Growth of Six Conifer Tree Species Under Early and Late-Season Drought Treatments

by

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Abstract

The projected increase in water stress in boreal forest ecosystems due to climate change is predicted to alter many phenological responses in trees. To test this prediction, under controlled conditions, I subjected seedlings of six Acadian Forest coniferous species to three drought treatments and documented their survival, height growth and biomass allocation patterns. The drought treatments included early-season drought, late season drought, and a control.

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1. Introduction

Greenhouse gases are thought to cause climate warming leading to increased occurrences and intensities of surface drought (Adler et al. 2017). While surface droughts have minimal impacts on mature trees (Aber and Driscoll 1997), they can lead to increased mortality in seedlings (Mueller et al. 2005, Moore et al. 2016) resulting in reduced regeneration and potential changes in the species composition (Redmond et al. 2018). Current research mainly focuses on the effects of drought with varying intensities on tree seedlings (Rajarajan and Handa 2020, McDowell et al. 2008), but there has been limited study on how the timing of drought within the growing season varies in the impacts on seedlings.

New Brunswick (NB) is a province in eastern Canada rich in forest resources (Government of New Brunswick 2011). Forests comprise about 85% of the landscape and, as such, the ecology and the economy of the province are largely based on the trees species that comprise the forests (Erdle 2019). The major native coniferous species that dominate NB forests include red spruce (Picea rubens), balsam fir（Abies balsamea), black spruce (Picea mariana), eastern white pine (Pinus strobus), eastern white cedar (Thuja occidentalis), and eastern hemlock (Tsuga canadensis). Some jack pine (Pinus banksiana) naturally occurs, and some Norway spruce (Picea abies) has been planted. Overall, conifers comprise about 45% of the forest composition (Canada 2018).

In the past 30 years, the annual average temperature in NB has risen by 1.1°C, and the province's average temperature is expected to rise by about 5°C under current projected rates of change (Government of New Brunswick 2011) , with some areas becoming warmer than others. Forecasts also indicate that the number of very hot days (days above

30°C) and the length of the growing seasons will increase significantly (Government of New Brunswick 2010). The implication is that drought may become more common and may persist for longer periods of time (Overpeck and Udall 2020).

Drought directly affects trees by slowing or preventing photosynthesis (Ryan 2011) and it can cause injury or death as well as limit growth (Pinheiro and Chaves 2011). Photosynthesis is required to produce the energy needed for growth and respiration (Molnar and Gair 2015). Carbon starvation occurs when trees close their stomata to maintain a safe level of xylem pressure (Sevanto et al. 2014, Chen et al. 2019). This results in a reduction or even cessation of photosynthesis (Salmon et al. 2019， Kulaç et al. 2012). When photosynthesis is halted, trees must rely on stored carbohydrates to support tissue metabolism (Adams et al. 2009). More severe droughts can lead to xylem cavitation and embolism (Trifilo et al. 2014). This further limits the transport of nonstructural carbohydrates (NSC) and nutrients between different organs (Mencuccini and Hölttä 2010). In studies of adult conifer species, early-season drought reduced current tree growth, while late-season drought significantly reduced growth in the following year (D'Orangeville et al. 2018， Foster et al. 2014, Mendivelso et al. 2014).

For seedlings, with limited capacity to store carbohydrates, drought can result in increased mortality rates (McDowell et al. 2008).

Drought resistance varies greatly among species. (Herrero and Zamora 2014). For the NB coniferous species, drought is likely to have different impacts depending on its timing, severity, and frequency (Gazol et al. 2020). For eastern hemlock, a series of mid-century low-water events coincided with the sudden decline of hemlock and interrupted

subsequent phases of hemlock recovery. (Marsicek et al. 2013). Most research has focused on the impacts of drought on forest insects and disease (Kolb et al. 2016; Domec et al. 2013). Studies of drought impacts on seedlings are lacking. For red spruce, there is little information regarding the impact drought has on the species. Red spruce showed a positive response to precipitation and radial growth was mainly limited by temperature (Ribbons 2014). In eastern white cedar, drought reduces shoot biomass (Steven and Gaddis 2017). Low water utilization also significantly reduces shoot biomass, root:stem ratio, and seedling stem diameter in cedar seedlings (Steven and Gaddis 2017). Studies on white spruce show that, under water stress, stomata close fast, and epidermal transpiration rates are lower (Trouvé et al. 2015). Drought increased root growth ability of white spruce but not the root quality (Tan 2007). White spruce survival rates under drought were 78 % - 97% of survival under non-drought conditions, indicating that drought may lead to increased mortality (Sang et al. 2019). While drought increased mortality, there was little effect on white spruce biomass (Lu et al. 2019). In balsam fir, drought reduced year-end fine root biomass growth (Olesinski et al. 2011). Balsam fir growth also declined with the onset of major droughts (Adams et al. 1985). For Norway spruce, a species native to Europe, growth was negatively impacted by drought (Svobodová et al. 2019). In young Norway spruce, crowns of severely drought-affected trees had significantly lower biomass and fewer tracheids and tracheid rows compared to trees not impacted by drought (Lu et al. 2019). Norway spruce root systems were more sensitive to drought than the aerial parts (Velasco-Conde et al. 2012). Much of the work focuses on mature trees with very few studies of seedlings. In addition, most

studies were observational rather than controlled, so factors other than drought may confound the results.

In this study, a greenhouse experiment was used to determine how the timing of extreme drought affects the growth, survival, and distribution of biomass in northern conifer seedlings. Specifically, we investigated how the timing of intense drought affected the survival, height growth and biomass allocation patterns of seedlings of conifer tree species common to New Brunswick. The study aims to answer the following questions:

(1) How does drought in different periods affect the growth of coniferous species, what differences exist between different species under drought treatment.

(2) How do different drought treatments affect the survival rate of seedlings, and how do survival rates vary across the different species.

(3) How does drought affect the distribution of seedlings biomass, and how does it vary among the different species.

2. Methods

2.1 Experimental design

To determine species response to the timing of extreme drought, a greenhouse experiment was conducted using 72 two-year-old seedlings Six species with 12 seedlings per species were divided into three groups (4 seedlings/species/group) and subject to one of three drought treatments: no drought; early drought; and late drought. Seedlings were grown over one growing season (18 weeks) under artificial light, heating, and the associated drought treatments.

Prior to the experiment, seedlings were germinated from seed in a growth chamber, transferred to a green house, then overwintered outdoors. At the beginning of the 2nd growing season each seedling was repotted into a 15cm ×15cm pot and grown a second season outdoors. Seedlings were then over wintered outdoors until January 2020 when this experiment was initiated. In January 2020, these 2-year-old seedlings were moved to a greenhouse, warmed, and watered for a week to break dormancy. The experiment began on January 31st, 2020, and ended 126 days later (June 5th, 2020).

Seedlings were grown in a greenhouse with uniform lighting conditions (175 μmol/m^-2/s^-1) for 12 hours a day. Seedlings were watered by hand every two days and water was applied until the soil was saturated (flowing out of the pots). Table 1 gives the watering schedule. For the no drought or control seedlings, watering was performed throughout the 18-week growing period. For the drought treatments watering was stopped for a 3-week period. The early drought treatment began on week 3 and the late

drought treatment on week 7. Normal watering resumed after the treatments ended. In order to study the impact of drought on different growth periods of seedlings, we identified two stages for drought treatment beginning at the end of the 3rd week of seedling growth and beginning at the end of the 6th week (Table 1).

Table 1. Watering schedule for the three drought treatments.

	Week 1- 3	**Week 4 -Week 6**	**Week 7-Week 9**	**Week 10-Week18**
No drought treatment	Seedlings were watered every 2 days			
Early drought treatment	Seedlings were watered every 2 days	Not watered	Seedlings were watered every 2 days	
Late drought treatment	Seedlings were watered every 2 days		Not watered	Seedlings were watered every 2 days

2.2 Data collection

Heights of seedlings were measured at day 0 and then remeasured weekly throughout the experiment or until the time of death. Heights were measured to the nearest 0.1cm from the soil surface to the seedling's apical tip.

Mortality was assessed during the weekly measurements. Seedlings that had wilted, stopped growing (no height growth for two consecutive weeks), or had dry foliage and branches were determined to be dead (Figure 1). The time of death (date) was noted.

Figure 1. Balsam fir death as recorded on April 11, 2020（11/4/2020 Balsam fir）

On day 127, the experiment ended, and each surviving seedling was removed from its pot. Pruning shears were used to cut the root from the stem at ground line. Seedlings were dissected and separated into component parts: foliage; woody material consisting of the stem and branches; and roots. The root together with the soil were immersed in a bucket of water to separate them. Components were placed in an oven and dried at 70°C for 48 hours, then weighed on an electronic scale (nearest 0.1 g).

2.3 Data analysis

Survival

Survival was assessed in terms of both overall survival rate and timing of mortality. The overall survival rates of seedlings were the ratio of the number of seedlings that live to the total number. Survival rates by treatment were determined for each species and each treatment. Survival rates before, during, and after drought treatments were assessed.

Height Growth

To determine effects of drought treatments on height growth three adjustments to the data were made. First, height growth is only reported for surviving seedlings. Second initial height was used to standardize seedling size. Finally, a logistic function was fitted to the height growth data to make the results easier to interpret.

Removing effects of mortality

Under drought treatment, some seedlings died. Dead seedlings do not have subsequent height growth. Height growth was only analyzed on seedlings that survived the duration of the experiment.

Controlling for initial height differences

One challenge in comparing height growth responses within a species is that initial seedling heights differed at the beginning of treatments. Initial size differences may mask treatment differences. To remove effects of different initial tree heights, the starting point was made the same by averaging height of the three largest seedlings for each species (1 for each treatment) and this value was used as the initial height for all seedlings for that species – treatment combination. The shape of each seedling's height growth curve remained the same, it was just shifted up or down. For example, The standardization formula was：

$$\text{Initial height} = \frac{H_1+H_2+\cdots H_n}{n} \qquad (1)$$

where H is the initial height of each seedling and n is the number of seedlings.

Smoothing height growth trends

Measured heights often varied up and down throughout the growing season. These variations may be caused by a loss of turgidity in the terminal bud or may be due to measurement errors. To minimize impacts of erratic height data on treatment interpretation, the height response curve for each treatment was fitted to a logistic model:

$$Height_t = H_0 + H_1(1 - e^{-R \cdot T})^S \qquad (2)$$

where t is the day of the year, In this model, T represents the time of the maximum growth rate. H_1corresponds to the total height growth, R corresponds to the maximum growth rate. Rstudio (*v3.5.2*; R Core Team 2018) was used to fit Eq. 2 to each seedling's height data (D'Orangeville and al., 2013)

Biomass Allocation

Seedling biomass was divided into foliage, aboveground wood (stem and branches) and belowground. Total biomass was calculated as the sum of the three components. Relative biomass was calculated as the proportion of a seedling's component biomass to it's total biomass:

$$Relative\ biomass = \frac{\text{component biomass}}{\text{Total dry biomass of the individual}} \qquad (3)$$

The aboveground/belowground biomass ratio was calculated as the sum of foliage and wood divided by the belowground (root) biomass (A:B = (W+F)/B). Similarly, the foliage/root biomass ratio was calculated as the foliage biomass divided by the root biomass (F:R = F/B).

3. Results

3.1 Survival

Under conditions of no drought, all seedlings of all species survived to the end of the 18-week experiment (Table 2). Red spruce survival was not impacted by either drought treatment, and all seedlings survived the entire 18-week experiment (Table 2). Similarly, Norway spruce had no observed mortality from early drought and minimal mortality (1 seedling) under late drought (Table 2). Early drought had a greater impact on eastern white cedar and white spruce than did late drought (Table 2). Balsam fir and eastern hemlock were very sensitive to both drought treatments with low survival rates under either treatment (Table 2).

Table 2. Number of trees surviving at the beginning and end of the experiment by species.

Species	Drought Treatment					
	None		Early		Late	
	Initial	Final	Initial	Final	Initial	Final
Eastern Hemlock	4	4	4	2	3	2
Red Spruce	4	4	4	4	4	4
Eastern White Cedar	4	4	4	1	4	3
Norway Spruce	4	4	4	4	4	2
White Spruce	4	4	4	2	4	3
Balsam Fir	4	4	4	2	3	1

With the exception of eastern hemlock, all mortality due to early drought occurred after the 3-week drought period ended and watering had restarted (Table 3). With later

drought, the mortality occurred either during the drought period or just after the drought period ended (Table 3).

Table 3. Seedling survival by week and species[1] by early and late drought treatments (Orange shading indicates the period of drought).

Week	Drought Treatment											
	Early						Late					
	EH	RS	EC	NS	WS	BF	EH	RS	EC	NS	WS	BF
0	4	4	4	4	4	4	4	4	4	4	4	4
1	4	4	4	4	4	4	4	4	4	4	4	4
2	4	4	4	4	4	4	4	4	4	4	4	4
3	4	4	4	4	4	4	4	4	4	4	4	4
4	4	4	4	4	4	4	4	4	4	4	4	4
5	4	4	4	4	4	4	4	4	4	4	4	4
6	2	4	4	4	4	4	4	4	4	4	4	4
7	2	4	3	4	2	2	2	4	4	4	4	3
8	2	4	1	4	2	2	2	4	4	4	4	3
9	2	4	1	4	2	2	2	4	3	4	3	3
10	2	4	1	4	2	2	2	4	3	2	3	2
11	2	4	1	4	2	2	2	4	3	2	3	2
12	2	4	1	4	2	2	2	4	3	2	3	2
13	2	4	1	4	2	2	2	4	3	2	3	2
14	2	4	1	4	2	2	2	4	3	2	3	2
15	2	4	1	4	2	2	2	4	3	2	3	2
16	2	4	1	4	2	2	2	4	3	2	3	2
17	2	4	1	4	2	2	2	4	3	2	3	2
18	2	4	1	4	2	2	2	4	3	2	3	2

[1]EH = eastern hemlock, RS = red spruce, EC = eastern white cedar, NS = Norway spruce, WS = white spruce, BF = balsam fir

3.2 Height growth

Tables 4 – 9 show the results of the fits of the von Bertalanffy – Richards equation to the individual seedlings by species and drought treatment. Figures 2 – 7 show the seedling height growth trajectories.

Red spruce (Table 6; Fig. 4) was the only species not sensitive to either drought treatment. The H_1 estimates ranged from 3.5 – 10.7 for the no drought seedlings and from 4.7 – 8.0 for the early drought seedlings and from 5.7 – 9.3 for the late drought seedlings. Similarly, there were no clear trends across the drought treatments for R or S (Table 6). The height growth trajectories reflect these observations with trajectories from all three drought treatments intermingled (Fig. 6).

Height growth of eastern white cedar (Table 7, Fig. 5), Norway spruce (Table 8, Fig. 6), and white spruce (Table 9, Fig. 7) were all sensitive to early drought, but not to late drought. Eastern white cedar height growth was the least impacted by early drought (Fig. 5). For both Norway spruce (Fig. 6) and white spruce (Fig. 7) maximum height growth was completed before the late drought treatment was applied.

Eastern hemlock (Table 4, Fig. 2) and balsam fir (Table 5, Fig. 3) height growth was sensitive to both drought treatments. Balsam fir height growth responded similarly to both drought treatments (Fig.3) with little or differences in responses between early and late drought treatments. Eastern hemlock height growth, on the other hand, was very sensitive to both drought treatments (Table 4, Fig. 2). Early drought had greater impacts on eastern hemlock height growth than later drought. The H_1 coefficient (asymptotic height growth) ranged from 7.4 cm to 13.9 cm for no drought trees, 5.0 cm to 7.0 cm for late drought, and 4.0 cm to 4.6 cm for early drought (Table 4). Early drought appeared to not only reduce asymptotic height growth, but also delayed the timing of maximum height growth (Fig. 2).

Table 4. Initial height (H_0), asymptotic maximum height growth (H_1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for eastern hemlock.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	29.5	8.3207	0.6440	24.4465	0.99	1.92
			(0.1009)	(0.0551)	(7.3200)		
None	2	35.5	13.946	0.4500	13.4240	0.99	7.63
			(0.1811)	(0.0318)	(2.7072)		
None	3	33.4	11.0975	0.5604	40.4343	0.98	23.36
			(0.2229)	(0.0651)	(18.3343)		
None	4	32.0	7.3613	0.5189	18.0525	0.98	10.45
			(0.1764)	(0.0746)	(8.2126)		
Early	1	30.6	4.6977	0.3662	8.5967	0.98	1.69
			(0.1496)	(0.0553)	(3.1082)		
Early	2	30.5	4.0576	0.5970	80.3313	0.92	34.87
			（0.2527）	（0.2119）	（129.8502）		
Late	1	24.7	7.0458	0.3282	8.1249	0.97	17.58
			(0.3190)	(0.0622)	(3.5077)		
Late	2	34.0	4.9991	1.2347	1737.3269	0.96	14.38
			(0.1517)	(0.3718)	(4041.2632)		

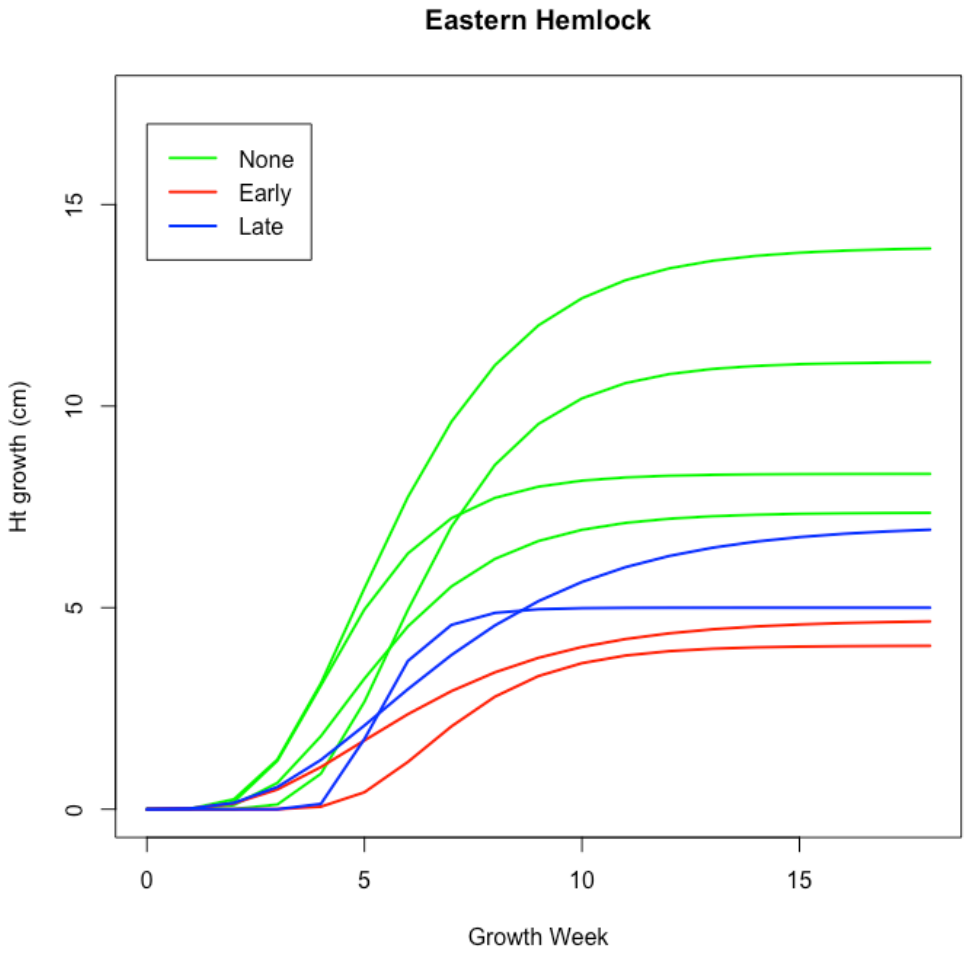

Figure 2. Height growth over the 18 week period for eastern hemlock by drought treatment.

Table 5. Initial height (H0), asymptotic maximum height growth (H1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for balsam fir.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	39.0	16.3991	0.5207	11.8898	0.99	27.57
			(0.2126)	(0.0436)	(2.8005)		
None	2	38.5	17.9793	0.6620	24.6337	0.98	389.09
			(0.3764)	(0.1002)	(13.0923)		
None	3	38.0	16.4281	0.6362	39.4325	0.99	66.46
			(0.2578)	(0.0660)	(16.0509)		
None	4	35.8	17.4921	0.5415	17.6568	0.99	120.89
			(0.3123)	(0.0607)	(6.2593)		
Early	1	39.2	6.5514	0.2319	2.5732	0.86	161.54
			(0.6996)	(0.1039)	(1.5411)		
Early	2	30.2	11.1761	0.4373	9.4055	0.97	98.03
			(0.3330)	(0.0740)	(4.0721)		
Late	1	33.7	8.1456	0.4521	6.5115	0.98	14.21
			(0.1879)	(0.0664)	(2.1917)		

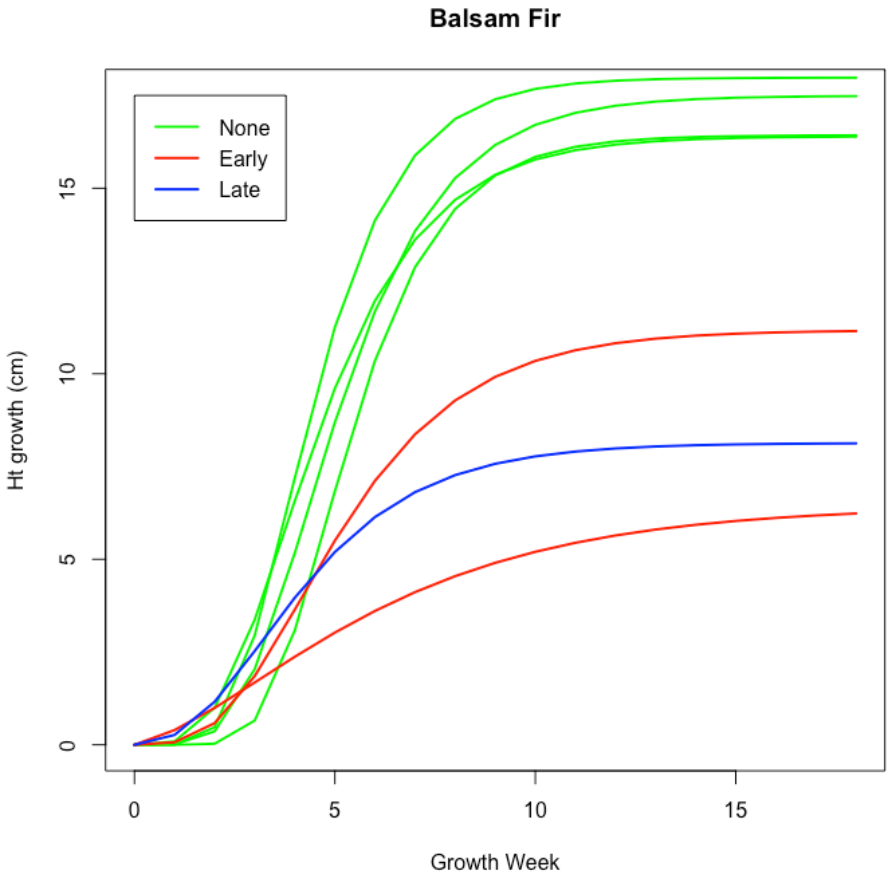

Figure 3. Height growth over the 18 week for Balsam fir by drought treatment.

Table 6. Initial height (H0), asymptotic maximum height growth (H1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for red spruce.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	27.1	3.5032	0.9679	148.7005	0.83	58.59
			(0.2149)	(0.5154)	(417.2940)		
None	2	31.3	5.2719	0.7649	210.7154	0.98	5.34
			(0.1387)	(0.1368)	(209.1667)		
None	3	30.4	5.9812	0.6973	81.9407	0.97	22.85
			(0.1973)	(0.1543)	(83.8990)		
None	4	28.2	10.7410	0.7668	72.5470	0.99	4.46
			(0.1218)	(0.0645)	(27.7131)		
Early	1	30.1	4.6977	0.3662	8.5967	0.99	4.34
			(0.1496)	(0.0553)	(3.1082)		
Early	2	25.5	5.4922	0.5742	17.0181	0.97	5.96
			（0.1399）	（0.0977）	（9.1155）		
Early	3	26.3	5.3268	0.7243	52.3327	0.94	32.72
			(0.2025)	(0.1995)	(60.8241)		
Early	4	31.7	7.9992	0.6447	65.4084	0.99	8.89
			(0.1624)	(0.0830)	(36.9894)		
Late	1	22.5	8.5555	0.7521	65.2644	0.99	1.33
			(0.0904)	(0.0585)	(22.4942)		
Late	2	30.5	9.3037	0.7983	95.7756	0.99	16.67
			(0.1687)	(0.1088)	(62.7994)		
Late	3	27.6	7.5003	0.6706	35.4980	0.99	2.30
			(0.1061)	(0.0666)	(13.5464)		
Late	4	27.0	5.7125	0.3303	4.0852	0.85	146.73
			(0.4397)	(0.1338)	(3.0117)		

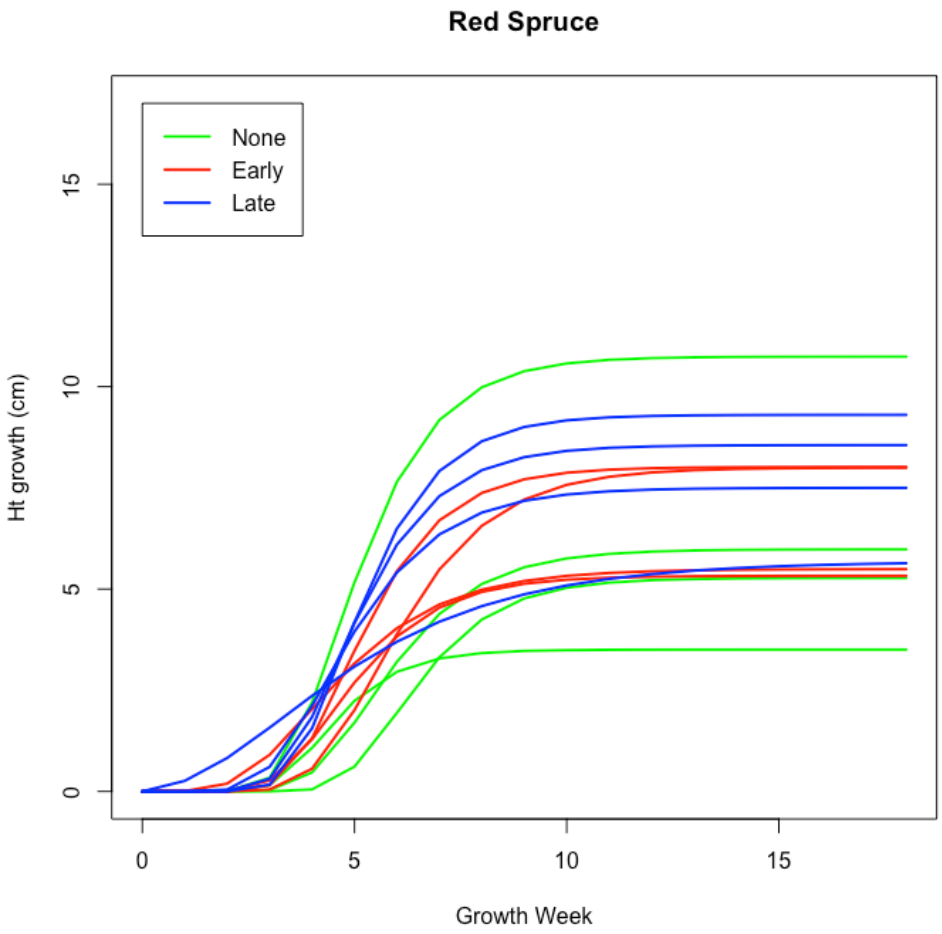

Figure 4. Height growth over the 18 weeks for red spruce by drought treatment.

Table 7. Initial height (H0), asymptotic maximum height growth (H1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for eastern white cedar.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	34.5	8.1457	0.2306	2.3192	0.95	47.93
			(0.4997)	(0.0620)	(0.7998)		
None	2	26.0	11.8388	0.2363	3.0796	0.98	20.27
			(0.4338)	(0.0342)	(0.6412)		
None	3	26.0	10.1290	0.2519	3.0191	0.98	16.14
			(0.3589)	(0.0385)	(0.6797)		
None	4	25.2	10.4977	0.2126	2.6633	0.99	2.97
			(0.3125)	(0.0235)	(0.3800)		
Early	1	20.5	8.3181	0.1634	1.7399	0.98	6.78
			(0.5379)	(0.0364)	(0.3638)		
Late	1	29.2	8.3182	0.1634	1.7399	0.97	54.39
			(0.5379)	(0.0364)	(0.3638)		
Late	2	24.2	11.6308	0.1585	1.5496	0.95	110.04
			(1.7934)	(0.0875)	(0.7530)		
Late	3	29.3	8.0872	0.3131	2.9117	0.98	37.98
			(0.6517)	(0.1412)	(2.0806)		

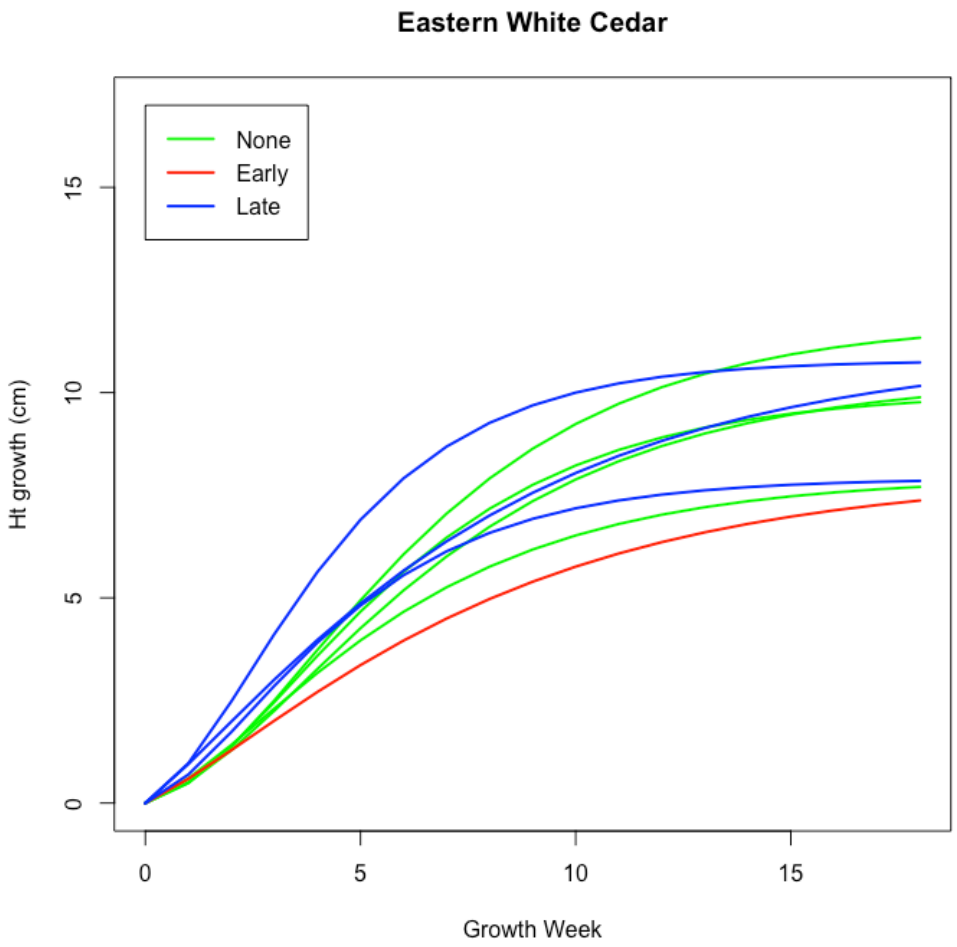

Figure 5. Height growth over the 18 weeks for eastern white cedar by drought treatment.

Table 8. Initial height (H0), asymptotic maximum height growth (H1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for Norway spruce.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	38.4	8.7493	0.6661	64.8468	0.98	31.69
			(0.2084)	(0.1041)	(44.5434)		
None	2	36.5	10.2570	0.8410	94.5479	0.99	2.82
			(0.1051)	(0.0681)	(36.7880)		
None	3	26.7	12.1479	0.7684	51.2436	0.99	23.34
			(0.1796)	(0.0867)	(24.3462)		
None	4	36.1	7.4424	0.9960	395.8372	0.98	11.44
			(0.1480)	(0.1662)	(411.1892)		
Early	1	35.5	5.9945	1.2471	439.8107	0.95	30.27
			(0.1726)	(0.3705)	(834.5009)		
Early	2	37.2	4.2392	0.5191	11.2202	0.95	6.53
			(0.1477)	(0.1176)	(7.0308)		
Early	3	32.5	6.9333	0.9204	262.1911	0.97	22.74
			(0.1791)	(0.1898)	(313.9792)		
Early	4	35.8	5.9007	0.5795	23.1370	0.99	2.04
			(0.1098)	(0.0696)	(9.4949)		
Late	1	43.3	6.9011	1.0345	194.6475	0.97	27.89
			(0.1757)	(0.2391)	(249.4311)		
Late	2	36.2	11.6286	0.9395	139.4810	0.99	0.34
			(0.0599)	(0.0411)	(31.7675)		

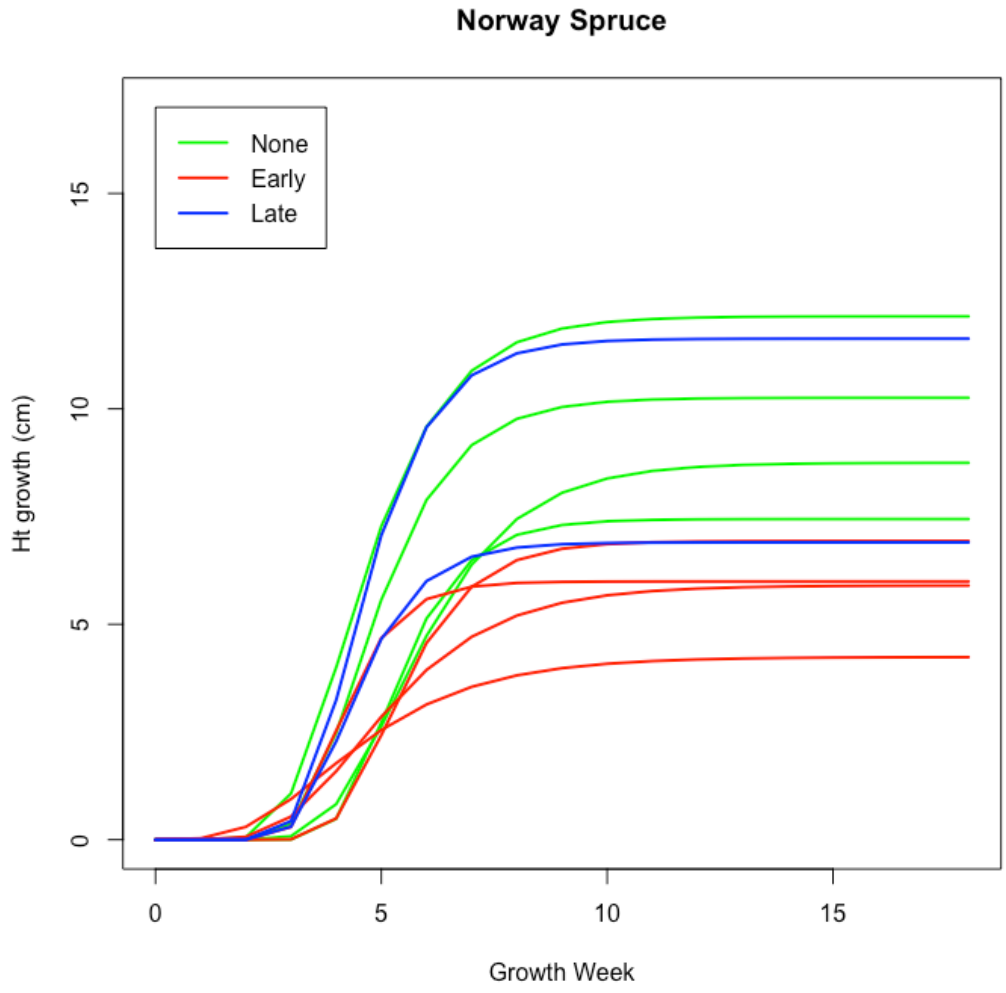

Figure 6. Height growth over the 18 weeks for Norway spruce by drought treatment.

Table 9. Initial height (H0), asymptotic maximum height growth (H1), intrinsic maximum height growth rate (R), inflection factor (S), the associated standard errors (in parentheses), and regression diagnostics for individual seedlings by drought treatment for white spruce.

Treatment	Tree	H_0	Regression Estimates			Regression Diagnostics	
			H_1	R	S	R^2	rMSR
None	1	31.5	10.4011	0.8292	34.0671	0.98	19.28
			(0.1611)	(0.1083)	(17.1247)		
None	2	29.0	7.8105	0.8062	37.1050	0.98	10.04
			(0.1392)	(0.1177)	(37.1050)		
None	3	31.4	9.7039	0.7099	21.6032	0.99	6.30
			(0.1272)	(0.0724)	(7.5057)		
None	4	32.2	8.8807	0.7471	22.8581	0.98	10.80
			(0.1425)	(0.0965)	(10.2390)		
Early	1	26.0	4.4704	0.4648	5.6580	0.85	59.62
			(0.2579)	(0.1810)	(4.8386)		
Early	2	26.5	7.7480	0.5287	13.4542	0.98	13.57
			(0.1785)	(0.0781)	(5.8077)		
Late	1	25.5	9.8245	0.7341	25.6981	0.99	3.86
			(0.1120)	(0.0657)	(8.2101)		
Late	2	24.5	14.5020	0.7601	17.6678	0.99	12.58
			(0.1447)	(0.0637)	(4.8003)		
Late	3	31.7	14.3290	0.7933	26.7878	0.99	27.85
			(0.1775)	(0.0816)	(9.9774)		

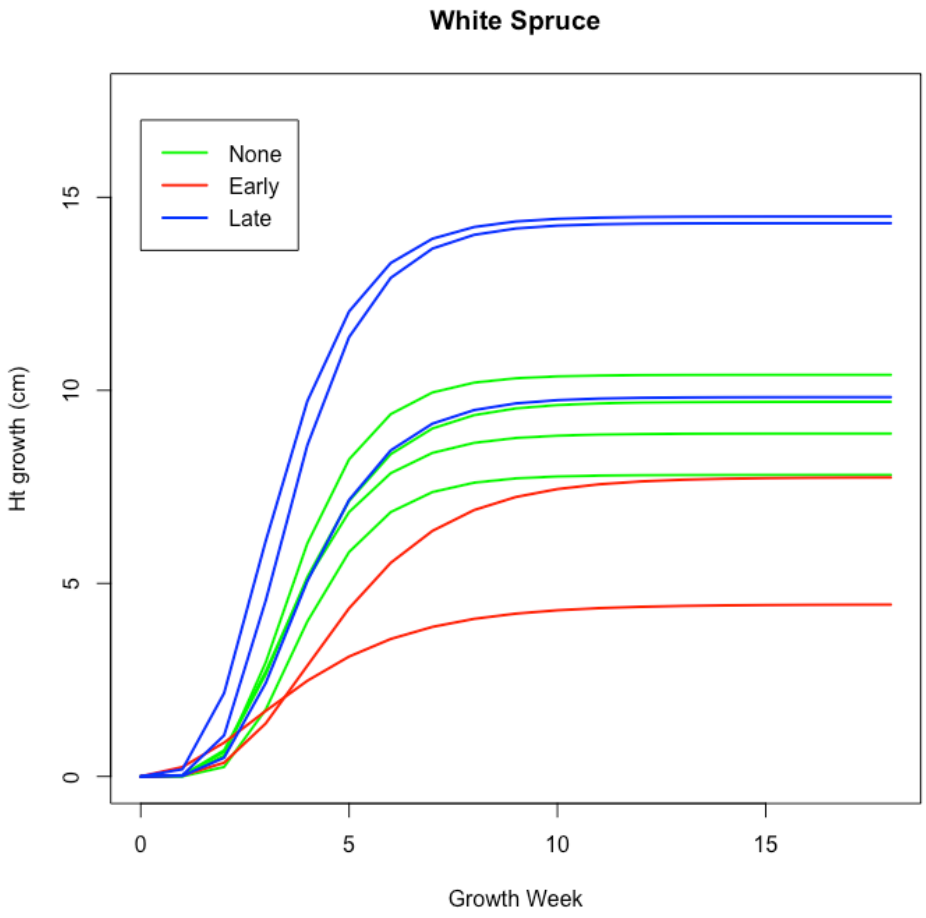

Figure 7. Height growth over the 18 weeks for white spruce by drought treatment

3.3 Biomass

Figures 8 – 13 show seedling biomass by component and species at the end of 18 weeks of growth. For all species and all treatments, foliage biomass was generally greater than stem and root biomass. As with height growth (Fig. 4), red spruce biomass was not impacted by drought treatment for any of the three biomass components (Fig. 9). For all other species, the results where not as consistent across the three biomass components. For white spruce (Fig. 12) and balsam fir (Fig. 13) early and late drought both impact all

three components, but there were minimal differences between early and late drought. For Norway spruce (Fig. 11) early drought had greater impacts on biomass for all three components, while late drought generally had minimum impacts. With eastern white cedar (Fig. 10), both drought treatments impacted all three components; however, early drought generally had greater impacts on all three components than late drought treatments. For eastern hemlock (Fig. 8), late drought impacted roots and stems more than foliage, while early drought impacted foliage more.

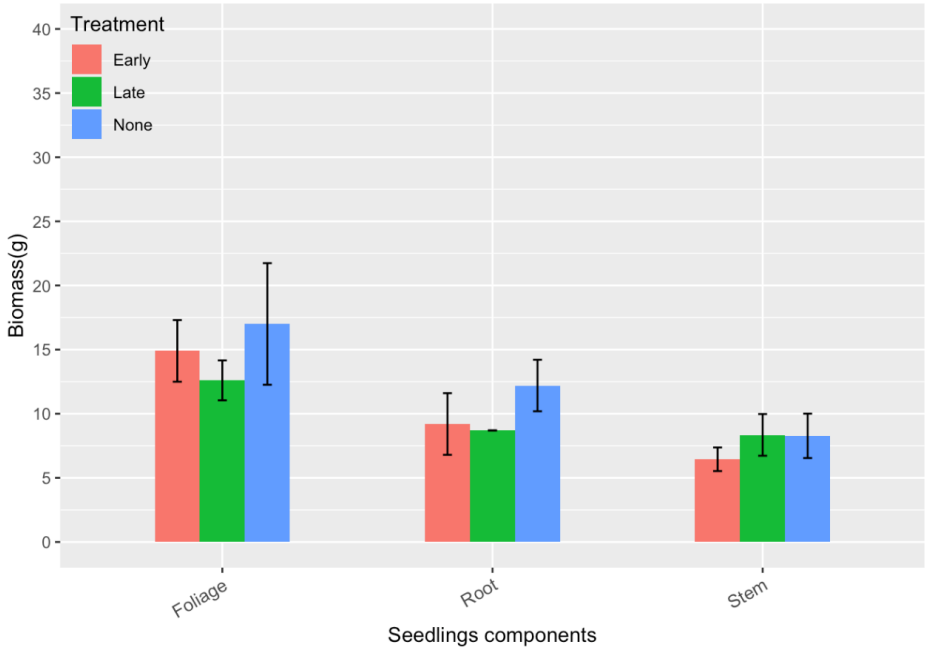

Figure 8. Biomass component by drought treatment for eastern hemlock. (vertical bars represent standard error).

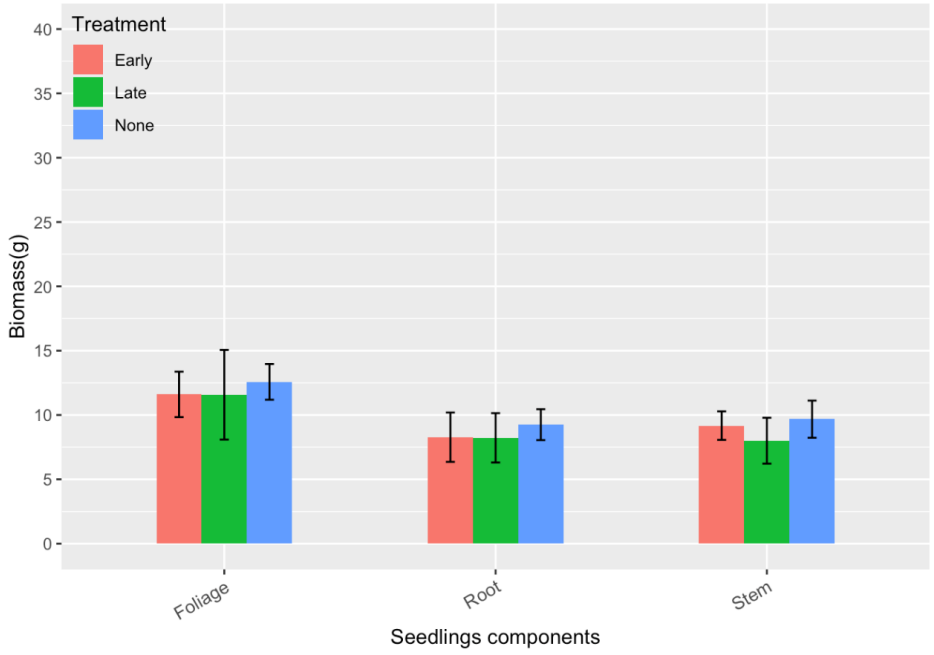

Figure 9. Biomass component by drought treatment for red spruce. (Vertical bars represent standard error).

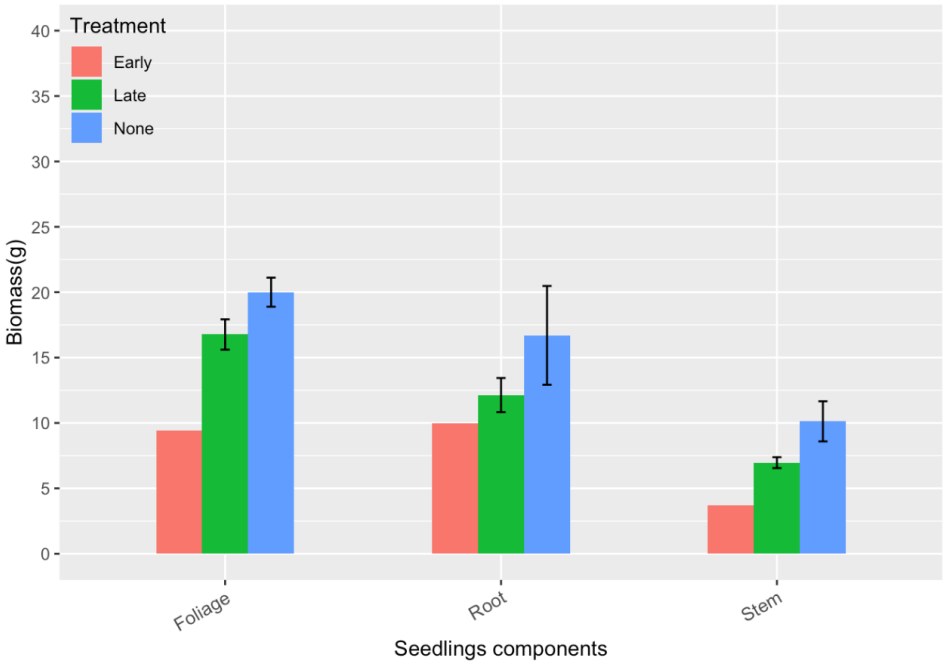

Figure 10. Biomass component by drought treatment for eastern white cedar. (Vertical bars represent standard error).

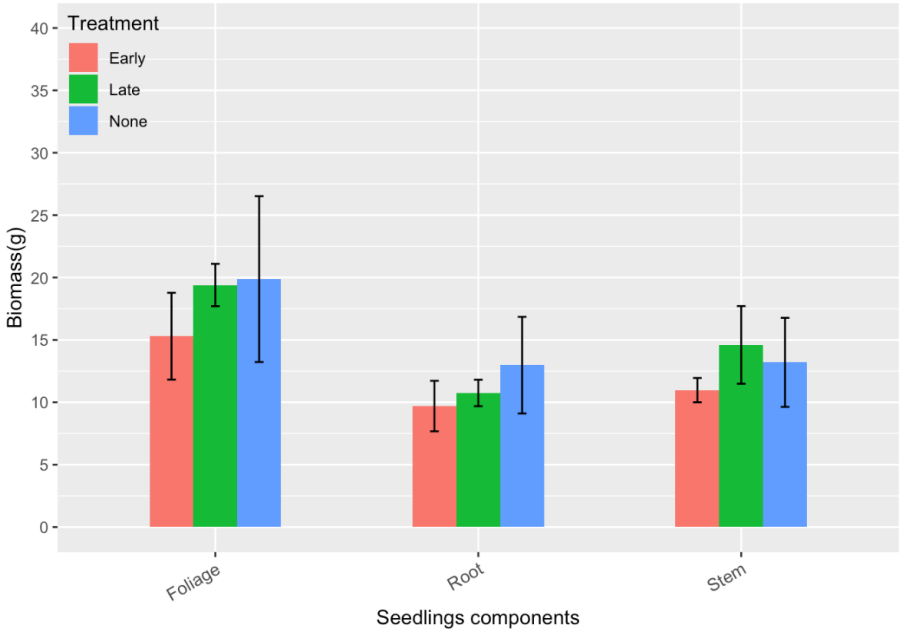

Figure 11. Biomass component by drought treatment for Norway spruce. (Vertical bars represent standard error).

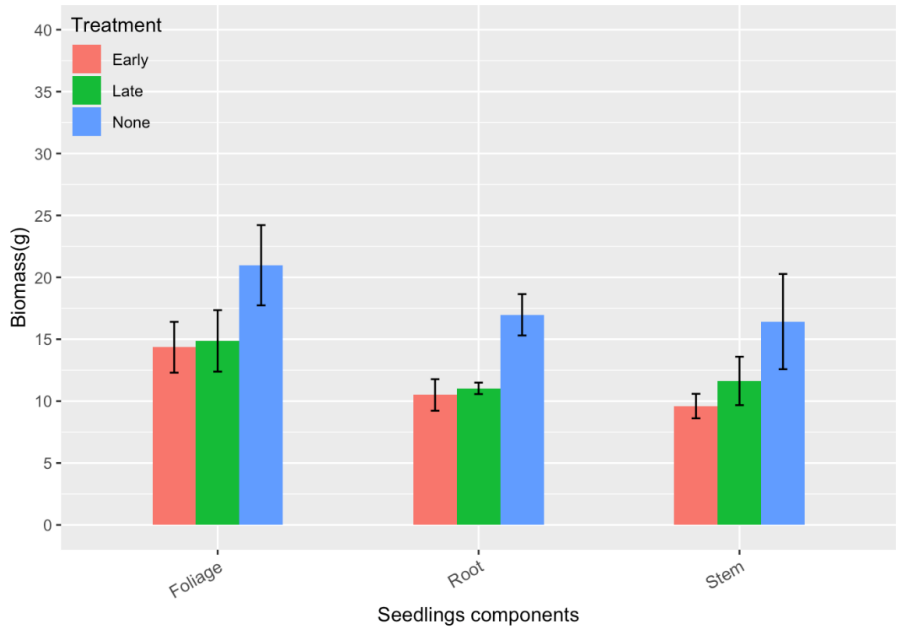

Figure 12. Biomass component by drought treatment for white spruce. (Vertical bars represent standard error).

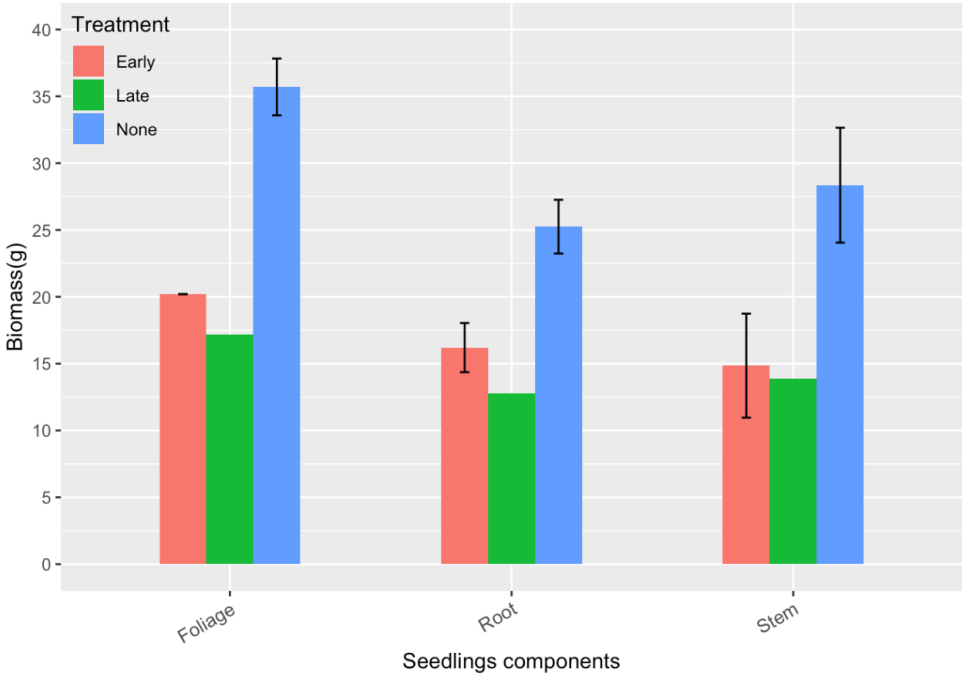

Figure 13. Biomass component by drought treatment for balsam fir. (Vertical bars represent standard error).

With the exception of eastern white cedar, neither aboveground: belowground (Fig. 14), nor foliage: root (Fig. 15) ratios were impacted by drought treatment. Drought had much larger impacts on totals (Figs. 8 – 13) and distributions (Figs 14 & 15).

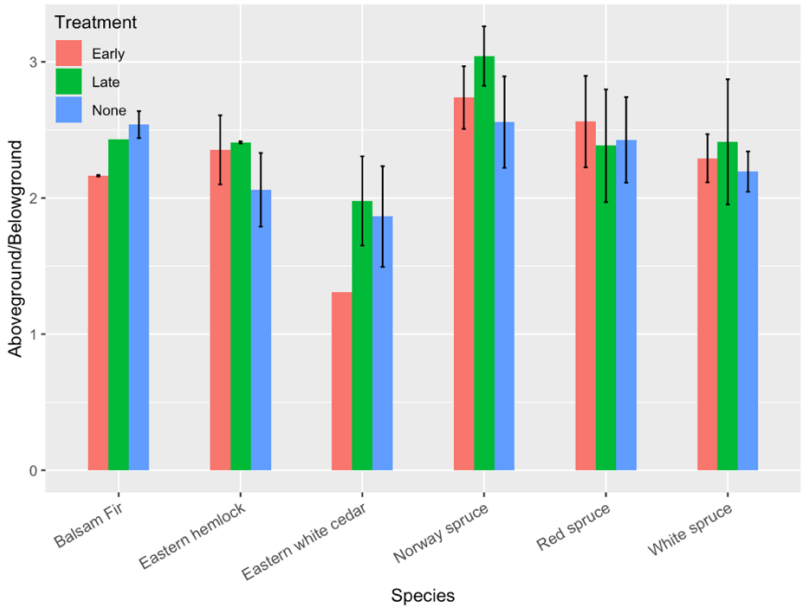

Figure 14. Biomass of aboveground: belowground ratio (A/B) of 6 species under 3 drought treatments.

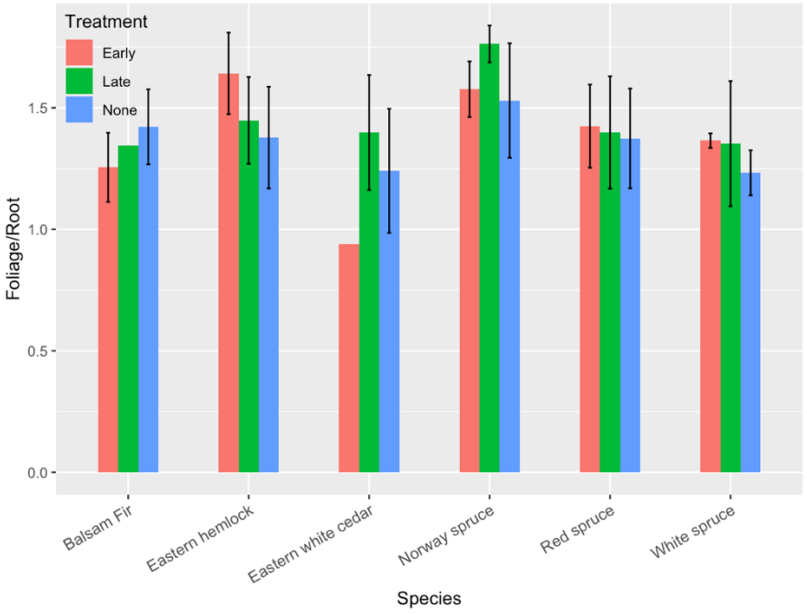

Figure 15. Biomass of leaves: root ratio (L/R) of 6 species under 3 drought treatments.

4 . Discussion and Conclusions

4.1 Effects of different drought timing on the survival of seedling

Drought and the timing of drought can induce seedling mortality. Drought stress produces residual air embolisms in the water delivery system, which reduce the plant's ability to provide water to the leaves for photosynthetic air exchange (Allen et al. 2010). Mortality varied among species; red spruce was least impacted by drought. This result is consistent with previous studies that reported red spruce to be relatively drought tolerant compared to other species (Vaughn et al. 2021). In contrast, the survival rate of balsam fir was only 58%. Similar results were reported in previous studies where drought stress resulted in significant reductions in survival and growth of balsam fir seedlings (Koç n.d.). Drought affects seedling mortality and the extent depends on timing (McDowell et al. 2008； Xu et al. 2023). The survival rate of seedlings in late drought treatment was three times greater than that of early drought treatment. Under the late drought treatment, the death of seedlings appeared 1 to 3 weeks later than that of the early drought treatment. with higher mortality under late drought treatment than early drought treatment, possibly due to the greater woody tissue development of seedlings in the late drought treatment. This is consistent with the findings of (Zhang et al. 2017) that age and wood density affect mortality, with mortality significantly decreasing as wood density increases.

4.2 Effects of different drought timing on height growth of seedling

Studies have shown that drought resistance is highly species-specific (Elliott and Swank 1994）The 6 conifer species studied respond to drought in different amounts and ways. Drought and more specifically, the timing of drought does affect the height growth of conifers (Jafarnia et al. 2018). The early life stages of trees are most sensitive and vulnerable to soil moisture deficits (Alexou 2013). The reason total height growth is reduced is two-fold. One is a change in the rate of height growth and the 2nd is the duration of height growth. Those two-fold also interact. Drought causes root morphology changes in seedlings (Zhou et al. 2018), Since root traits are related to plant growth rate (Comas et al. 2002) eventually lead to the maximum rate of height growth was reduced (Amissah et al. 2015) both drought treatments. Drought results in the closure of seedlings' stomata (Cao 2000), reduced photosynthesis, and reduced activity of growth-promoting enzymes, which ultimately inhibit growth. Both drought treatments occurred after seedlings began to grow rapidly (week 3). Therefore, the drought didn't affect the start time of rapid growth, but rather the end time of seedlings. Since the late drought occurred in week 7, the growth of seedlings slowed down at this time, and the drought prompted the seedlings to finish growing more quickly.

While drought and the timing of drought affects height growth of conifers in general, the impact is variable depending on species. In general, red spruce showed better resistance to drought, with little effect on growth at both drought treatment heights. seedlings at the height of balsam fir are more susceptible to drought.

4.3 Effects of different drought time on the biomass collection of seedlings

Drought affects biomass allocation to varying degrees (Eziz et al. 2017) While the timing of drought did not differentially affect total biomass reductions compared to no drought, and these were significant reductions. The two types of drought treatment mainly inhibit the accumulation of foliage biomass; However, the inhibition degree of stem and root are different under the two drought treatments. Drought mainly inhibited stem growth under early drought treatment and root growth under late drought treatment. Early drought-induced reduction in root biomass was less than shoot biomass, resulting in a lower above/below ground (A/B) mass ratio (Zhou et al. 2018).

For eastern hemlock and white spruce, early period drought inhibited root growth. Drought prevented foliage biomass accumulation more than root under late drought treatment. All other species early drought inhibited biomass accumulation in shoots less than shoots. The main reason is that drought promoted the growth of the root (Helenius et al. 2002). Eastern white cedar, Norway spruce drought inhibits the root to a lesser extent. For balsam fir late drought inhibition degree of late drought on foliage , stem and root of seedlings are relatively consistent (D'Orangeville et al. 2013).

5. Recommendations

There are imperfections in the experiment. In order to better study the factors that affect the growth of seedlings, the following is the direction that the next experiment can be optimized and studied.

1. Since the sample size of this experiment is small and the measurement is based on manual work, there will be individual differences in seedlings and measurement errors. The experiment was therefore repeated with more seedlings of each species to determine an average response rather than simply a potential response based on the largest surviving seedling.

2. The growth of seedlings includes height growth and radial growth. This experiment only studies height growth. In order to make the research on seedlings growth more comprehensive, it is necessary to check the results of diameter growth to see if they change and how.

3. Factors affecting the growth of seedlings include water, temperature, light. This experiment only focused on drought as a variable, in order to fully understand the factors affecting the growth of seedlings. In addition to precipitation, temperature control should be added in the experiment to observe the growth changes of seedlings at different temperatures.

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