hydrological models suggest 20%–40% reductions in soil moisture for the period 2070–99 compared to 1971–2000 levels (Houle et al. 2012).

In boreal forests, tree growth is strongly related to water supply (Hofgaard et al. 1999). Drought in 2002–2003 was associated with reductions of 6–34% of net ecosystem

productivity in boreal forest stands, compared to productivity in 2000 (Kljun et al. 2007). Tree-ring records from Alaska indicate significant reductions in carbon uptake in a large portion of that region's boreal forests due to drought (Barber et al. 2000). However, in humid boreal forests of eastern North American, the water supply may still exceed what the trees need to grow (Isabelle et al. 2020).

Drought timing matters in tree growth (D'Orangeville et al. 2018). Moisture availability in the early growing season, when many water-dependent activities are in progress has great impact on growth. The 2004 summer drought in Alaska was associated with decreases of gross primary production of 12% in deciduous forests and by 9% in coniferous forests (Welp et al. 2007). A spring drought in 2010 also was associated with reduced primary productivity in southwestern China (Zhang et al. 2012). At the end of summer, growth slows down, cells become dehydrated, and the cambial tissue prepares for winter dormancy (Duchesne et al. 2012). Late summer droughts can significantly reduce root depth, growth, and survival rates of shallow rooted seedlings (Padilla and Pugnaire 2007). However, high moisture in the late growing season may result in lower soil respiration and lower radiation inputs, which may impact growth in the next growing season (Schuur et al. 2001, Lavigne et al. 2004).

Delayed effects of drought also are thought to influence growth (Anderegg et al. 2013). Balsam fir (*Abies balsamea* (L.) Mill.) seedlings showed delayed cell differentiation associated with drought stress in the previous year (D'Orangeville et al. 2013). Drought-

induced tissue damage (embolism) can limit a tree's capacity to conduct water beyond the duration of a drought (Yin and Bauerle 2017). Water deficits can delay the hardening of buds and inhibit cell differentiation, which affect height growth in the following growing season (Grossiord et al. 2017). Extreme droughts in 2018 and 2019 in Europe showed clear legacy effects, with greatly reduced tree radial growth in the growing seasons following drought (Scharnweber et al. 2020).

The main species of the boreal forests of Québec are white spruce (*Picea glauca* (Monech) Voss), black spruce (*Picea mariana* (Mill.) BSP.), jack pine (*Pinus banksiana* Lamb.) and balsam fir (*Abies balsamea* (L.) Mill.) (Rayfield et al. 2008). White spruce often dominates well-drained floodplains and warm upland soils that lack permafrost (Wirth et al. 2008). Black spruce is the single most abundant boreal tree species in Québec, and is typically associated with poorly drained lowlands and north-facing slopes where permafrost restricts drainage (Wirth et al. 2008). Natural black spruce stands cover most cool, humid areas; however, because of its resistance to most forest pests, it is a preferred species for artificial reforestation on warmer and drier sites (Bernier 1993). Jack pine can grow on very dry sandy or gravelly soils, but the best site for jack pine is well drained loamy sands; it is also a pioneer species on burned or other severely disturbed sites (Rudolph and Laidly 1990). Balsam fir usually grows on moist, well-drained shallow soils (Wenger 1984).

Drought timing could influence these species' responses to drought and influence

their growth in the subsequent year. For example, radial growth of black spruce was observed to increase in the year following higher precipitation during the previous growing season (Gewehr et al. 2014). Summer moisture is one of the most limiting factors of the growth of white spruce (Barber et al. 2000, Griesbauer and Green 2012). Late growing season conditions might have a greater impact on white spruce seedlings' growth in the following year than the conditions in summer (Renard et al. 2016). Summer droughts are associated with slight reductions in jack pine's growth (McCollum and Ibáñez 2020). After a summer drought, balsam fir seedlings showed reduced growth and reduced leaf water potential, and both the number and diameter of tracheids were reduced (D'Orangeville et al. 2013). Either too dry or too wet autumn soil conditions appear to limit root activities of balsam fir, and were associated with growth reductions in the next year (Lavigne et al. 2004). Much research focuses on drought in the early growing season, the influence of drought in the late growing season in these boreal species is lacking.

In most studies, species-specific responses to drought are compared under short-term drought conditions. Under these conditions, jack pine consistently had the fastest growth rates under water stress (Buxton et al. 1985, Marshall et al. 2000); however, the legacy effects indicate the importance of long-term experiments. Furthermore, effects of drought in the current and previous growing seasons are not well documented. Diameter growth, as a secondary growth event, is the result of cell division and expansion in the cambium layer, which relies on a direct water supply (Deslauriers et al. 2016). Height growth is partly

determined during bud formation in the previous year, along with climate conditions during the actual growing season (Grossiord et al. 2017).

In this study, a water manipulation treatment was used to examine effects of four years of varying water deficit on the height and diameter growth of planted seedlings of four species in a recently harvested boreal forest stand in Québec. Our hypotheses were that (1) diameter and height growth decline with lower soil water content in the current early growing season (July and August) and with increased soil water content in the previous year's late growing season (September and October), (2) diameter growth is more sensitive to soil water content in current growing season, while height growth depends on moisture levels in the previous growing season, because of their different patterns (secondary versus primary growth), and (3) jack pine will show faster total growth under drought treatments, followed by black spruce, balsam fir, and white spruce, because of their different adaptability to dry condition.

Methodology

Study site

The study was located in the balsam fir dominated boreal forest of Québec, located within the Forêt Montmorency north of Québec City (Québec, Canada; 47°15' N, 71°11' W, 780-840 m above sea level, Figure 1A). The site was a mature fir stand that was clear-cut in the summer of 2013 following a hemlock looper (*Lambdina fuscicollis*) epidemic. Soil drainage was mesic, and the site was characterized by a 12% slope to the north. The average annual temperature (1971-2000) was -0.5°C and the average annual precipitation was 1605mm.

Experimental design

The experiment was designed with 18 plots distributed at three blocks along the slope (upper, middle and lower slopes; Figure 1B). Deep trenches were dug above each plot to minimize seepage and water flow along the slope. Different levels of rain exclusion treatments ranging between 0% (exclusion of all rainfall) to 150% of rainfall were randomly applied to each plot within each slope level, including a control treatment (100N) receiving natural precipitation directly, and a procedural control treatment (100R) receiving the same amount of precipitation through the rain-exclusion system described below.

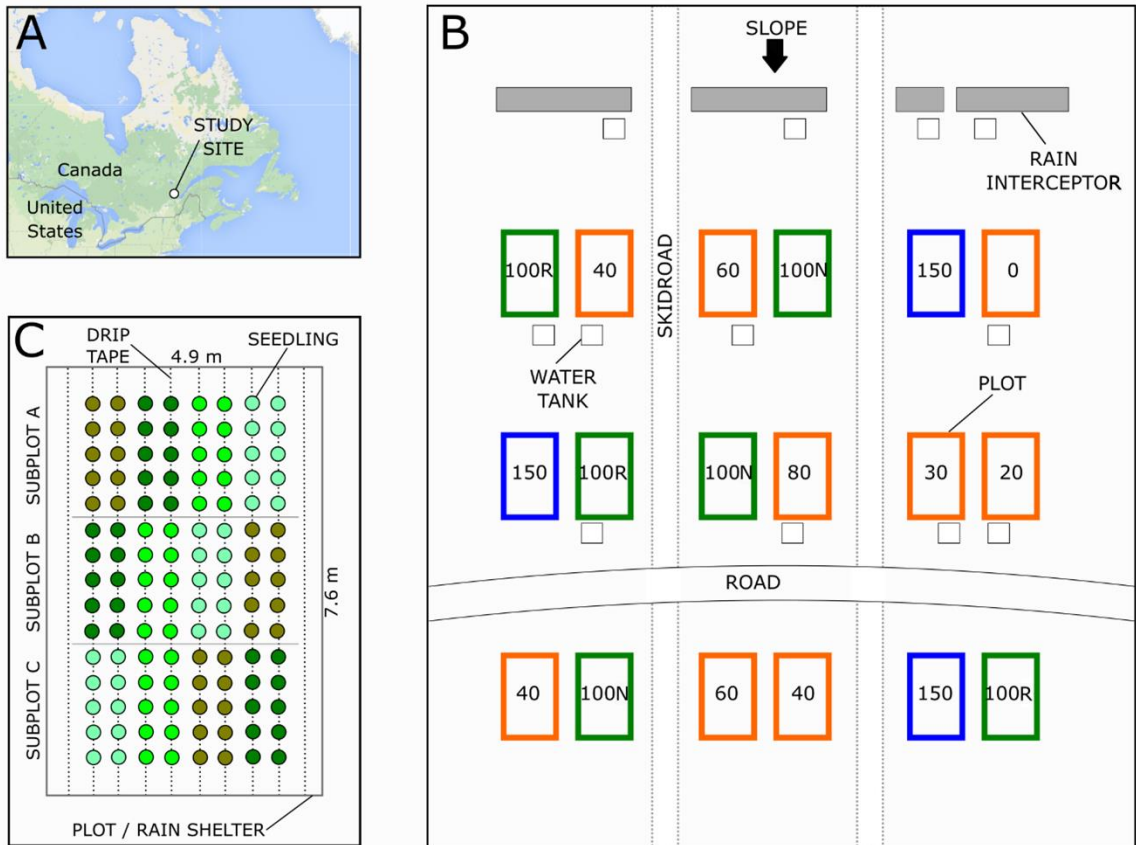


Figure 1. A. Location of the study site. B. Schematic diagram of experimental design. Values at the center of each plot correspond to the percentage of precipitation received. Treatments 100N and 100R correspond to control and procedural control, respectively. C. Example of the distribution of seedlings in each plot. Each color corresponds to one of the four species tested: white spruce, black spruce, jack pine, and balsam fir.

Treatments

Rainwater was completely intercepted within all but two treatments: non-interception control (100N) and 150% treatments. Rain was intercepted by a combination of a 37 m² (7.6 m x 4.9 m) transparent, 0.15-mm thick, polyethylene tarp held 2-2.5m above ground

with a galvanized steel structure and gutters on the sides of the tarp. The proper circulation of air under the tarp helped limit the accumulation of heat (Figure 2). Levels of intercepted rain were controlled by varying lengths of rain gutters. The collected water was redistributed by drip-irrigation, an approach that achieves good watering consistency with low water pressure (6psi). Twelve rows of 30 cm pierced hoses (Aqua-TraXX PBX, TORO Agricultural Irrigation, Fiano Romano, IT) were placed along each row of seedlings, and distributed $2.65\text{-}3.78 \text{ l}\cdot\text{min}^{-1}$ of water under each shelter. Such a flow was equivalent to a rain of $4\text{-}6 \text{ mm}\cdot\text{hour}^{-1}$, comparable to the natural precipitation flow of $2\text{-}10 \text{ mm hour}^{-1}$ measured in the area. Sufficient pressure was achieved using the differences in altitude between blocks based on the moderate slope of the site (9-12%). Following this logic, the water collected upslope was redistributed to the mid slope plots, and mid slope plot water was redistributed to downslope plots. To irrigate upslope plots, wooden panels covered with a polyethylene tarp were installed upslope to collect the necessary amounts of water.



Figure 2. Aerial view of the experiment (left) and example of plot in spring before tarp installation (right). Photographs by Charles Massicotte (left) and Loïc D'Orangeville (right).

A total of 2,160 nursery-grown seedlings of black spruce, white spruce, jack pine and balsam fir were planted in June 2014 (540 trees per species). All seedlings were 35-cm high except jack pine, which were 20-cm tall. The seeds used to produce the plants came from seed orchards, except for the balsam fir, which were naturally sourced. Each of the 18 plots was planted with 120 seedlings (30 per species) with a 40-cm equal spacing. Each plot was divided into three subplots perpendicular to the slope

A. Location of the study site. B. Schematic diagram of experimental design Values at the center of each plot correspond to the percentage of precipitation received. Treatments 100N and 100R correspond to control and procedural control, respectively. C. Example of the distribution of seedlings in each plot. Each color corresponds to one of the four species tested: white spruce, black spruce, jack pine, and balsam fir. Each subplot contained ten seedlings of

each species in randomly arranged pairs of rows. A 1-m buffer zone surrounded the edge of each plot within the footprint of the rain-exclusion system.

Preliminary moisture manipulation treatments were initiated in August-October 2014 and June-October 2015 to assess the treatment effects on soil moisture. Tarps were removed before winter to avoid potential breakage due to snow accumulation. A spatial and temporal analysis of soil moisture variations during 2015 revealed a persistent moisture gradient perpendicular to the slope driven by differences in bedrock depth. While the treatments did redistribute the expected amounts of water, soil moisture levels remained lower in parts of the study area with shallower soil, confounding some of the treatment effects on soil water content. Because of this, a decision was made to modify the focus of the “experimental unit” away from the “treatment label”, since it was not an accurate descriptor of plant available water. Instead, each tree became our focus unit, along with records of soil water content measured at the tree level. We also decided to amplify the observed moisture gradient by increasing the rain exclusion in certain treatments (upper slope: 80% became 0% of incoming rain; mid slope: 80% and 60% became 40% and 30% of incoming rain, respectively; lower slope: 80% became 40% of incoming rain; Figure 1). Following these changes described above, the experiment was followed through 2016 (June 6 to October 5), 2017 (June 21-September 26) and 2018 (June 13-September 11). ANOVA on SWC in 2015 and 2016, before and after treatment change, showed no significant difference

($P < 0.01$), so data in 2015 was analyzed with following years. Only these four years (2015-2018) were included in this analysis.

Data collection

Height and diameter of each seedling were recorded annually from 2015 to 2018 at the end of the growing season or the very beginning of the following growing season. Growth was obtained by subtracting the initial values (i.e., heights at the beginning of the growing seasons) from the values at the end of the growing seasons. Only seedlings that survived the 2015-2018 duration of the study were analyzed here. Because mortality due to drought treatment could not be differentiated from mortality due to other causes (e.g., insect damage, frost heave, snow damage, etc.) this eliminated survival selection bias and allowed a more complete and independent assessment of soil moisture effects. Soil moisture effects on survival were not considered in this study. Outliers were eliminated by a visual assessment. The final dataset consisted of 111 white spruce, 234 black spruce, 104 jack pine, and 156 balsam fir.

Volumetric soil water content (SWC) was measured every two weeks during each growing season using a systematic sampling scheme of 32 sample points within each plot using a FieldScout TDR-300 soil moisture probe with 20 cm rods (precision: 3% SWC; Spectrum Technologies Inc., Plainfield, USA). Soil water content for each seedling was estimated by using inverse distance squared weighted interpolation, expressed as percentage of volumetric soil water content. The four values closest to each seedling

(distances varied from 28 to 85 cm) were used to interpolate a water content for that seedling. Interpolation consisted of averaging the four values weighted by corresponding inverse of the square of the distance from each seedling.

Data analysis

One-way ANOVA was used to test the differences of soil water content across years and species. To test the difference of total growth under drought treatments between species (hypothesis 3), the growth of each specie was compared and one-way ANOVA was used to test the differences between species.

To test the relationship between soil water content in the early/ late season and two types of growth (hypothesis 1 and 2), a mixed effects regression model was fitted. July (J) and August (A) were defined as the months where water was limiting for early season tree growth, and the soil water content in this period was defined as the average SWC over these two months (SWC_{JA}). Similarly, September (S) and October (O) were the months when most current season growth was completed but soil moisture could impact the following-year growth, the soil water content during this period was estimated as the average over these months (SWC_{SO}). Soil water contents (SWC_{JA} and SWC_{SO}) and tree size were considered as fixed effects and year was considered as a random effect in a mixed effects regression model:

$$G = I + aX + b * SWC_{JA} + c * SWC_{SO} + d * X * SWC_{SO} + e \quad (1)$$

where G was the annual growth in diameter or height, I was the intercept term (with random effects associated with year, $I = i_0 + \omega_{year}$ where ω_{year} = random effect associated with year), X was tree size (diameter or height), i , ω_{year} , a , b , c and d were coefficients, fitted separately to each species, and e was the random residual error. All models were fitted using the lmer function in the NLME package (Pinheiro and Bates 2000), in R ((R Development Core Team 2019).

Results

SWC

Average SWC for each tree across years varied from 5%- 62% for July-August SWC (SWC_{JA}) and from 5%-50% for the September-October SWC in the previous year (SWC_{SO}). The SWC_{JA} were generally higher than the SWC_{SO} with the exception of 2017 (Figure 3); 2017 was significantly drier than all other years ($p < 0.01$, ANOVA). All species within plots were subject to similar SWC levels ($p = 0.89$, ANOVA) and the number of seedlings were evenly distributed across the SWC gradient.



Figure 3. Distribution of the July-August (left) and the previous year's September-October (right) soil water content (SWC) by growing season year.

Growth

Jack pine showed the greatest growth among species, while white spruce showed the least. Annual diameter growth increased over time, jack pine had the greatest in 2018 ($0.82 \pm 0.29 \text{ cm} \cdot \text{yr}^{-1}$; Figure 4), followed by black spruce, balsam fir, and white spruce. Height growths increased first, then decreased in 2017 due to the lowest annual SWC (Figure 3 and 5). White spruce showed the lowest annual height growth ($10.77 \pm 7.88 \text{ cm} \cdot \text{yr}^{-1}$; Figure 5), the growth of black spruce and balsam fir was double that ($21.04 \pm 12.20 \text{ cm} \cdot \text{yr}^{-1}$ and $20.91 \pm 9.80 \text{ cm} \cdot \text{yr}^{-1}$, respectively), jack pine was more than triple that ($38.54 \pm 12.19 \text{ cm} \cdot \text{yr}^{-1}$). This level of growth consisted to 2018. After four years of SWC control, jack pine showed a significantly higher growth, while white spruce was significantly lower than others ($P < 0.01$, ANOVA). The difference between black spruce and balsam fir was not significant ($P > 0.1$). In addition, the high standard deviation reflected the wide effect range of SWC treatments.

Jack pine annual diameter growth usually showed the greatest intercept while white spruce showed the least. For example, the intercept of jack pine was $0.568 \text{ cm} \cdot \text{yr}^{-1}$ in 2018, while that of white spruce was $0.278 \text{ cm} \cdot \text{yr}^{-1}$ (Figure 6). The slopes were initially flat and some species were negative, but generally transitioned to positive and increased with time. For instance, the slope between SWC_{SO} and annual diameter growth of balsam fir was $-0.003 \text{ cm} \cdot \text{yr}^{-1}$ in 2014 but $0.306 \text{ cm} \cdot \text{yr}^{-1}$ in 2017, while that of white spruce was $-0.001 \text{ cm} \cdot \text{yr}^{-1}$ in 2014 but $0.002 \text{ cm} \cdot \text{yr}^{-1}$ in 2017 (Figure 6).

As same as diameter growth, height growth of jack pine showed the greatest intercept and white spruce showed the least. In 2018, the intercept of jack pine was $35.4 \text{ cm}\cdot\text{yr}^{-1}$ while that of white spruce was only $3.79 \text{ cm}\cdot\text{yr}^{-1}$ (Figure 7). The slope was initially flat but sharper with time. For instance, the slopes of balsam fir and black spruce between SWC_{JA} and annual diameter growth were $-0.117 \text{ cm}\cdot\text{yr}^{-1}$ and $-0.069 \text{ cm}\cdot\text{yr}^{-1}$ in 2015, however, that of balsam fir and black spruce became $0.511 \text{ cm}\cdot\text{yr}^{-1}$ and $0.178 \text{ cm}\cdot\text{yr}^{-1}$ in 2018 (Figure 7). In addition, level of the effect of SWC mainly ranging from 5-40 % (Figure 6 and 7).

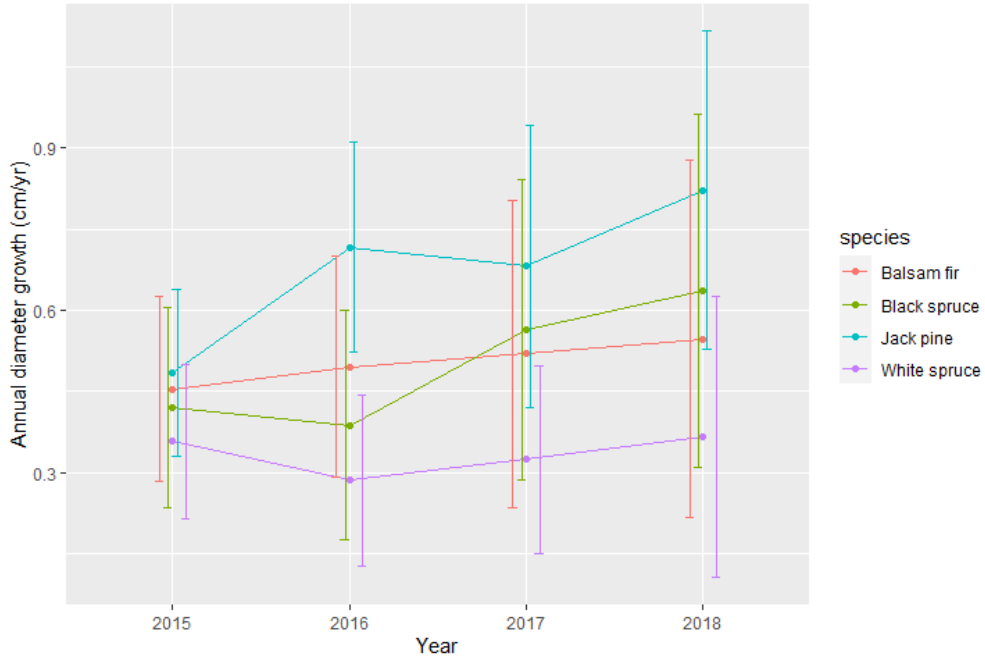


Figure 4. Average diameter growth by year and species (vertical bars indicate ± 1 sd).

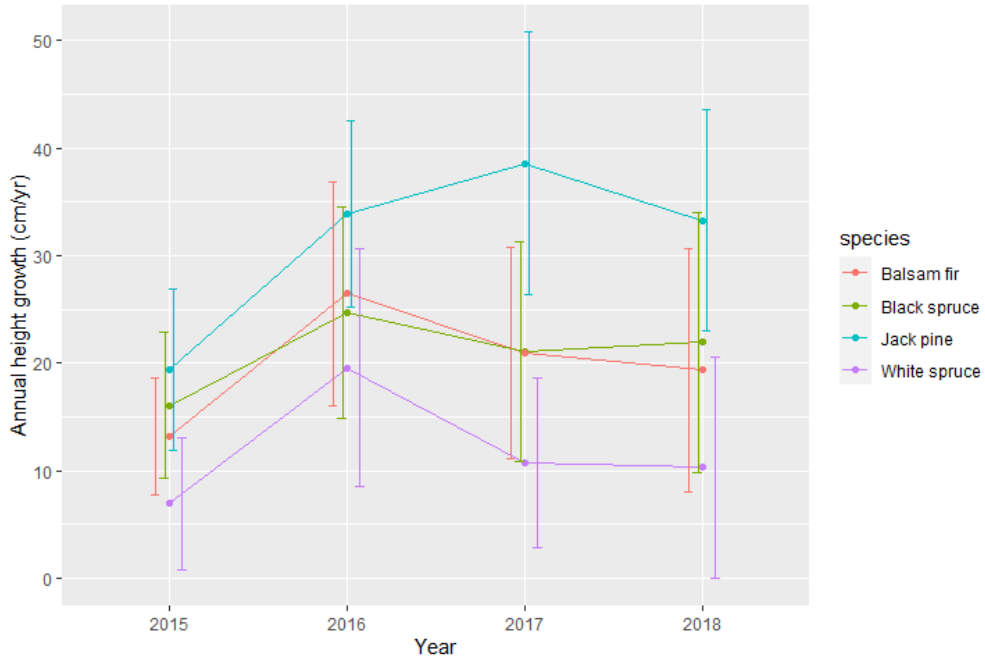


Figure 5. Average height growth by year and species (vertical bars indicate ± 1 sd).

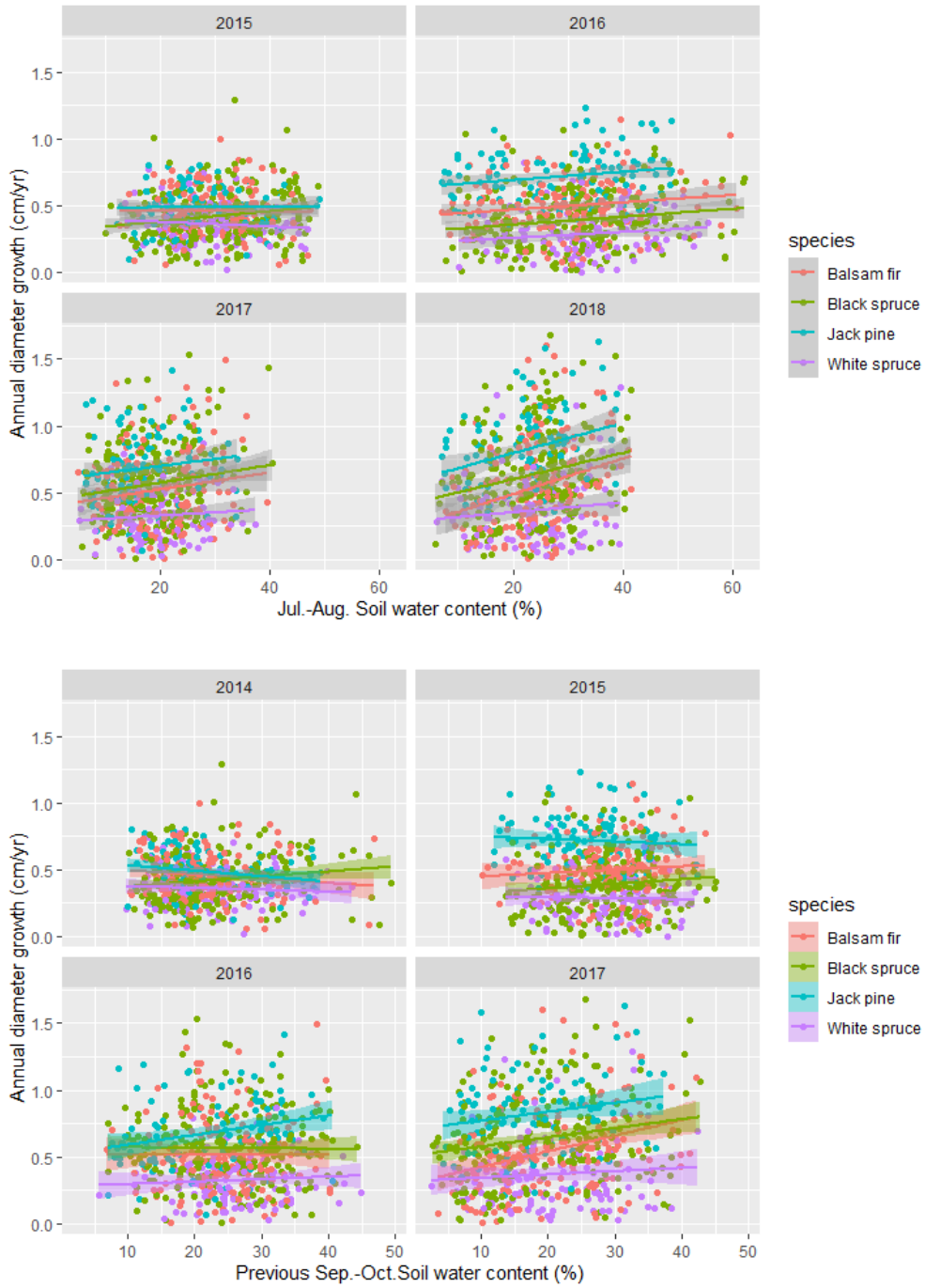


Figure 6. Annual diameter growth across the July-August and the previous year's September-October soil water content by species, using linear smoother.

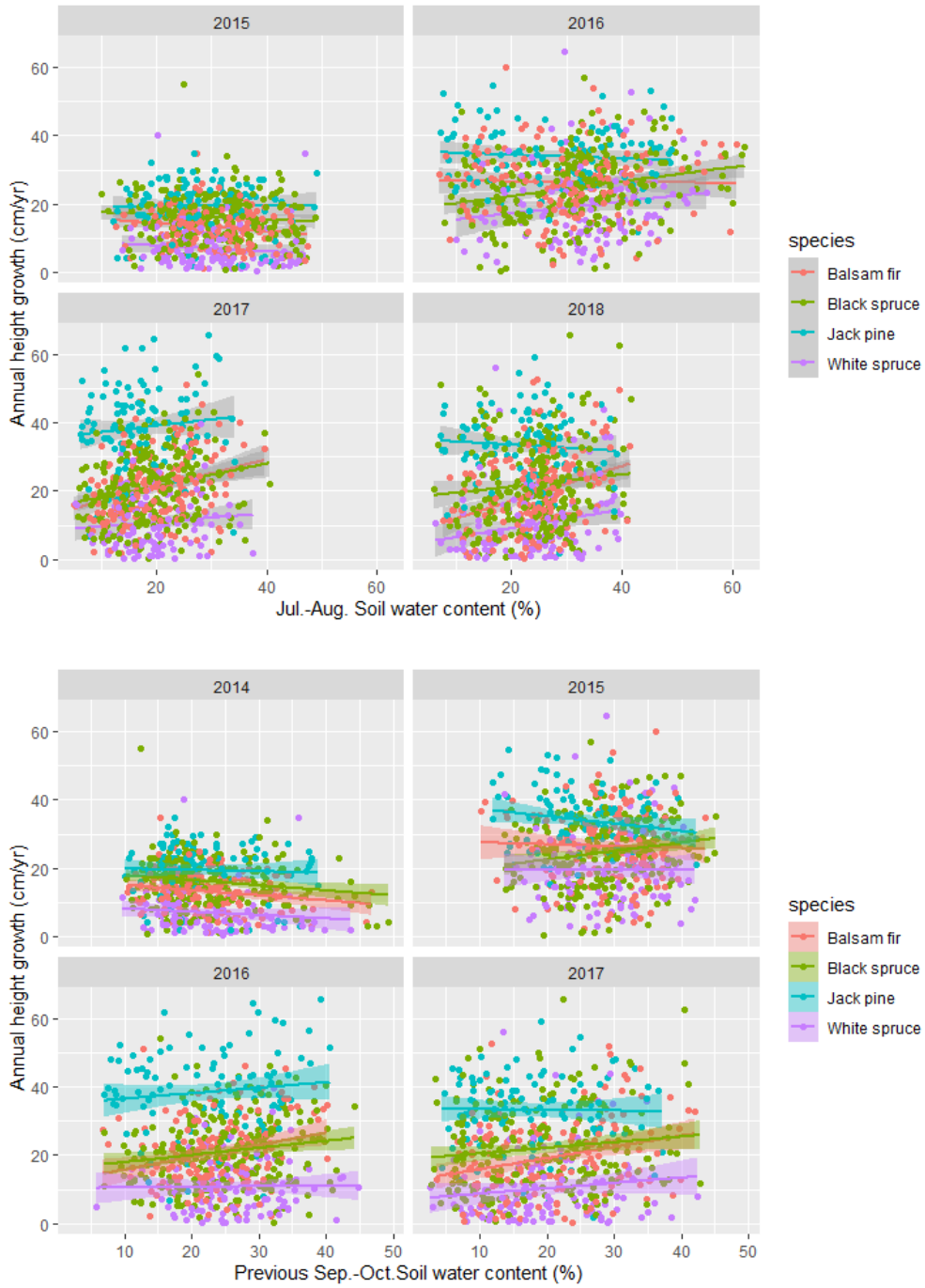


Figure 7. Annual height growth across the July-August and the previous year's September-October soil water content by species, using linear smoother.

Mixed Effects Modeling

- Increasing SWC_{JA} significantly increased the diameter growth of jack pine and balsam fir, while increasing SWC_{SO} was significantly associated with their reduced diameter growth (Table 1). Increasing SWC_{JA} was also significantly associated with increased black spruce diameter growth (Table 1). When SWC_{JA} increased from 18% to 32%, the annual diameter growths of black spruce, jack pine and balsam fir was predicted to increase by $0.061 \text{ cm}\cdot\text{yr}^{-1}$, $0.082 \text{ cm}\cdot\text{yr}^{-1}$ and $0.049 \text{ cm}\cdot\text{yr}^{-1}$, respectively (Figure 6a, c, d). The diameter parameter was not significant for any species, but the interaction between diameter and SWC_{SO} was significant and positive for jack pine and balsam fir (Table 1). As a result, large trees would display increased growth while small trees display decreased under higher SWC_{SO} . The threshold where there was a difference in diameter growth related to SWC_{SO} was about 2 cm (Figure 8). When previous-year fall moisture (SWC_{SO}) increased from 17% to 30% and seedling diameter was 4cm, the annual diameter growth was predicted to show the greatest increase, $0.237 \text{ cm}\cdot\text{yr}^{-1}$ for jack pine (Figure 8c) and $0.242 \text{ cm}\cdot\text{yr}^{-1}$ for balsam fir (Figure 8d). Intercepts were from $0.3081 \text{ cm}\cdot\text{yr}^{-1}$ to $0.5938 \text{ cm}\cdot\text{yr}^{-1}$ for black spruce, jack pine and balsam fir, but only $0.1125 \text{ cm}\cdot\text{yr}^{-1}$ for white spruce (Table 1). Estimates for significant SWC or interaction was all small, which was consistent with the flat slopes (Figure 6)

The height growth of black spruce significantly increased with increasing SWC_{JA} but significantly decreased with increasing SWC_{SO} (Table 2). Increasing SWC_{JA}

significantly increased white spruce height growth, while SWC_{SO} was significantly and negatively associated with balsam fir height growth. When SWC_{JA} increased from 18% to 32%, the annual height growth was predicted to increase $2.309 \text{ cm}\cdot\text{yr}^{-1}$ (black spruce; Figure 9a) and $2.341 \text{ cm}\cdot\text{yr}^{-1}$ (white spruce; Figure 9b). The height parameter was not significant for any species, but the interaction between height and SWC_{SO} was significant for black spruce and balsam fir (Table 1). Consistent with diameter growth, higher SWC_{SO} would increase the height growth of large trees but decrease that of small trees. The threshold where there was a difference in height growth related to SWC_{SO} was about 70cm, 60cm, 60cm and 55cm, for black spruce, white spruce, jack pine and balsam fir, respectively (Figure 9). While when seedlings were 150cm high and the same SWC_{SO} was increased, the annual height growth increased from $3.403 \text{ cm}\cdot\text{yr}^{-1}$ for black spruce (Figure 9a) and $8.112 \text{ cm}\cdot\text{yr}^{-1}$ for balsam fir (Figure 9d). Intercepts were from $14.6787 \text{ cm}\cdot\text{yr}^{-1}$ to $33.9122 \text{ cm}\cdot\text{yr}^{-1}$ for black spruce, jack pine and balsam fir, significantly, but only $0.03 \text{ cm}\cdot\text{yr}^{-1}$ for white spruce and not significant.

Table 1. Parameter estimates and associated standard errors (in parentheses) and regression summary statistics for the linear mixed effects model (Eq. 1) for diameter growth by species. Bold values indicate statistically significant ($p < .05$) parameter estimates.

Factor	Parameter	Species			
		Black spruce	White spruce	Jack pine	Balsam fir
Fixed effect	Intercept	0.3081	0.1125	0.5938	0.5425
		(0.0818)	(0.1154)	(0.0901)	(0.0927)
	Diameter	0.0578	0.1249	-0.0056	-0.0909
		(0.0454)	(0.0725)	(0.0489)	(0.0487)
	SWC _{JA}	0.0043	0.0021	0.0059	0.0035
		(0.0012)	(0.0013)	(0.0016)	(0.0013)
	SWC _{SO}	-0.0032	-0.0052	-0.0132	-0.0112
		(0.0027)	(0.0040)	(0.0037)	(0.0038)
	Diameter* SWC _{SO}	0.0025	0.0040	0.0079	0.0075
		(0.0015)	(0.0027)	(0.0019)	(0.0020)
Random effect	s(Intercept)	0.0872	0.0834	0.0721	0.0000
Goodness-of-fit					
	Fixed	R ²	0.0645	0.1633	0.2047
Fixed+random					
		R ²	0.1650	0.3097	0.2803
	RMSE	0.2560	0.1866	0.2244	0.2476

Table 2. Parameter estimates and associated standard errors (in parentheses) and regression summary statistics for the linear mixed effects model (Eq. 1) for height growth by species. Bold values indicate statistically significant parameter estimates ($p < .05$).

Factor	Parameter	Species			
		Black spruce	White spruce	Jack pine	Balsam fir
Fixed effects	Intercept	14.6787	0.0302	33.9122	18.9766
		(3.5916)	(5.9614)	(5.4036)	(4.7698)
	Height	0.0304	0.1306	-0.0346	-0.0413
		(0.0399)	(0.0727)	(0.0508)	(0.0502)
	SWC _{JA}	0.1650	0.1672	-0.0068	0.0951
		(0.0458)	(0.0627)	(0.0734)	(0.0543)
	SWC _{SO}	-0.2677	-0.1586	-0.1576	-0.3816
	(0.1239)	(0.1963)	(0.1457)	(0.1431)	
	Height* SWC _{SO}	0.0035	0.0018	0.0024	0.0067
		(0.0014)	(0.0028)	(0.0017)	(0.0018)
Random effects	s (Intercept)	3.2646	5.8900	8.0056	5.6298
Goodness-of-fit					
	Fixed	R ²	0.0732	0.0861	0.0052
Fixed+random					
		R ²	0.1676	0.3724	0.4013
	RMSE	9.8545	9.3682	10.8845	9.7569

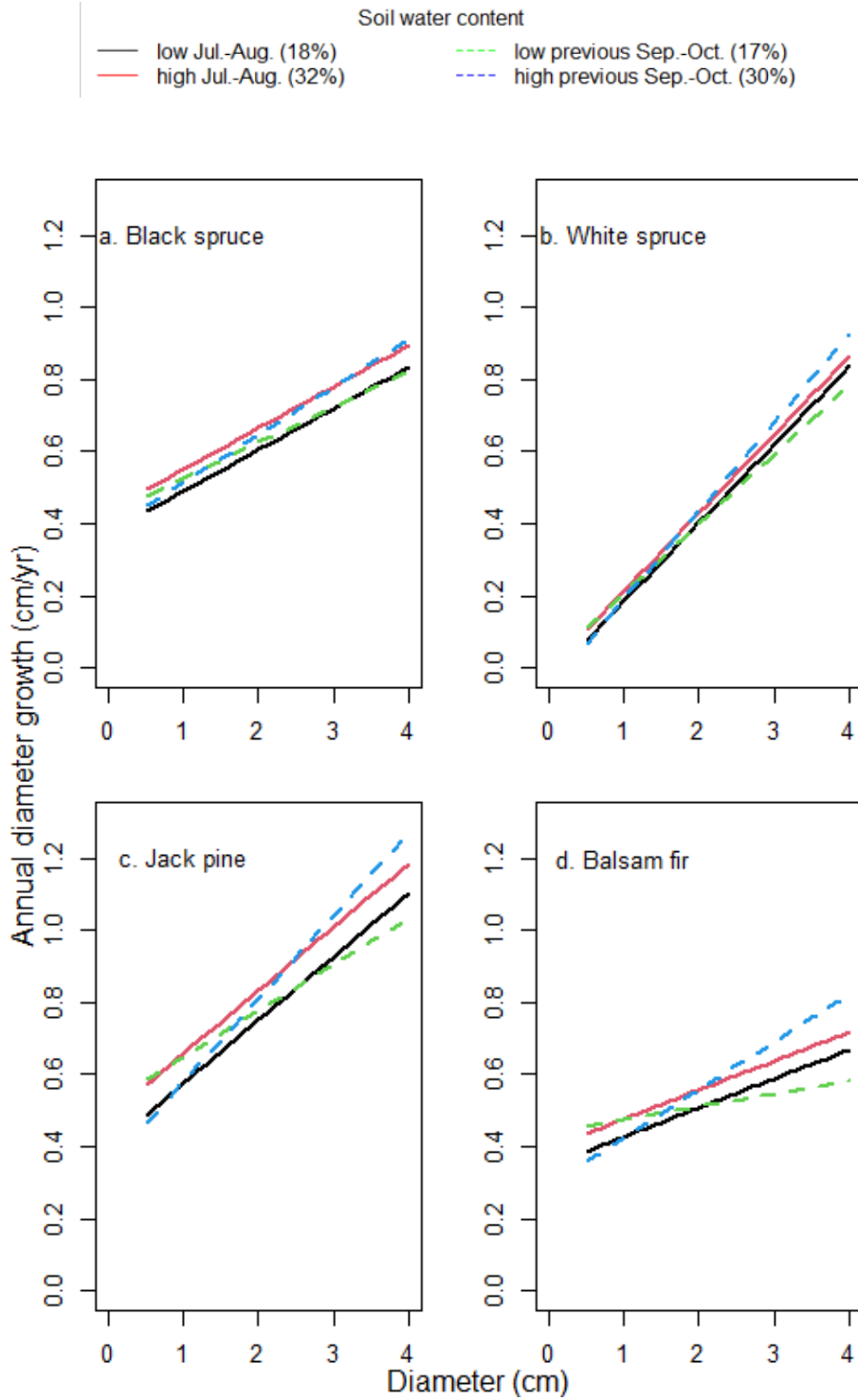


Figure 8. Fitted diameter growth by diameter, species, and soil water content based on estimates from equation 1 (Table 1).

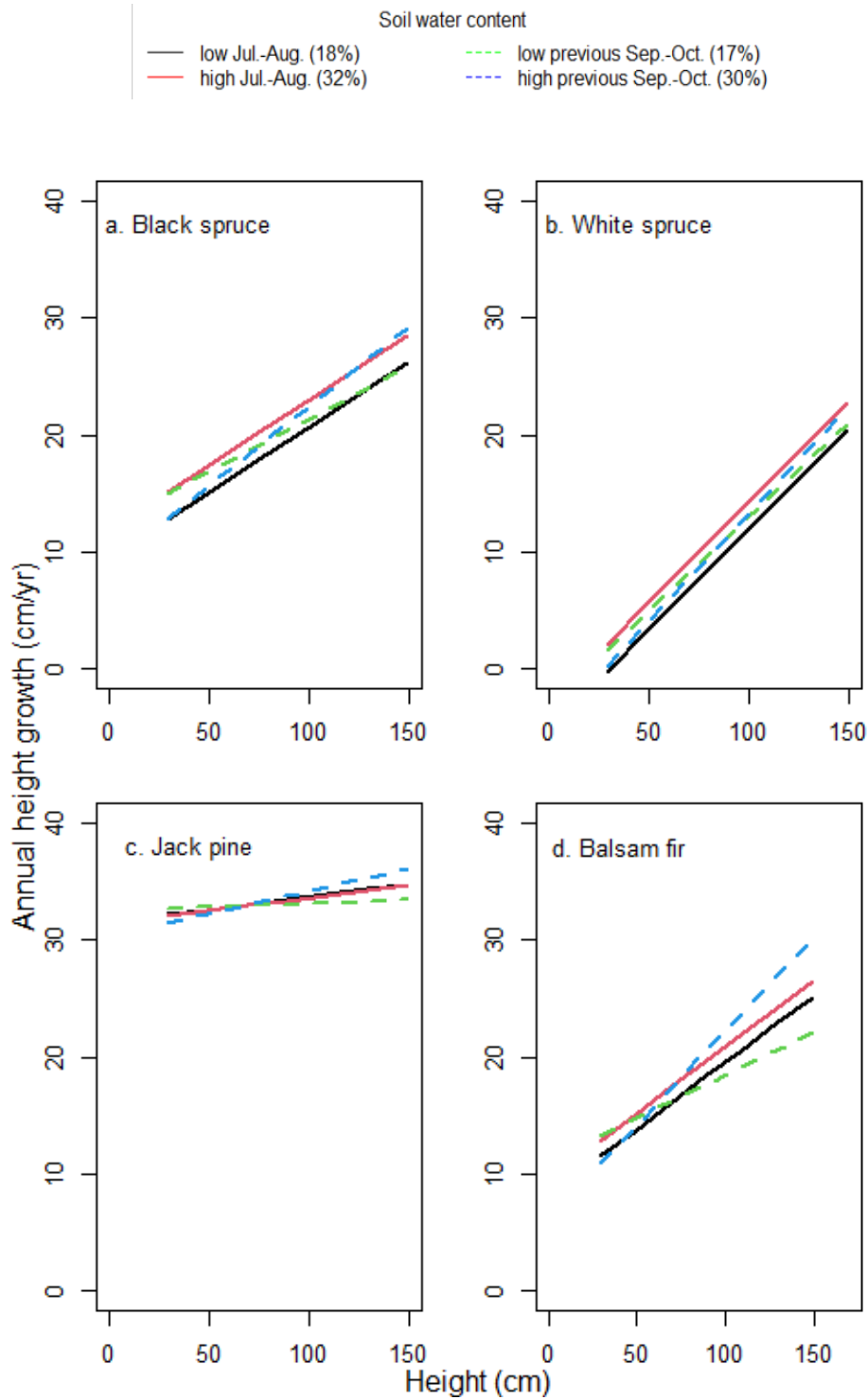


Figure 9. Fitted height growth by height, species, and soil water content based on estimates from equation 1 (Table 2).

Discussion

Our hypotheses were that (1) diameter and height growth decline with lower SWC_{JA} and with higher SWC_{SO} , (2) diameter growth is more sensitive to SWC_{JA} while height growth depends on SWC_{SO} and (3) jack pine will show faster total growth under drought treatments, followed by black spruce, balsam fir, and white spruce. Our models show lower SWC_{JA} reduced diameter growth of black spruce, jack pine and balsam fir and height growth of black and white spruces, while lower SWC_{SO} decreased jack pine and balsam fir diameter growth and black spruce and balsam fir height growth (Table 1 and 2), except for smaller seedlings (Figure 8 and 9). Therefore, the correlations between SWC and diameter and height are identical (Table 1 and 2). Those results are partly against our first hypothesis and totally counter to the second hypothesis. Finally, the total growth order is jack pine, black spruce/balsam fir and white spruce (Figure 6 and 7), as same as our third hypothesis.

Consistent with previous findings and our first hypothesis, our results show summer drought would reduce height growth of two spruce species and diameter growth of black spruce, jack pine and balsam fir. However, the effects from soil water content are quite small, perhaps the water requirements of those seedlings are relatively small, given their current size. Sullivan et al. (2017) confirmed that water supply in August had a positive correlation with the growth of black and white spruce. Black spruce also showed reduced

diameter growth under summer drought treatment (Belien et al. 2012). Many water-dependent activities are ongoing in summer, which require sufficient quantities of water (Tardif et al. 2001). Tree height growth is a product of the apical meristem whose cells divide and elongate at the base of the bud (Koch et al. 2004). Diameter growth is driven by cell division and expansion in the cambium layer, which relies on a direct water supply (Deslauriers et al. 2016). Cell division and enlargement last from May to July in Québec boreal forests, with another month to complete cell wall formation (Deslauriers et al. 2003). This explains the dependence of radial growth on summer moisture (Table 1). However, diameter growth, as a secondary growth event, is also controlled by the foliage biomass and water that the stem needs to transport, which is associated with height growth (Hoyle 1965). The link between diameter and height makes them both affected by moisture in the current and previous growing seasons, counter to our second hypothesis.

Our results suggest higher soil water content in the previous year's late growing season (SWC_{SO}) leads to more jack pine and balsam fir diameter growth and black spruce and balsam fir height growth (Table 1 and 2), except for smaller seedlings (Figure 8 and 9), partly against our first hypothesis. In a throughfall exclusion experiment of balsam fir seedlings, 32% reduction of terminal growth was observed after one year treatment (D'Orangeville et al. 2013). Renard et al. (2016) also reported that the survival and growth rate of white spruce seedlings was more sensitive to the late growing season

conditions rather than summer conditions. Late growing season drought can significantly reduce root depth, growth, and survival rates of shallow rooted seedlings (Padilla and Pugnaire 2007). Water deficits in the late growing season can delay the hardening of buds and inhibit cell differentiation, thus affect the growth in the following growing season (Grossiord et al. 2017). Drought will cause hydraulic damage, which will affect various water-dependent processes within a few years after the event (Anderegg et al. 2013). Adequate water supply in autumn can also be seen as the release of summer drought. Without it, the damage caused by summer drought may not be fixed, thus the accumulated damage will reduce the growth in next year.

A model fitting for jack pine and black spruce in boreal Ontario showed diameter growth would increase with increasing moisture in summer but decrease with increasing total precipitation (Subedi and Sharma 2013). Our models split the total moisture, or precipitation, to summer and previous fall and explain this situation from another aspect. Such results could indicate the possibility that growth rates are constrained by moisture in summer directly, while high moisture in fall reduces smaller seedlings growth the following year (Figure 8 and 9). In the early growth period, biological activities need large quantities of water; however, in the late growth period, where water-dependent activities slow down, water supply is perhaps greater than what is needed. High soil water content can limit microbial activity and decomposition rate, thereby decreasing

nutrient availability for plant growth; high moisture associated with high precipitation may indirectly reduce tree growth by decreasing radiation inputs (Schuur 2003). Isabelle et al. (2020) reported a wet boreal forest, dominated by mature balsam fir, in Montmorency always received excess precipitation than its physiological limit, over 60% of rainfall was not used and flowed away. However, this report focused on energy and water budget but not growth.

Interestingly, our results showed soil water content effects generally increase with tree size (Figure 6 and 7). It could be explained by the difference between small and large seedlings. Generally, small seedlings usually have a small and superficial rooting system, which makes them more vulnerable to soil conditions (Martín-Benito et al. 2008). Either too dry or too wet soil conditions would lead to poor soil respiration, thus limit root activities and are associated with growth reductions in the next year (Lavigne et al. 2004). However, small seedlings don't need as much water as large seedlings, thus the microsite moisture may be sufficient even high for them (Merlin et al. 2015). Large seedlings usually have higher resource and maintenance needs than small seedlings (Zang et al. 2012). Along with seedling growth, the water demand is increasing, the past high water for small seedlings is transiting to current insufficient water for large seedlings. Those factors may explain the opposite responses to the high previous fall moisture between smaller and larger seedlings.

Jack pine showed the highest growth under drought treatment, followed by black spruce, balsam fir, and white spruce (Figure 6 and 7), as same as our third hypothesis. Jack pine is just growing, whatever size and moisture, while the other species are more regulated by their size and moisture (Table 1 and 2). Jack pine can grow on very dry sandy or gravelly soils and has strong adaptability to drought (Rudolph and Laidly 1990). Black spruce and balsam fir usually compete in wet environments and grow well with adequate water (Nijssen and Lettenmaier 2002). White spruce can tolerate variable moisture conditions but prefer fertility soil (Wirth et al. 2008). Jack pine and black spruce are drought-resistant species, resisting drought by keeping stomatal conductance to maintain high transpiration and photosynthesis rates (Boucher et al. 2020). Black spruce will maximize its photosynthesis rate, while jack pine will optimize photosynthesis in balance with water loss, which is more suited to continuous drought (Tan et al. 1992, Stewart et al. 1995, Hébert et al. 2006). Jack pine has larger, deeper and faster growing root systems and is able to absorb water from deep soil layer rather than shallow layer (Blake and Li 2003). On the other hand, drought-resilient species, like white spruce, will control stomata conduction to reduce water loss but not maintain photosynthesis rates (Bigras 2005), which directly limits their growth rate. Balsam fir is also a drought-resilient species, but adjusting fine root production and mortality allows it to adapt to the environment (Olesinski et al. 2011). White spruce likes wet condition but cannot tolerant excessive water, in addition, its growth will not increase if only increase moisture without

increased fertility (Nienstaedt and C. Zasada 1990) , might be another reason for its low growth in this area.

Conclusions

In order to study the impact of water limitation on boreal forest growth, a water manipulation experiment consisting of soil water content control during the growing season was conducted for 4 consecutive years in a humid boreal forest of Québec, Canada. A linear mixed model was built to predict the effects of soil water content on growth. Increasing SWC in early growing season of the current year increased diameter growth for black spruce, jack pine and balsam fir and height growth for black spruce and white spruce. Higher SWC in the later growing season of the previous year increased the diameter growth for jack pine and balsam fir and height growth for black spruce and balsam fir, except for small seedlings. Diameter and height growth are associated with each other and are both affected by SWC in two growing seasons. Jack pine showed the highest growth under drought treatment, followed by black spruce, balsam fir, and white spruce. Our experiment suggests drought has a chronic and cumulative growth-reduction effect, highlighting the importance of further research on species-specific mechanisms under chronic drought. Warming may increase evapotranspiration during summer and reduce the availability of soil moisture, but the risk of water stress in this wet area is less than other area. Fall drainage may be needed to maintain the growth of seedlings when they were small.

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Curriculum Vitae

Detian Zhao

Nanjing Forestry University

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