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Early Life Stage Characteristics of Six Acadian Conifer Species: Germination and Seedling Development in a Changing Climate

Jason D. Schatz

EARLY LIFE STAGE CHARACTERISTICS OF SIX ACADIAN CONIFER SPECIES: GERMINATION AND SEEDLING DEVELOPMENT IN A CHANGING CLIMATE

By

Jason D. Schatz

B.S. Iowa State University, 2004

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Forestry)

The Graduate School

The University of Maine

August, 2007

Advisory Committee:

Michael S. Greenwood, *Ruth Hutchins* Professor of Tree Physiology, advisor

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By Jason D. Schatz

Thesis Advisor: Dr. Michael S. Greenwood

An Abstract of the Thesis Presented
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Global climate change will drastically alter regional climates. The influence of these changes on the distribution and relative abundance of forest trees is both critically important and subject to substantial uncertainty. It will be particularly important to understand the effects of different climate scenarios on the early life stages of major tree species, because: 1) Early life stage performance and survival strongly influence the abundance of mature trees of a given species, 2) Trees are most sensitive to environmental variation during their early life stages, and 3) Our knowledge of the response of Acadian Forest tree species to environmental variation is very limited.

In Experiment 1, we monitored the germination, growth, and development of six major Acadian Forest conifers: *Abies balsamea, Picea glauca, Picea mariana*, *Picea rubens*, *Pinus strobus*, and *Tsuga canadensis*. Seedlings were grown in two light environments: high light (60% of full sun), typical of canopy gaps, and low light (10% of full sun), typical of the understory beneath full canopies.

In terms of germination, the *Picea* species germinated most rapidly and completely, *P. strobus* and *A.balsamea* germinated less completely and more gradually, and *T. canadensis* germination was strongly inhibited by higher soil temperatures associated with the high-light environment.

Growth and biomass allocation varied widely among the six species. In the high-light environment, *P. strobus* and *A. balsamea* quickly developed extensive root systems, while the *Picea* species concentrated their growth on shoot development. In the low-light environment, *A. balsamea* maintained higher root allocation relative to the other species. In the high-light environment, the *Picea* species exhibited season-long neoformed shoot growth, while relatively early budset limited the shoot growth of the other species.

In Experiment 2, we studied the relative sensitivity of *P. rubens* and *A. balsamea* growth and development to different light, soil moisture, and root competition treatments over the seedlings' first growing season and the first two months of their second growing season. We found that the growth and development of both species was similarly sensitive to variation in belowground nutrient competition and soil moisture. So, any interspecific differences in the response of *P. rubens* and *A. balsamea* to dry conditions would probably arise due to differences in mortality rates during severely dry conditions rather than long-term growth effects of non-lethal variation in soil moisture.

The results of Experiments 1 and 2 will provide insights into the relative fitness of these species in various climate change scenarios.

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$$RGR = \frac{\ln\left(\text{harvest 3 dry mass}\right) - \bar{x}\left[\ln\left(\text{harvest 1 dry masses}\right)\right]}{\text{\# days between harvests 1 and 3}}$$

$$RLR = \ln\left(\text{magnitude in light}\right) - \bar{x}\left[\ln\left(\text{magnitudes in shade}\right)\right]$$

$$RCR = \ln\left(\text{magnitude in comp trt}\right) - \bar{x}\left[\ln\left(\text{magnitudes in no comp trt}\right)\right]$$

$$RWR = \ln\left(\text{magnitude in wet trt}\right) - \bar{x}\left[\ln\left(\text{magnitudes in dry trt}\right)\right]$$

Chapter 1: First Season Germination, Growth, and Development of Six Acadian Conifer Species in Two Light Environments

1.1. Introduction:

Global climate change could drastically alter regional climates (Houghton et al. 2001). The combination of increased temperatures and altered precipitation patterns could have a significant impact on soil water availability (Aber et al. 2001), which could contribute to large shifts in species distributions and local abundance (Overpeck et al. 1991; Iverson and Prasad 1998; Hansen et al. 2001; Aber et al. 2001).

Palynological evidence reveals that species have historically undergone immense range shifts in response to climate change. In Maine, for example, white pine (*Pinus strobus* (L.)) was relatively abundant 9,000 to 5,000 years ago when the climate was considerably warmer and drier than it is today (Jacobson and Dieffenbacher-Krall 1995). But as the climate became cooler and wetter, white pine abundance declined and spruce (*Picea* sp.) and fir (*Abies balsamea* (L.) Mill) abundance increased in Maine's forests (Schauffler and Jacobson 2002). There is also strong evidence that eastern hemlock (*Tsuga canadensis* (L.) Carr.) declined sharply in response to a drier climate and recovered when the climate became wetter and cooler (Foster et al. 2006). So clearly trees can react strongly to climate change.

Among other things, climate change can significantly affect seasonal patterns of water availability. For instance, increased temperatures in New England could cause an increased proportion of winter precipitation to come in the form of rain, which could lead to decreased snow accumulation. This could increase winter runoff and evaporation and decrease the amount of snowmelt feeding soil water recharge and runoff in the spring. In

a model of future precipitation of the north-central US and southern Europe, Gregory et al. (1997) found that soil water could increase somewhat in the fall and winter and decrease somewhat in the spring and summer, which could further diminish the amount and reliability of available water during the spring and summer months.

In New England, general circulation models (GCMs) predict increases in both mean annual temperature and precipitation (Houghton et al. 2001). The increase in mean annual precipitation seems to suggest a wetter environment for plants, but the true implications of such changes are unclear. Plant communities not only respond to precipitation amounts but also to the pattern in which they receive that precipitation.

GCMs predict that future precipitation patterns will be characterized by less frequent, more intense storms (Easterling et al. 2000; Houghton et al. 2001; but see Bengtsson et al. 2006). So although total annual precipitation will increase, there will be longer dry periods between rainfall events. Knapp et al. (2002) tested the effects of precipitation variability on a native prairie by altering the frequency and intensity of precipitation events but keeping total precipitation constant. Under the different watering regimes, community composition and productivity proved more sensitive to precipitation variability than to total precipitation or mean soil water content, which demonstrates the importance of precipitation patterns to plant communities.

Knapp et al. (2002) conducted their study in a Kansas prairie, which is generally more water-limited than New England's forests. But even in relatively water-rich forests, droughts can still strongly affect species growth and competitive interactions, particularly at the seedling level (DeStevens et al. 1991a; Joslin et al. 2000; Holmgren 2000; Engelbrecht et al. 2006). Many researchers have attributed high conifer seedling

mortality to drought. Such mortality is caused largely by the interaction between seedling desiccation and root growth inhibition caused by the hardening of dried soil (Moore 1926; Baldwin 1934; Place 1955; Walsh and Voigt 1977; DeStevens 1991a; Royo et al. 2001; Lee et al. 2004). Also, relative to larger trees, germinants and young seedlings have higher proportions of their root systems within the litter layer, which dries more rapidly than the deeper mineral soil (Moore 1926; Ahlgren and Ahlgren 1981).

This raises the possibility that Maine's future forests could be significantly affected by changes in the frequency of droughts, the severity of which could be exacerbated by increased temperatures. Increased CO_2 concentrations should offset drought stress somewhat by increasing water use efficiency (Wayne et al. 1998), but the degree to which this will occur for a given plant species in a given microenvironment on a given timescale is unclear (Aber et al. 2001; Wullschleger et al. 2002).

Due to its relatively abundant precipitation, New England is at lower risk of future droughts compared to many other areas of North America (Aber et al. 1995; Hanson and Weltzin 2000; Weltzin et al. 2003), but this does not make New England immune to occassional droughts. Even during the water-rich rainy season of tropical forests, seedlings have proved vulnerable to short dry spells (Engelbrecht et al. 2006). Given the potential weather pattern changes discussed above, it seems prudent to address the possibility that drought will play an increasingly prominent role in New England as the climate continues to change. Among the questions that need to be addressed is how climate change could affect the performance and distribution of tree species (Joslin et al. 2000; Hanson and Weltzin 2000; Hanson et al. 2001).

It will be particularly important to understand the probable effects of different climate scenarios on trees' early life stages, including seed germination, germinant establishment, and seedling growth, development, and survival. Studying these early life stages is crucial for three major reasons:

1) Early life stage performance and survival exert strong influences on the overall population of a given species by limiting the number of trees reaching later life stages (Harper 1977). Various studies have linked early seedling and sapling performance to eventual canopy attainment (Kobe et al. 1995; Kobe 1997; Canham et al. 1999; Messier and Nikinmaa 2000; Clark and Clark 2001; Claveau et al. 2002; Lin et al. 2002; Wyckoff and Clark 2002).

2) Trees are most sensitive to drought and other environmental stresses during their early life stages (Harper 1977; Schlesinger et al. 1982; Wellington 1984; Hanson et al. 2001), which suggests that tree early life stages will be among the most responsive components of forests to climate change (Joslin et al. 2000; Hanson et al. 2001). Relative to older, more-well-established trees, germinants and seedlings have less extensive root systems and lower carbohydrate reserves with which to endure periods of stress (Donovan and Ehlinger 1991; Flanigan et al. 1992). Seeds (particularly germinating seeds) can also be highly sensitive to desiccation and other stresses (Fenner 1985; Tweddle et al. 2003). There are exceptions to this, of course, particularly in very arid environments where the smallest trees tend to be the most shaded by neighboring vegetation, thus making them more protected from evaporative water stress during drought conditions (Mueller et al. 2005). But in general, germinating seeds and seedlings are more vulnerable than adults to stress. Most studies find that, after the first growing

season, mortality rates drop sharply (Place 1955; Harper 1977; Harcombe 1987; DeSteven 1991b; Hill et al. 1995; Boerner and Brinkman 1996).

3) Our knowledge of the early life stages of Acadian Forest species is very limited. Data regarding the response of major species to environmental variation during their early life stages will be useful regardless of the future climate.

Maine lies within the transition zone between the boreal and temperate forests, and the northern or southern range limits of many woody taxa fall within Maine's forests (McMahon 1990). At their range limits, species' responses to climate change could be particularly dramatic (Loehle 2000). Even slight changes in climatic conditions could cause range shifts, with some species expanding into novel areas and other species' ranges being constricted via local extinction. As such, climate change stands to have a dramatic impact on the composition of Maine's forests.

Early life stage traits may be able to help us predict local species dynamics under various climate scenarios. For instance, if the early life stages of a given species have traits typically associated with enduring dry conditions, then the early life stages of that species should perform relatively well in a drier climate. Or, if the early life stages of a given species appear adapted for cooler, moister conditions, then the early life stages of that species should perform relatively well in a cooler, moister climate and relatively poorly in a warmer, drier climate.

In assessing a given species, however, it is important to bear in mind that seedling traits are subject to significant intraspecific variation. As such, using seedling traits to predict a species' performance requires knowledge of the full range of the plasticity of those traits. Variation in available light can significantly influence seedling growth,

physiology, morphology, and biomass allocation (Givnish 1988; Abrams 1994; Poorter and Nagel 2000). So, measuring seedling traits under disparate light conditions can provide a simple and effective way to capture much of a species' phenotypic plasticity.

1.2. Materials and Methods

1.2.1. Species Descriptions

We monitored the germination and first-season growth and developmental of six major Acadian Forest conifers: balsam fir (*Abies balsamea* (L.) Mill), white spruce (*Picea glauca* (Moench)), black spruce (*Picea mariana* (Mill) B.S.P.), red spruce (*Picea rubens* (Sarg.)), white pine (*Pinus strobus* (L.)), and eastern hemlock (*Tsuga canadensis* (L.) Carr.).

In Maine, red spruce is near its northern range limit (Blum 1990), black spruce, white spruce, and balsam fir are near their southern range limits (Viereck and Johnston 1990; Nienstaedt and Zasada 1990; Frank 1990), and white pine and hemlock are near the middle of their ranges (Wendel and Clay 1990; Godman and Lancaster 1990). Hemlock and balsam fir are considered very shade tolerant, red spruce is anywhere from shade tolerant to very shade tolerant, black and white spruce are shade tolerant, and white pine is of intermediate shade tolerance (Baker 1949; Barnes et al. 1998). All six species are major components of Maine's forests (Griffith and Alerich 1996).

1.2.2. Experiment Location

Seedlings of all six species were grown in an open-air hoophouse in Orono, ME. The hoophouse floor was comprised of crushed gravel to facilitate draining. The climate

of Orono is cool and moist, with a 30-year (1971-2000) mean annual temperature of 6.5º C and mean annual precipitation of 1023 mm. May through October (the approximate growing season in Orono) has an average temperature of 14.9º C and average precipitation of 527 mm (Climatography of the United States No. 81). Temperature and humidity data for this experiment are detailed in Table 1.

1.2.3. Experimental Design and Procedure

The seedlings were germinated and grown in a split plot design that was split into two light environments: high light (60% of full sun) and shade (10% of full sun), which are typical light levels in large gaps and beneath full overstories, respectively (Kuppers et al. 1996; Messier et al. 1998). The two light environments were created using different densities of neutral shade cloth; Table 1 details the mean daily fluence in each treatment.

In mid-April, 2005, approximately 18 seeds were sown at a depth of 0.5 cm in three 20-cm-diameter plastic pots in each light environment for each species (Table 2). Treatments were replicated in three blocks for a total of nine pots of each species randomly placed in each light environment (Fig. 1). A few pots contained 18 ± 1 seeds, causing the total seeds planted per species-treatment to vary slightly from the target of 162 seeds (= 18 seeds * 9 pots); but such deviations were quite small (Table 2) and were assumed to not significantly affect experimental results. Seeds were surface sterilized with 1% H_20_2 prior to sowing. Pots were filled with a mixture of 2:1:1 peat:vermiculite:perlite and 4 kg/m^3 Osmocote 18-6-12 (Scott-Sierra, Milipitas, CA, USA). Seeds were provided by The National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada). Seed sources were chosen for

Period	Treatment	Mean air temp (˚C)	Relative humidity	Mean daily fluence
04/21 - 05/31	Light	19.9	60	13845
	Shade	19.9	60	1794
06/01 - 08/31	Light	20.4	80	17743
	Shade	20.4	80	1362
09/01 - 11/15	Light	11.7	85	7933
	Shade	11.7	85	158
04-21 - 11/15	Light	17.1	78	13437
	Shade	17.1	78	1013

Table 1. Climate data for Experiment 1.

	Date	Treatment	Species					
			Balsam fir	Black spruce	White spruce	Red Spruce	White pine	Hemlock
Seeds planted	4/21/2005	Light	163	160	162	162	162	162
		Shade	162	164	164	163	162	163
Harvest 1	7/7/2005	Light	17	25	27	27	9	0
		Shade	18	27	27	27	9	18
Harvest 2	9/3/2005	Light	27	27	24	23	25	9
		Shade	27	27	27	27	27	9
Harvest 3	11/15/2006	Light	26	27	25	25	13	21
		Shade	24	27	25	27	21	17

Table 2. Number of seeds planted and number of seedlings harvested at each of three harvests for Experiment 1.

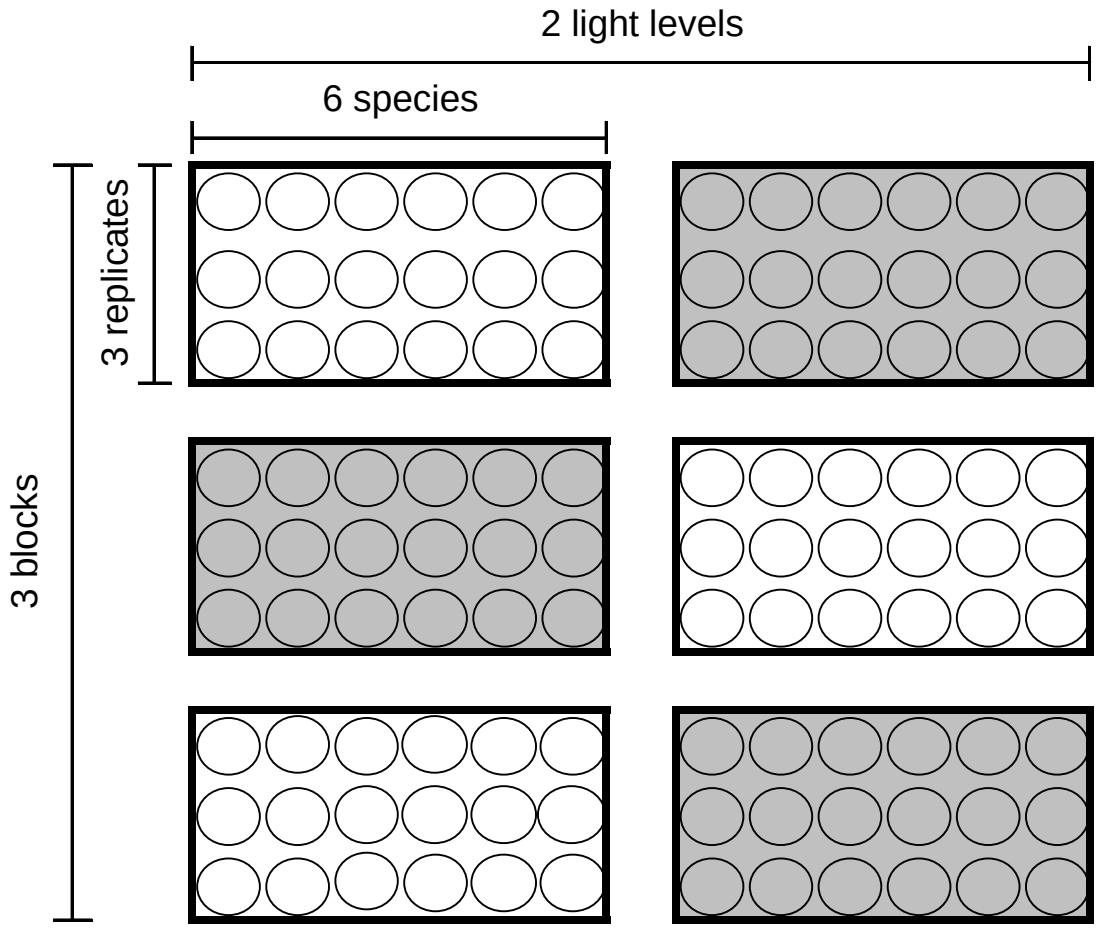

Figure 1. Schematic of Experiment 1. Each circle represents one 20 cm diameter monospecific pot sown with approximately 18 seeds of either *A. balsamea, P. mariana, P. glauca, P. rubens, P. strobus,* or *T. canadensis*. The gray-shaded squares represent the shade treatment (10% full sunlight); the unshaded squares represent the light treatment (60% full sunlight).

their proximity to our study site. Five seed sources were used for each species to minimize genetic and site biases (Table 3). For each species, equal weights of seed from each seed source were mixed before sowing.

All pots were kept well watered and fertilized throughout the experiment, ensuring that light was the primary limiting growth factor.

1.2.4. Data Collection

Germinants were counted approximately every-other-day for the first 47 days after seeds were sown. However, we actually did not measure germination, per se, because seeds were shallowly buried in peat, and we could not directly monitor their germination. Rather, we recorded germinant emergence, because germinants were counted only after they emerged from the peat. But given the consistently shallow depth and permeability of the peat overlying the seeds, emergence is hereafter assumed to be equivalent to germination for this experiment.

Approximately three seedlings from each pot were harvested 70, 140, and 200 days after seeds were sown (Harvests 1, 2, and 3, respectively), yielding approximately 27 seedlings per species per light treatment per harvest (Table 2). Shoot length, root length, and dry mass of roots and shoots were measure soon after harvest. Shoot biomass was divided into leaf and stem components for Harvests 2 and 3. Dry masses were obtained after drying plant materials for at least 72 hours at 60^{o} C. For Harvest 3, leaf areas were obtained from 10 randomly selected seedlings of each species from each light environment. To obtain leaf areas, a representative sample of approximately 40 fresh needles per seedling were removed from the stem, scanned with a flatbed scanner, and

Species	Province	Location	Latitude (ºW)	Longitude (ºN)	Elevation (m)	% Germ
Black spruce	Quebec	Lac Taibi	45.27	77.41	287	99
	Ontario	Alice	45.45	77.17	-	100
	Quebec	Granby	45.24	72.44	120	97
	Nova Scotia	Cogmagon River	45.05	64.03	30	95
	Nova Scotia	Oxford	45.40	63.57	60	98
White spruce	Ontario	Prairie Point	45.52	81.41	-	99
	Quebec	Granby	45.24	72.44	142	91
	Quebec	Granby	45.24	72.44	142	87
	Quebec	Lac Belisle	45.48	75.05	650	92
	Quebec	Ste-Anne-du-Lac	46.50	75.20	-	91
Red spruce	Nova Scotia	Abraham Lake	45.10	62.38	150	84
	Nova Scotia	Spencers Island	45.21	64.42	30	92
	Nova Scotia	Abraham Lake	45.10	62.38	150	94
	Ontario	Bear Pond Road	45.02	77.19	320	100
	Nova Scotia	New Yarmouth	45.22	64.50	200	97
Balsam fir	Nova Scotia	Spar Lake	45.05	62.23	61	58
	Nova Scotia	Onslow Mountain	45.25	63.18	155	63
	Nova Scotia	Bishop Mountain	45.02	64.59	175	55
	New Brunswick	Canoose	45.21	67.23	100	53
	Quebec	Lac Etchemin	45.20	70.55	800	75
White pine	Ontario	Algonquin Park	45.53	77.42	200	97
	New Brunswick	Upper Brockway	45.35	67.05	200	83
	Nova Scotia	Caledonia	44.21	65.05	100	97
	Nova Scotia	Caledonia	44.21	65.05	100	86
	Quebec	Riviere Niger	45.05	72.05	150	81
Hemlock	New Brunswick	Pow Brook	45.53	64.56	225	91
	New Brunswick	Pirate Lake	45.43	67.40	200	92
	New Brunswick	Hamtown Corner	46.07	66.44	210	96
	Nova Scotia	Williamsdale	45.36	63.54	175	92
	New Brunswick	Fredericton	45.57	66.40	80	96

Table 3. Seed sources for Experiment 1. Seeds were acquired from the National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada). % germ is the viability reported by the National Tree Seed Centre.

analyzed using WinSEEDLE image analysis software, version 2007a (Regent Instruments Inc., Quebec, Canada).

Air temperature and relative humidity were monitored throughout the experiment (Table 1). In each light environment, light levels and soil surface temperature were monitored with LI-190 quantum sensors (Licor Inc., Lincoln, Nebraska) and type-T thermocouples, respectively, attached to a Campbell Scientific CR10X data logger (Campbell Scientific, Logan, UT).

The experiment described above will hereafter be referred to as Experiment 1.

1.2.5. Statistical Analysis

1.2.5.1. Statistical Software

This analysis will use the germination data and data from Harvests 1 and 3. All analyses were carried out in R (R version 2.4.1 © 2006--The R Foundation for Statistical Computing).

1.2.5.2. Germination Analysis

To analyze the germination data, each pot (containing approximately 18 seeds) was defined as one replicate, yielding 9 replicates per species per light treatment (Fig. 1). ANOVAs were performed with species, light, and block effects accounting for variation in germination initiation time, germination completion time, germination rate, and percent germination. The following model was used for all germination ANOVAs:

Y ~ treatment:block + species + treatment + block + species:treatment

where treatment = light treatment. The MS of the 'treatment:block' term was used as the error MS in the F-ratios of the 'treatment' term in order to account for light-environment splits and blocking effects (Appendix).

Germination initiation time was defined as the number of days after planting before 10% of eventual germinants in a given pot had germinated. Germination conclusion time was defined as the number of days after planting before 90% of eventual germinants in a given pot had germinated. Germination rate was calculated as the mean germination rate (germinants per day) during the period in which approximately the middle 80% of germination occurred within a given pot (for example, if 10 of 18 seeds germinated in a given pot, the germination rate for the days in which germinants 2-9 germinated would be used to calculate the mean germination rate for that pot).

Models were assessed for normality and constant variance by examining normal QQ plots and residual plots, respectively. For the germination data, all models satisfied the assumptions of ANOVA except for germination initiation and conclusion times, which appeared to have non-constant variance. Closer examination of the models revealed that the non-constant variance associated with the germination initiation and conclusion time ANOVAs was largely due to the high-light hemlock germination data. This was not unexpected. Germination data were difficult to estimate for high-light hemlock because most high-light hemlock seeds germinated after we stopped monitoring germination on day 47 of the experiment. So other than knowing that high-light hemlock seeds germinated sometime after day 47, we had little basis for our estimates. As such,

germination initiation, conclusion, and rate for high-light hemlock should be viewed as educated guesses, not exact numbers. But since the high-light hemlock seeds germinated so much later than any other species-treatment combination, the uncertainty associated with high-light hemlock estimates did not affect conclusions regarding germination initiation times.

There were similar problems with estimates of germination conclusion dates for the shade-environment hemlock and shade-environment balsam fir. Several replicates of each species concluded germination sometime after we had stopped monitoring on day 47. Again, this makes estimates of exact germination rates and conclusion dates very uncertain, but it still allows us to safely conclude that shade-environment hemlock and shade-environment balsam fir concluded germination much later and had generally lower germination rates than the three spruces, white pine, and high-light balsam fir. This will all be discussed in greater detail in sections 3.1 and 4.1 of this chapter.

All germination ANOVAs showed highly significant species:treatment interactions ($p<0.001$; Appendix). Tukey's HSD test was used to compare the means of each species:treatment combination.

1.2.5.3. Seedling Growth and Development Analysis

ANOVAs were performed with species, light treatment, and block effects accounting for variation in shoot length, plant dry mass, R:S mass ratio (R:S mass = root dry mass/shoot dry mass), primary root length, and R:S length ratio (R:S length = primary root length/shoot length). These measurements were log- or square-root-transformed as necessary to better approach normality (Appendix). For the Harvest 3

data, additional ANOVAs were performed with species, light treatment, and block effects accounting for variation in root mass ratio (RMR = root dry mass/whole plant dry mass), stem mass ratio (SMR = stem dry mass/whole plant dry mass), leaf mass ratio (LMR = leaf dry mass/whole plant dry mass), specific leaf area (SLA = leaf area/leaf mass), foliar-area-to-root-mass-ratio (FARM = plant leaf area/root dry weight), and seedling relative growth rate (RGR). FARM ratios were calculated based on leaf areas measured on a subsample of 10 seedlings per species per light environment.

For RGR calculations, the ln-transformed Harvest 1 dry masses were averaged in each species-treatment combination and subtracted from each ln-transformed Harvest 3 dry mass in the same species-treatment combination. The difference was then divided by the number of days between Harvests 1 and 3 as follows:

$$\text{(1)} \qquad \text{RGR} = \frac{\ln\left(\text{harvest 3 dry mass}\right) - \bar{x}\left[\ln\left(\text{harvest 1 dry masses}\right)\right]}{\#\text{ days between harvests 1 and 3}}$$

Harvest 1 dry masses were averaged across blocks, so RGR was analyzed with a simple two-way ANOVA with species and light environment accounting for variation in RGR.

For all other seedling traits, the following ANOVA model was used:

Y ~ treatment:block + species + treatment + block + species:treatment

where treatment = light treatment. The MS of the 'treatment:block' term was used as the error MS in the F-ratios of the 'treatment' term in order to account for light-treatment splits and block effects (Appendix).

Sample sizes for the different species-treatment combinations were somewhat unbalanced (Table 2). This should be borne in mind when considering results of these ANOVAs.

Models were assessed for normality and constant variance by examining normal QQ plots and residual plots, respectively. The results of those models failing to meet those criteria should be considered somewhat cautiously.

All Harvest 1 models met assumptions of normality except perhaps for the R:S mass ratio ANOVA. Similarly, all of the Harvest 1 models met assumptions of constant variance except perhaps for the R:S mass ratio ANOVA. The failure of the R:S mass ratio models to consistently meet the assumptions of ANOVA appeared to be due to several very small root dry masses. The implications of this observation for our results will be discussed in the last paragraph of section 3.2 of this chapter.

All Harvest 3 models met assumptions of normality except for the SMR ANOVA. All Harvest 3 models also met assumptions of constant variance except for the height and SMR ANOVAs. The fact that SMR so consistently failed to meet the assumptions of ANOVA was a concern, but since the SMR data is not critical to our conclusions, more complex/appropriate analyses were not conducted.

Harvest 1 and 3 ANOVAs for all seedling traits showed highly significant ($p<0.001$) species:treatment interactions, except for SLA for Harvest 3 and R:S mass ratio for Harvest 1, which were non-significant ($\alpha=0.05$; Appendix).

In order to assess seedling trait differences at the species level, species means within each light environment were compared using Tukey's HSD test. Sample sizes of the six species were somewhat unbalanced, particularly during Harvest 1 (Table 2),

raising some concerns about the validity of Tukey's HSD test for this dataset. The Tukey's HSD test in R does include an adjustment to accommodate mildly unbalanced designs, but the unbalanced sample sizes should still be borne in mind when considering results based on Tukey's HSD test.

For the Harvest 3 data, species' relative responses to the two light environments were evaluated by calculating a relative light response (RLR) statistic. RLRs were calculated for each seedling trait by averaging the ln-transformed values of a given parameter in the shade and subtracting that average from each individual value in the light. For each high-light value, RLR was calculated as follows:

$$\text{(2)} \qquad \text{RLR} = \ln\left(\text{magnitude in light}\right) - \bar{x}\left[\ln\left(\text{magnitudes in shade}\right)\right]$$

$$\text{e.g.} \quad \text{RLR} = \ln\left(\text{height in light}\right) - \bar{x}\left[\ln\left(\text{heights in shade}\right)\right]$$

A positive RLR indicates that a trait was greater in magnitude in the high-light environment than in the shade environment for a given species. A negative RLR indicates that a trait was lower in magnitude in the high-light environment than in the shade environment for a given species. RLR puts the responses of various seedling traits on a common scale, which allows us to explore their relative responses to the two light environments. One-way ANOVAs were performed for the RLRs of each seedling trait, with species accounting for variation in RLR. Block effects were ignored because shade values were averaged across blocks. All RLR models appeared to meet assumptions of normality and constant variance, which were evaluated by examining normal QQ plots and residual plots, respectively. Species effects for all RLR ANOVAs were highly

significant ($p<0.001$; Appendix), and species means were compared using Tukey's HSD procedure.

1.3. Results

1.3.1. Germination

Cumulative percent germination trajectories for the six species in both light environments can be seen in Figure 2.

Red and black spruce had the highest percent germination in either light environment, followed by white spruce, which germinated somewhat (but non-significantly) more completely than balsam fir (Fig. 3). In the shade environment, hemlock had similar percent germination to balsam fir and white spruce; but in the high-light environment, hemlock had the lowest percent germination of any species (Fig. 3). White pine had the lowest percent germination in the shade environment and germinated only slightly (but non-significantly) more completely than hemlock in the high-light environment (Fig. 3).

Percent germination was not significantly affected by light environment for any species except hemlock, which germinated more completely in the shade environment than in the high-light environment (Fig. 3).

Black and red spruce had the highest germination rates of any species (Fig. 4). In both light environments, white pine, balsam fir, and hemlock germinated significantly more slowly than the spruces (Fig. 4). Of the three slower-germinating species, white pine germinated fastest in the high-light environment, followed by balsam fir and eastern hemlock (Fig. 4). In the high-light environment, white spruce germinated at similar

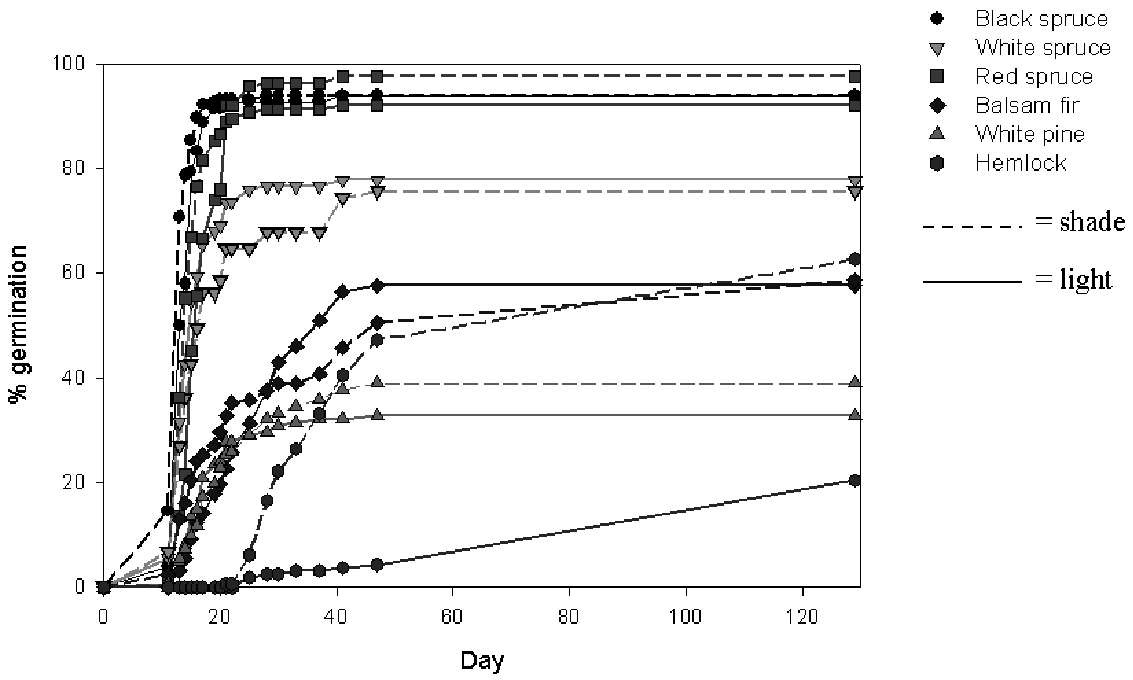

Figure 2. Cumulative percent germination trajectories for Experiment 1. (n=9/species/treatment; 18 ± 1 seeds per replicate).

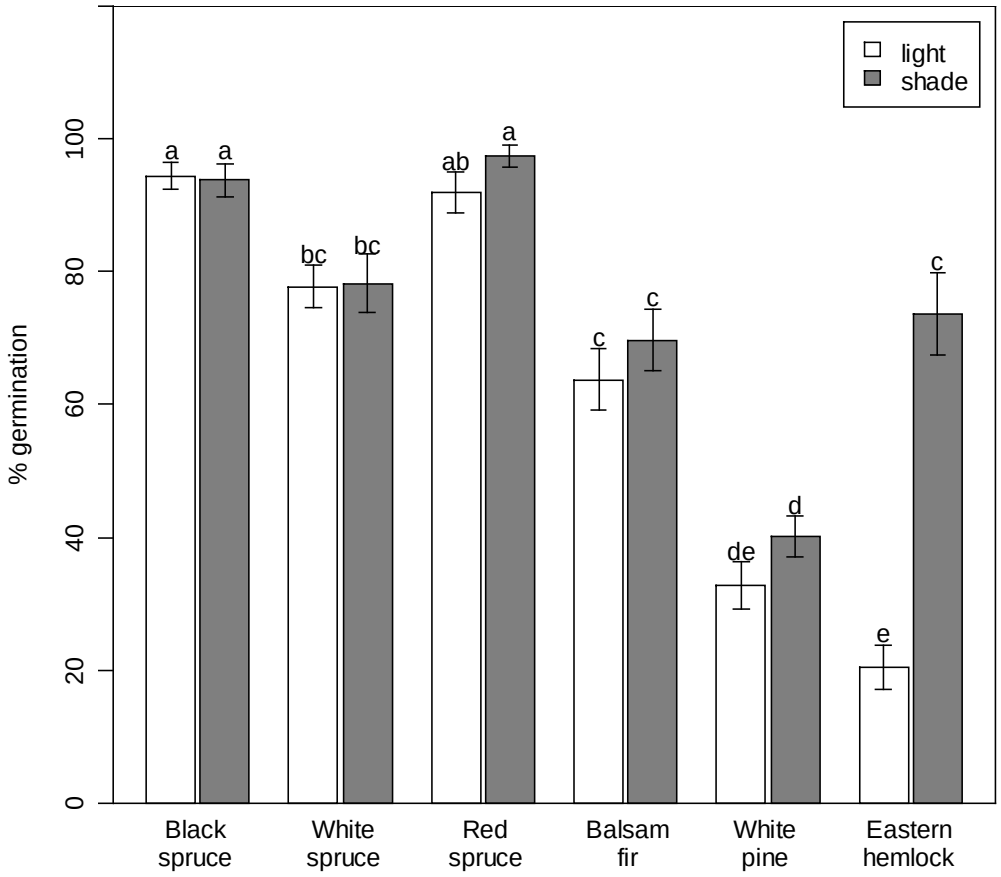

Figure 3. Mean final percent germination (± 1 SE) for Experiment 1. Different letters indicate significant differences determined by Tukey's HSD test. (n=9/species/treatment; 18 ± 1 seeds per replicate).

rates to red and black spruce, but in the shade environment, white spruce germinated significantly more slowly than the other spruces (Fig. 4). However, the differences between the germination rates of white spruce and the other two spruces appears to have been due to an anomaly in the white spruce germination trajectory. In Figure 2, note the unique 'lull' from day 20 to day 40 in the germination trajectory of white spruce in the shade environment. This lull likely caused the rate calculations to indicate that white spruce had a slower germination rate in the shade environment because white spruce did not complete 90% of its eventual germination until after the lull broke. Examination of the maximum slopes of the high-light and shade germination trajectories of the spruces clearly show that white spruce underwent most of its germination at a similar rate as red and black spruce in both light environments. As such, the significant differences between white spruce in the shade and all other spruce germination rates (Fig. 4) probably should be disregarded.

In response to the high-light environment, white pine germinated significantly faster and hemlock germinated significantly more slowly (Fig. 4). The germination rates of black spruce, red spruce, and balsam fir were not significantly different between the two light environments (Fig. 4).

The three spruces, white pine, and balsam fir initiated germination relatively soon after their seeds were sown (Fig. 5). In both light environments, hemlock initiated germination much later than any of the other species (Fig. 5). In the high-light environment, hemlock initiation was particularly slow, occurring over 20 days after the other species' germination initiated (Fig. 5).

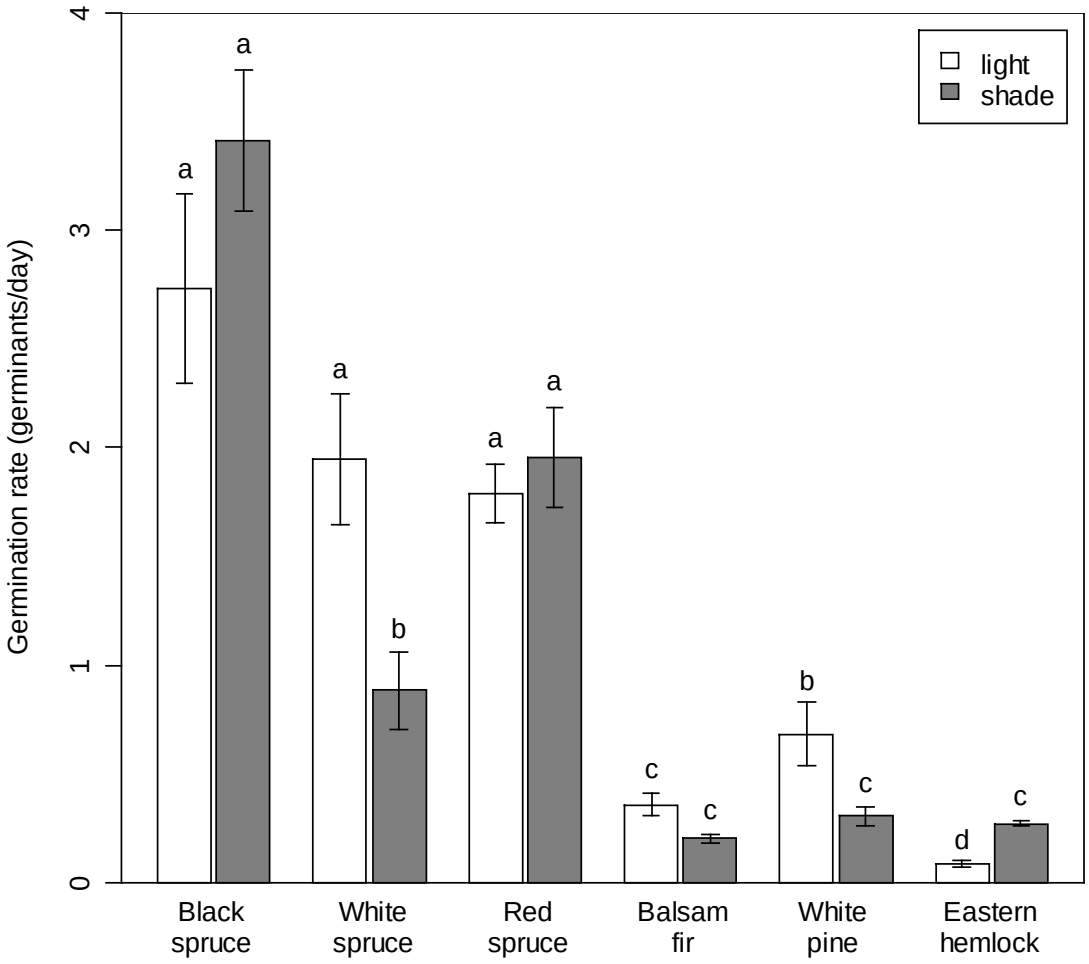

Figure 4. Germination rates (± 1 SE) in germinants/day (of the 18 ± 1 seeds planted in each replicate) for Experiment 1. Germination rate calculated as the mean rate/day of the period during which 80% of eventual germinants in a given replicate germinated. For instance if 10 of 18 seeds germinated in a given pot, the germination rate for the days in which germinants 2-9 germinated would be used to calculate the germination rate for that pot. Different letters indicate significant differences determined by Tukey's HSD test. (n=9/species/treatment; 18 ± 1 seeds per replicate).

In both light environments, black, white, and red spruce had similar germination duration and concluded germination sooner than most other species (Fig. 5; recall also the previous discussion of white spruce germination rates and the anomaly shown in Figure 2). The one exception to this was white pine in the high-light environment, which concluded germination at a similar time as red spruce (Fig. 5). In the high-light environment, balsam fir took much longer to complete germination than white pine or the three spruces (Fig. 5). As discussed in section 2.5.2 of this chapter, the germination durations of hemlock and shade-environment balsam fir were difficult to estimate. Nonetheless, we can safely conclude that hemlock began germinating much later than any of the other species and that both hemlock and shade-environment balsam fir concluded germination significantly later than any of the other species (Fig. 5).

The timing of germination for black, white, and red spruce was not significantly different between the two light environments (Fig. 5). Balsam fir and white pine concluded germination sooner in the high-light environment than they did in the shade environment (Fig. 5). Hemlock initiated germination much later in the high-light environment than it did in the shade environment (Fig. 5), but we have no data on how the length of hemlock's germination period was affected by light environment.

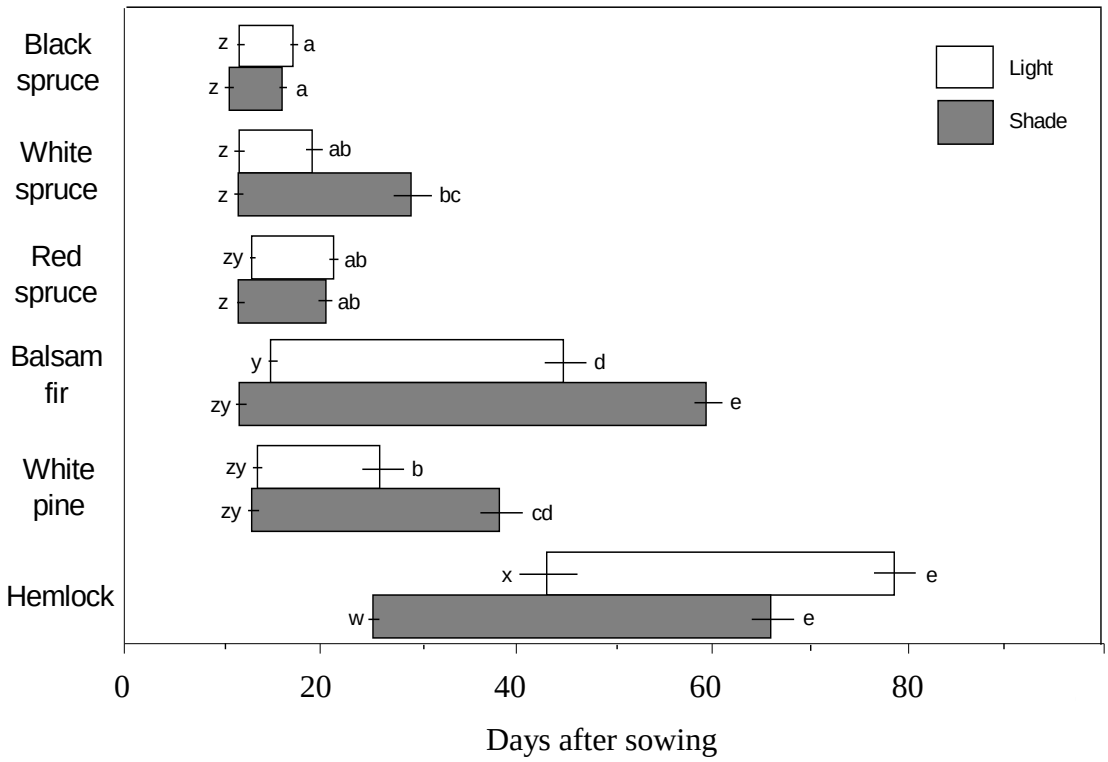

Figure 5. Timing of germination initiation and conclusion (± 1 SE) for Experiment 1. Germination initiation is defined as the time at which at least 10% of eventual germinants in a given replicate had germinated. Germination conclusion is defined as the time at which at least 90% of eventual germinants in a given replicate had germinated. So, for instance, if 15 of 18 seeds germinated in a given replicate, initiation is defined as the day on which germinant 2 germinated, and conclusion is the day on which germinant 14 germinated. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for initiation (w-z) than for conclusion (a-e). The two sets of letters do not refer to each other, meaning that one cannot make comparisons of an initiation mean with a conclusion mean. (n=9/species/treatment; 18 ± 1 seeds per replicate).

1.3.2. Harvest 1

Abbreviations for the various ratios and statistics discussed here are detailed in Table 4. For the Harvest 1 data, light-grown hemlock is excluded because there were few germinants by Harvest 1.

For all species, seedlings grown in the high-light environment had higher dry masses, higher R:S mass ratios, longer roots, and longer roots per unit height than their shade-grown counterparts (Fig. 6B-E). At Harvest 1, height was relatively unaffected by light level (Fig. 6A).

In both light environments, white pine was by far the tallest of any of the six species (Fig. 6A). In the high-light environment, black spruce was the second tallest, followed by white spruce, red spruce, and balsam fir, which were all very similar in height (Fig. 6A). In the shade environment, the three spruces and balsam fir were very similar in height. Hemlock was significantly shorter than black and white spruce in the shade environment, but in absolute terms hemlock was only 0.9 cm shorter, on average, than those two species (Fig. 6A).

In both light environments, white pine was by far the most massive of any of the six species (Fig. 6B). In the high-light environment, black spruce, white spruce, and balsam fir had similar masses and were all significantly more massive than red spruce (Fig. 6B). In the shade, hemlock was the least massive species (Fig. 6B). Balsam fir was significantly more massive (about 2x more) than the three spruces, whose dry masses were very similar to one another (Fig. 6B).

In the high-light environment, white pine and balsam fir had R:S mass ratios over 2x higher than those of the three spruces, whose R:S mass ratios were very similar to one

Parameter	Abbreviation or symbol	Units or definition
Root-to-shoot length ratio	R:S length	cm primary root length/cm shoot length
Root-to-shoot mass ratio	R:S mass	g root dry mass/g shoot dry mass
Root mass ratio	RMR	g root dry mass/g plant dry mass
Stem mass ratio	SMR	g stem dry mass/g plant dry mass
Leaf mass ratio	LMR	g leaf dry mass/g plant dry mass
Specific stem length	SSL	cm stem length/g stem dry mass
Specific leaf area	SLA	cm^2 leaf area/g leaf dry mass
Foliar-area-to-root-mass-ratio	FARM	cm^2 plant leaf area/g leaf dry mass
Specific root length	SRL	cm total root system length/g root dry mass
Relative growth rate	RGR	$\frac{\text{mg plant dry mass/g plant dry mass}}{\text{day}}$
Relative light response	RLR	$\frac{\ln(\text{magnitude in high light}) - \ln(\text{magnitude in low light})}{\textit{for any given plant trait}}$
Relative water response	RWR	$\frac{\ln(\text{magnitude in high water}) - \ln(\text{magnitude in low water})}{\textit{for any given plant trait}}$
Relative competition response	RCR	$\frac{\ln(\text{magnitude in comp treatment}) - \ln(\text{magnitude in no-comp treatment})}{\textit{for any given plant trait}}$

Table 4. Morphological ratios and statistics, with their acronyms and units of measure.

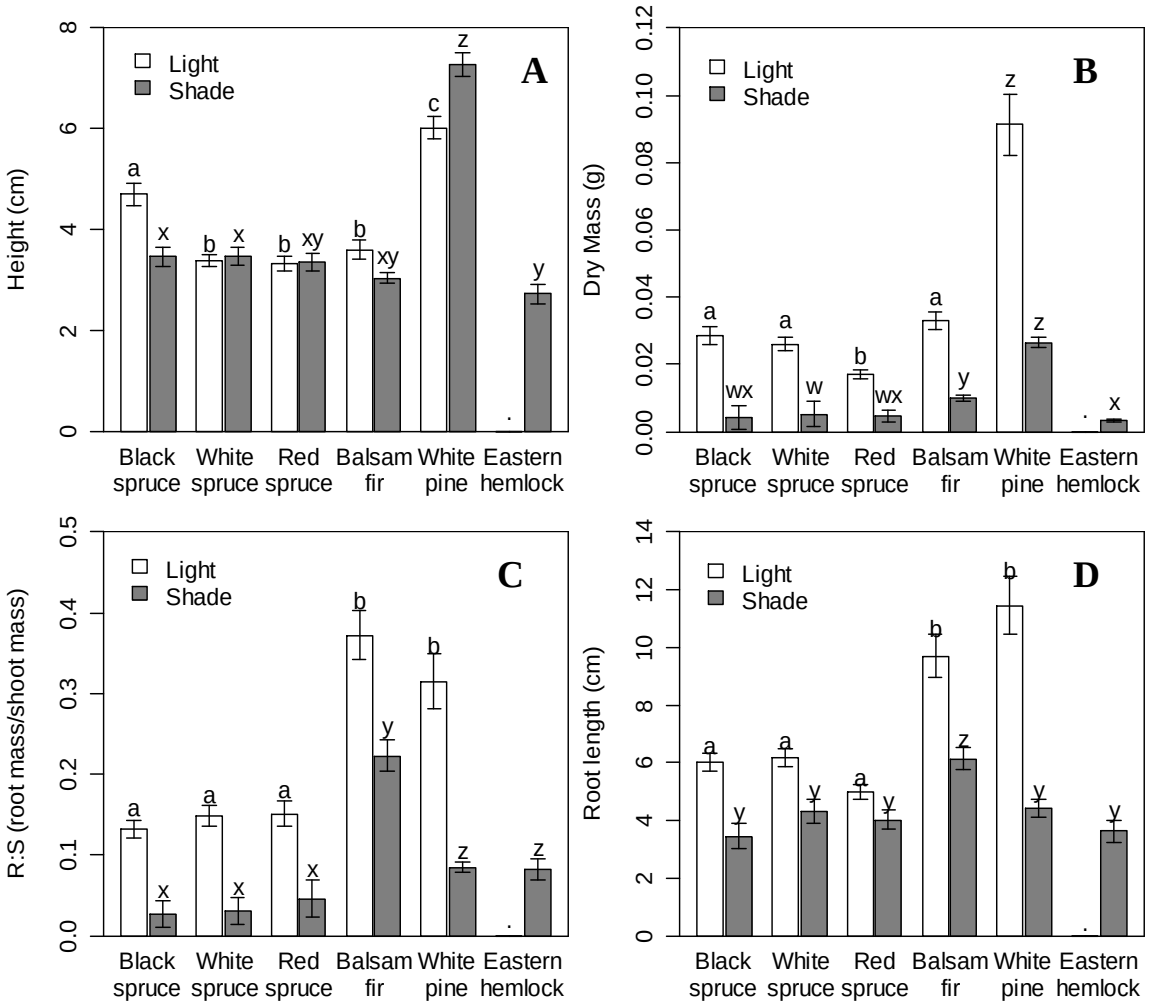

Figure 6 A-D. Harvest 1 means (± 1 SE) of height (A), dry mass (B), R:S mass ratio (C), and root length (D) for Experiment 1 70 days after planting. Acronyms are described in Table 4. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for light (a-d) than for shade (u-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. (n: black spruce-light = 25; white spruce-light = 27; red spruce-light = 27; balsam fir-light = 17; white pine-light = 9; hemlock-light = 0; black spruce-shade = 27; white spruce-shade = 27; red spruce-shade = 27; balsam fir-shade = 18; white pine-shade = 9; hemlock-shade = 18).

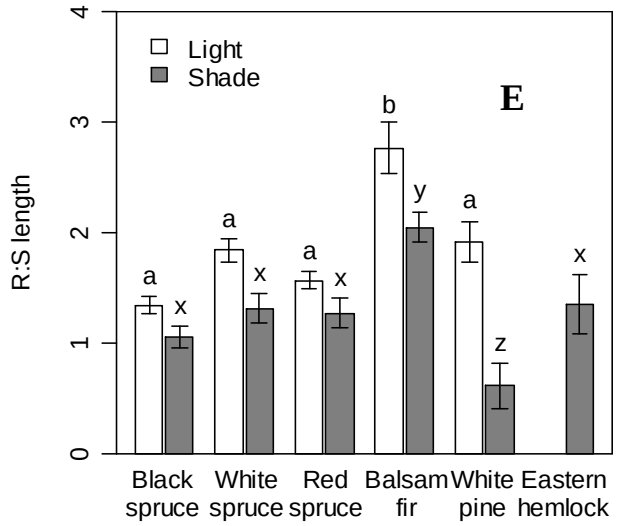

Figure 6E. Harvest 1 means (± 1 SE) of R:S length ratio (E) for Experiment 1 70 days after planting. Acronym is described in Table 4. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for light (a-d) than for shade (u-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. (n: black spruce-light = 25; white spruce-light = 27; red spruce-light = 27; balsam fir-light = 17; white pine-light = 9; hemlock-light = 0; black spruce-shade = 27; white spruce-shade = 27; red spruce-shade = 27; balsam fir-shade = 18; white pine-shade = 9; hemlock-shade = 18).

another (Fig. 6C). In the shade, balsam fir seedlings had R:S mass ratios almost 2x higher than those of any other species (Fig. 6C). The R:S mass ratios of white pine and hemlock were similar to one another and were significantly higher than the R:S mass ratios of the three spruce species, whose R:S mass ratios were very similar to one another (Fig. 6C).

In the high-light environment, white pine and balsam fir primary roots were nearly 2x longer than those of the three spruces, whose root lengths were very similar to one another (Fig. 6D). In the shade, white pine, hemlock, and the three spruces had similar primary root lengths, while balsam fir had significantly longer roots than any other species (Fig. 6D). In both light environments, balsam fir developed significantly longer primary roots relative to its height than did any other species (Fig. 6E).

There were some problems with non-constant variance in the R:S mass ratio ANOVAs, apparently due to several very low R:S mass ratios. Closer examination of the data revealed that the small R:S mass ratios were largely due to the root dry masses of red and black spruce, many of which weighed $\leq$0.0001 g at Harvest 1. Red and black spruce were among the first species to initiate and complete germination (Fig. 5), thus giving them the longest time to develop their root systems. Despite this head start, at Harvest 1 the root systems of black and red spruce were still much smaller than those of the other species. This further highlights the fact that, compared to the other species, red and black spruce seedlings strongly favor early shoot development over root development.

1.3.3. Harvest 3

1.3.3.1. Species Growth and Morphology

In the high-light environment, black and red spruce were the tallest of the six species (Fig. 7A). White pine and white spruce were significantly shorter than black and red spruce (Fig. 7A). In turn, balsam fir was significantly shorter than white pine and white spruce, while hemlock was significantly shorter than all of the other species (Fig. 7A).

In the shade, white pine was significantly taller than balsam fir, hemlock, and the three spruces, which were all similar to one another in height (Fig. 7A).

In the high-light environment, white pine was the most massive (Fig. 7B). The three spruces were similar in dry mass and were all significantly shorter than white pine (Fig. 7B). In turn, balsam fir was significantly less massive than the three spruce species, while hemlock was significantly less massive than all of the other species (Fig. 7B).

In the shade, white pine was significantly more massive than any of the other species (Fig. 7B). And despite some statistically significant differences, dry masses in the shade were relatively similar among the other five species (Fig. 7B).

In the high-light, R:S mass ratios[1] were similar among the three spruces, while fir and pine had significantly higher R:S mass ratios than the spruces or hemlock (Fig. 7E; 7F). Hemlock had the lowest R:S mass ratios in the high-light environment, though its mean R:S mass ratio was not significantly different from that of black spruce (Fig. 7E).

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[1]Most remarks about R:S mass ratios can also be applied to RMR (and vice versa): R:S mass = RMR/(1-RMR).

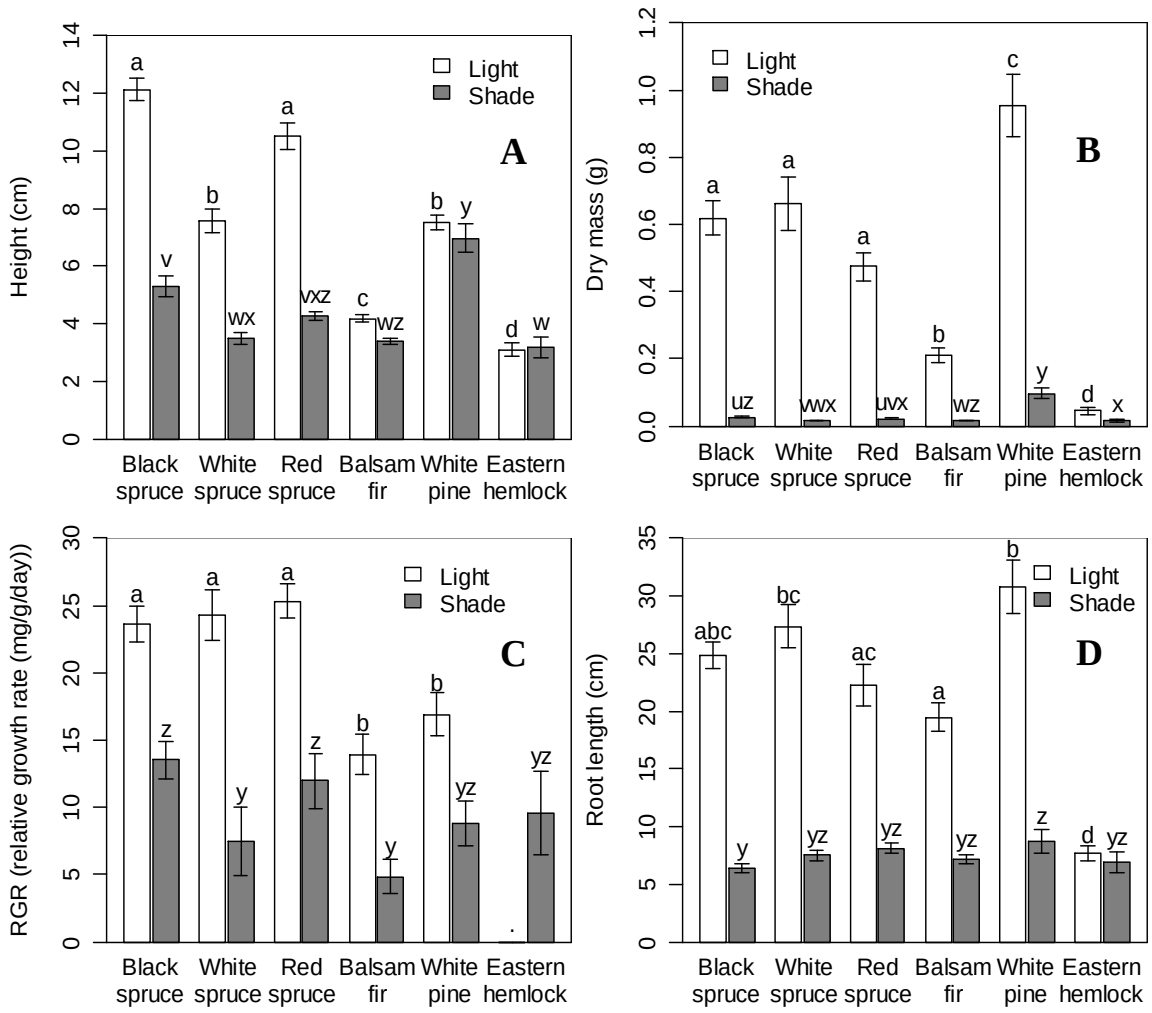

Figure 7A-D. Harvest 3 means (± 1 SE) of height (A), dry mass (B), RGR (C), and primary root length (D) for Experiment 1 200 days after planting. Acronyms are described in Table 4. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for light (a-d) than for shade (u-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. (n: black spruce-light = 27; white spruce-light = 25; red spruce-light = 25; balsam fir-light = 26; white pine-light = 13; hemlock-light = 21; black spruce-shade = 27; white spruce-shade = 25; red spruce-shade = 27; balsam fir-shade = 24; white pine-shade = 21; hemlock-shade = 17. Replicates for RGR calculations: black spruce-light = 27/25; white spruce-light = 25/27; red spruce-light = 25/27; balsam fir-light = 26/17; white pine-light = 13/9; black spruce-shade = 27/27; white spruce-shade = 25/27; red spruce-shade = 27/27; balsam fir-shade = 24/18; white pine-shade = 21/9; hemlock-shade = 17/18—the first number is the number of Harvest 3 seedlings and the second number indicates the number of Harvest 1 seedlings on which RGR calculations were based.

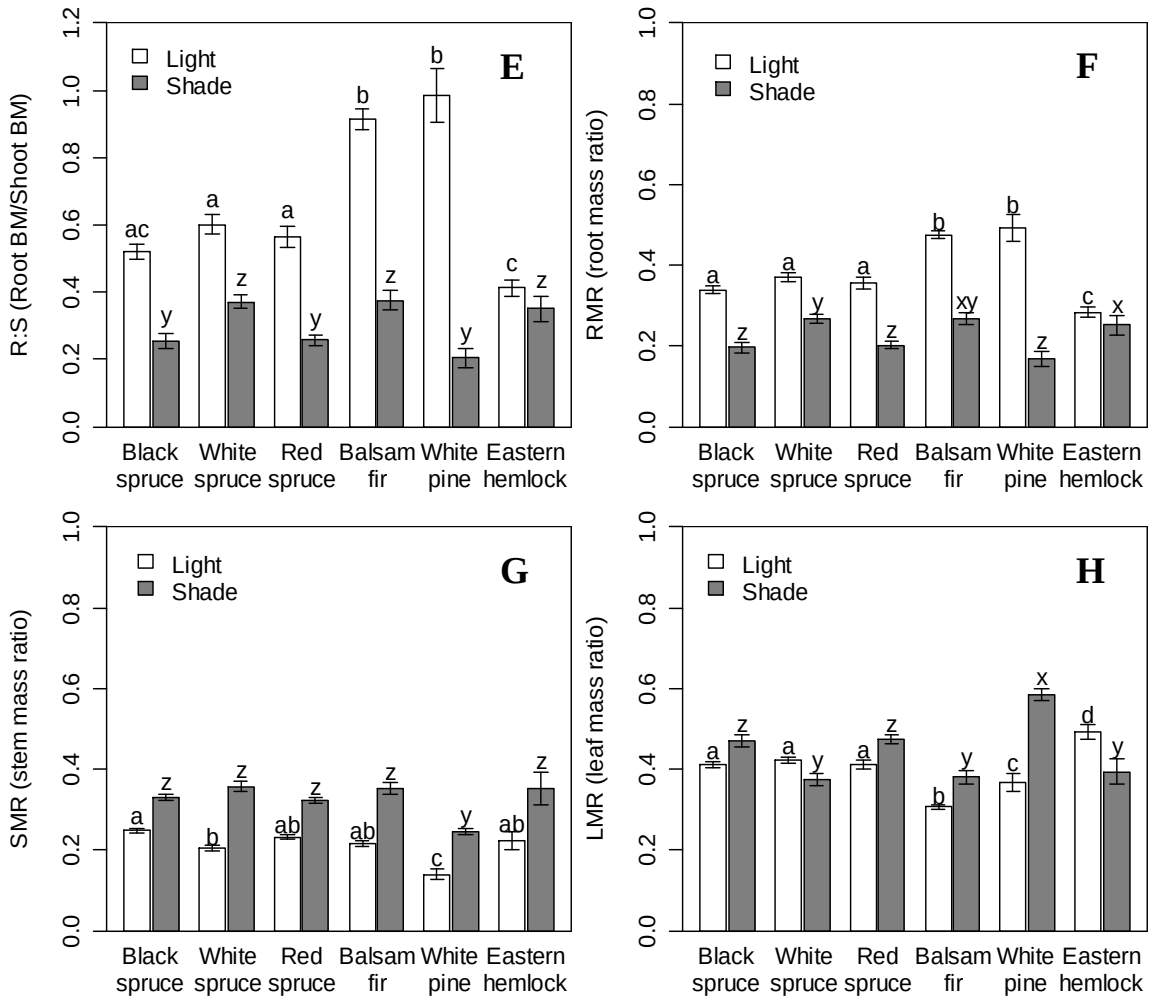

Figure 7E-H. Harvest 3 means (± 1 SE) of R:S mass ratio (E), RMR (F) SMR (G), and LMR (H) for Experiment 1 200 days after planting. Acronyms are described in Table 4. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for light (a-d) than for shade (u-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. (n: black spruce-light = 27; white spruce-light = 25; red spruce-light = 25; balsam fir-light = 26; white pine-light = 13; hemlock-light = 21; black spruce-shade = 27; white spruce-shade = 25; red spruce-shade = 27; balsam fir-shade = 24; white pine-shade = 21; hemlock-shade = 17).

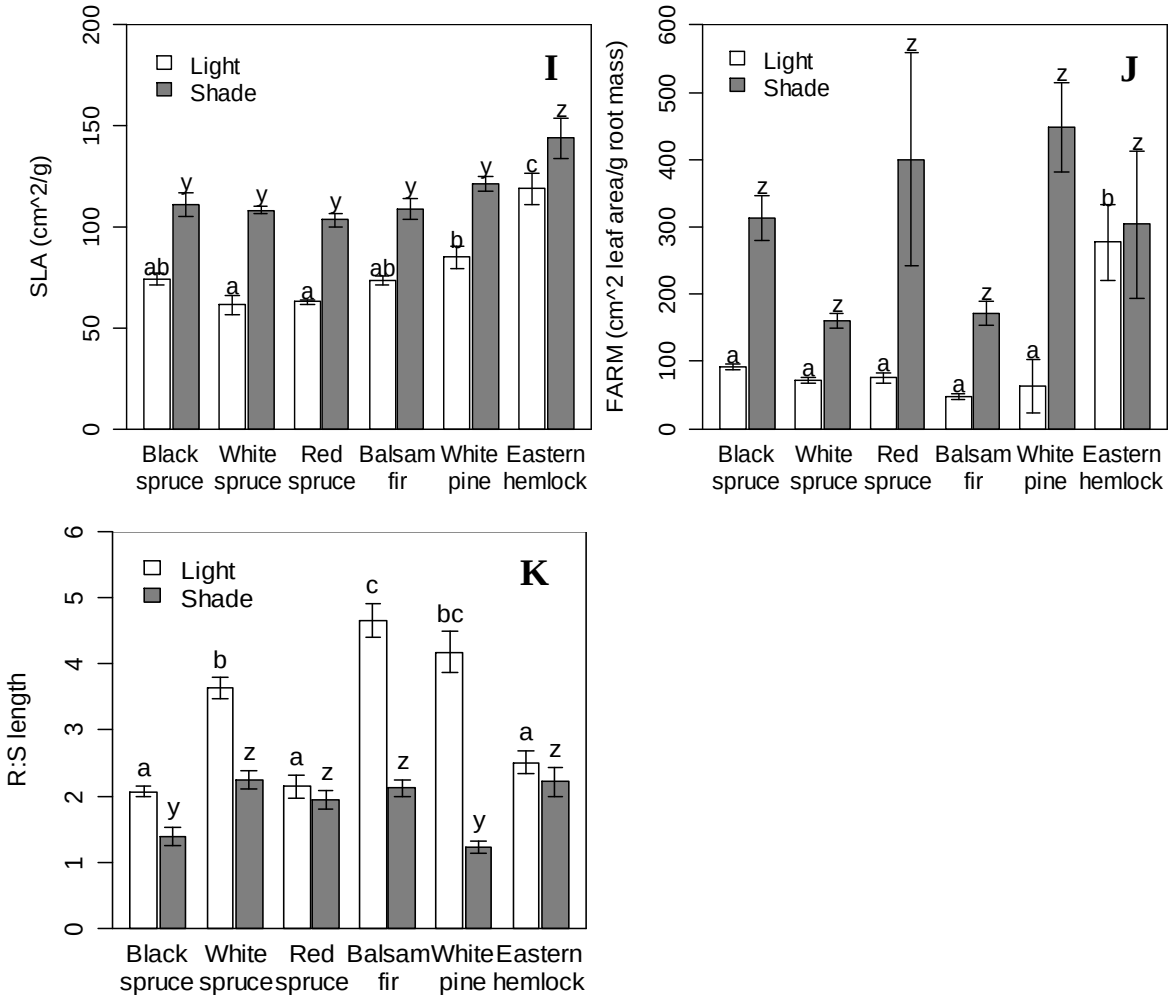

Figure 7I-K. Harvest 3 means (± 1 SE) of SLA (I), FARM ratio (J), and R:S length ratio (K) for Experiment 1 200 days after planting. Acronyms are described in Table 4. Different letters indicate significant differences determined by Tukey's HSD test. Different sets of letters are used for light (a-d) than for shade (u-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. (n*: black spruce-light = 27; white spruce-light = 25; red spruce-light = 25; balsam fir-light = 26; white pine-light = 13; hemlock-light = 21; black spruce-shade = 27; white spruce-shade = 25; red spruce-shade = 27; balsam fir-shade = 24; white pine-shade = 21; hemlock-shade = 17). *SLAs based on 10 samples/species-treatment.

In the shade, black spruce, red spruce, and white pine had similar R:S mass ratios, all of which were significantly lower than the R:S mass ratios of white spruce, balsam fir, and hemlock (Fig. 7E).

Root lengths in the high-light environment were fairly similar for all species except white pine, which had significantly longer roots than red spruce, balsam fir, and hemlock. Hemlock had much shorter primary roots than the other species (Fig. 7D). In the high-light environment, balsam fir and white pine had significantly longer primary roots relative to their heights than the other species (Fig. 7K). Among the spruces and hemlock, white spruce had the highest R:S length ratios (Fig. 7K).

Despite some statistically significant differences, primary root lengths in the shade were relatively similar for all species (Fig. 7D). Relative to their heights, in the shade environment, black spruce and white pine had significantly shorter primary roots than the other species, none of which were significantly different from each other in terms of R:S length (Fig. 7K).

In the high-light environment, the RGRs of the three spruces were similar, and they were all significantly higher than the RGRs of balsam fir and white pine (Fig. 7C). In the shade, black and red spruce had the highest RGRs, which were significantly higher than the RGRs for white spruce and balsam fir (Fig. 7C). White pine and hemlock RGRs in the shade were moderate among the study species and were not significantly different from the RGRs of any other species. (Fig. 7C).

In both light environments, SLAs of all species were similar, except for hemlock whose SLA in both light environments was significantly higher than those of the other species (Fig. 7I).

In the high-light environment, the FARM ratios of all species were similar except for hemlock, whose FARM ratios were significantly higher than those of the other species (Fig. 7J). There were no significant interspecific FARM ratio differences in the shade, where FARM ratios were highly variable (Fig. 7J).

1.3.3.2. Responses to Light Environment

As previously discussed, the relative responses of various traits to the different light environments were calculated using the relative light response (RLR) statistic. A positive RLR indicates that a given trait for a given species was greater in magnitude in the high-light environment than in the shade environment. A negative RLR indicates that a given trait for a given species was lower in magnitude in the high-light environment than in the shade environment. Larger absolute RLRs (i.e. more positive or more negative) indicate a larger response to light treatments. RLRs for hemlock were skewed by the disparate germination initiation times hemlock exhibited in the two light environments (i.e. light-shade comparisons could be between seedlings of significantly different ages), and thus are not discussed here.

Of the size metrics (i.e. dry mass and height), $RLR_{dry\ mass}$ was higher than $RLR_{height,}$ meaning that plant dry mass responded more strongly than height to the different light environments (Table 5). The three spruces had the highest $RLR_{dry\ masses}$, followed by white pine and balsam fir, whose $RLR_{dry\ masses}$ were significantly lower than those of the spruces (Table 5). The three spruces also had significantly higher $RLR_{heights}$ than fir or pine, whose $RLR_{heights}$ were not significantly different from one another (Table

	Height	Root length	Plant BM	R:S	LMR	SMR	RMR
Black spruce (n=27)	0.88 ± 0.09 a	1.42 ± 0.07 a	3.21 ± 0.12 a	0.79 ± 0.09 ab	-0.12 ± 0.04 a	-0.29 ± 0.03 c	0.59 ± 0.07 ab
White spruce (n=25)	0.77 ± 0.07 a	1.27 ± 0.10 ab	3.67 ± 0.15 a	0.49 ± 0.07 bd	0.14 ± 0.04 b	-0.55 ± 0.04 b	0.34 ± 0.05 bd
Red spruce (n=25)	0.90 ± 0.05 a	0.97 ± 0.10 b	3.02 ± 0.09 a	0.79 ± 0.07 ab	-0.13 ± 0.03 a	-0.34 ± 0.04 acd	0.57 ± 0.05 ab
Balsam fir (n=24)	0.22 ± 0.05 b	1.02 ± 0.08 b	2.44 ± 0.10 b	0.94 ± 0.07 a	-0.20 ± 0.04 a	-0.48 ± 0.04 bd	0.61 ± 0.05 a
White pine (n=13)	0.06 ± 0.07 b	1.26 ± 0.14 ab	2.37 ± 0.20 b	1.61 ± 0.08 c	-0.46 ± 0.03 c	-0.59 ± 0.05 b	1.11 ± 0.06 c
Hemlock (n=16)	0.01 ± 0.11 b	0.19 ± 0.13 c	1.01 ± 0.30 c	0.36 ± 0.15 d	0.22 ± 0.08 b	-0.53 ± 0.11 bd	0.28 ± 0.13 d
All species (n=130)	0.55 ± 0.04	1.06 ± 0.05	2.76 ± 0.09	0.79 ± 0.05	-0.08 ± 0.02	-0.44 ± 0.02	0.56 ± 0.03

	SLA (***n=10)	FARM	Reps (all traits but SLA)
Black spruce	-0.40 ± 0.06 abc	-1.12 ± 0.11 abc	(27/27)
White spruce	-0.57 ± 0.03 ab	-0.77 ± 0.08 b	(25/25)
Red spruce	-0.49 ± 0.03 ab	-1.28 ± 0.13 c	(25/27)
Balsam fir	-0.39 ± 0.08 abc	-1.21 ± 0.09 abc	(26/24)
White pine	-0.36 ± 0.06 abc	-1.92 ± 0.09 d	(13/21)
Hemlock	-0.19 ± 0.12 c	-0.09 ± 0.25 e	(21/17)
All species	-0.40 ± 0.03	-1.05 ± 0.07	(137/141)

Table 5. Mean RLRs (relative light responses) (± 1 SE) of height, primary root length, plant BM (biomass; i.e. dry mass), R:S mass ratio, LMR, SMR, RMR, FARM, SLA. Acronyms are described in Table 4. RLR calculations are described in section 2.5.3 of chapter 1. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot, for instance, compare a height mean with a primary root length mean. Replicates in parentheses indicate the number of replicates in the light (first number) and the number of replicates in the shade (second number) on which calculations are based.

5). In other words, the size of the spruces was more responsive to light environment than was the size of any of the other species.

Before discussing the allocation RLRs, it is extremely important to note that the RLRs of these allocation metrics only represent the actual differences in allocation between seedlings in different light conditions; they do not distinguish between ontogenetic drift and phenotypic plasticity as the driver of those changes. That is, biomass allocation can change a great deal with seedling size, and anything that can affect seedling size (e.g. light) can in turn affect allocation without any sort of plastic response on the part of the seedling (Poorter and Nagel 2000). So, the RLRs of allocation traits should be viewed only as descriptors of how allocation differed between high-light and low-light seedlings rather than indicators of true seedling plasticity in response to different light conditions.

In terms of carbon allocation, SMR and RMR changed more than LMR in response to light environment, with SMR decreasing from the low-light to the high-light environment, RMR increasing in the higher light environment, and LMR responding relatively little (and more variably) to light environment (Table 5).

The exception to this was white pine, whose LMR changed significantly more in response to the different light conditions than it did for any of the other species (Table 5). Increases in RMR from the low-light to the high-light environment were similar for all species except white pine, for which RMR increased significantly more in response to higher light than it did for any other species (Table 5). R:S mass ratios responded similarly to light environment as the related quantity, RMR. That is, the response of R:S mass ratio to higher light was similarly positive among all species except white pine, for

which R:S mass ratio responded significantly more positively to higher light than it did for the other species (Table 5).

RLR_{SLA} was fairly uniformly negative for all species (Table 5). That is, SLAs were always lower in the high-light environment. RLR_{FARM} was also negative for all species, and RLR_{FARM} was significantly more negative for white pine than it was for the other species (Table 5).

1.4. Discussion

1.4.1. Germination

The seeds used for this experiment were sorted for viability at the National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada), so the absolute germination percentages we observed may not apply directly to field conditions. Nonetheless, the percent germination values we recorded are in general agreement with other studies, with black and red spruce having a very high percent germination around 80-90% (Place 1955; Safford 1974; Greenwood et al. in preparation), white spruce having a slightly lower percent germination around 70% (Safford 1974), balsam fir and white pine germinating about 40-50% of their seeds (Place 1955; Franklin 1974; Kruglin 1974; Kanoti 2005; Greenwood et al. in preparation), and hemlock germinating a relatively low proportion of their seeds in the warmer high-light environment (Olson et al. 1959). Kanoti (2005) found that red spruce germinated faster and more completely than balsam fir or white pine, which agrees with our findings (Fig. 4).

The two light environments imposed very different soil temperature regimes on the germinating seeds (Fig. 8). These temperature differences presumably were the primary drivers of differences in germination dynamics between the two light environments. Except for hemlock, the light treatments did not significantly affect percent germination of any of the study species (Fig. 3). However, the light environment did affect the timing and rate of germination for various species (Fig. 4). White pine germinated significantly more rapidly in the high-light environment, while the germination initiation of hemlock was much delayed in the high-light environment (Fig. 5). White pine is considered less shade tolerant than the other study species (Baker 1949; Barnes et al. 1998), and its seedling establishment and regeneration is generally most successful in relatively exposed, higher-light environments (Wendel and Clay 1990). So perhaps white pine's more rapid germination in higher-light environments allow it to gain an early competitive foothold in its favored niche.

Balsam fir germination showed a limited response to temperature in this experiment (Fig. 5). In previous experiments, however, Greenwood et al. (in preparation) found that balsam fir germination rates consistently increased in warmer conditions (30/20ºC day/night temperature) than in cooler conditions (20/10ºC day/night temperature), while red spruce germination rates were unresponsive to the same temperature treatments. This suggests that the germination rates of both pine and fir can respond positively to higher temperatures, but that soil temperature differences between the two light environments in this experiment (Fig. 8) were perhaps insufficient to elicit that positive response in fir.

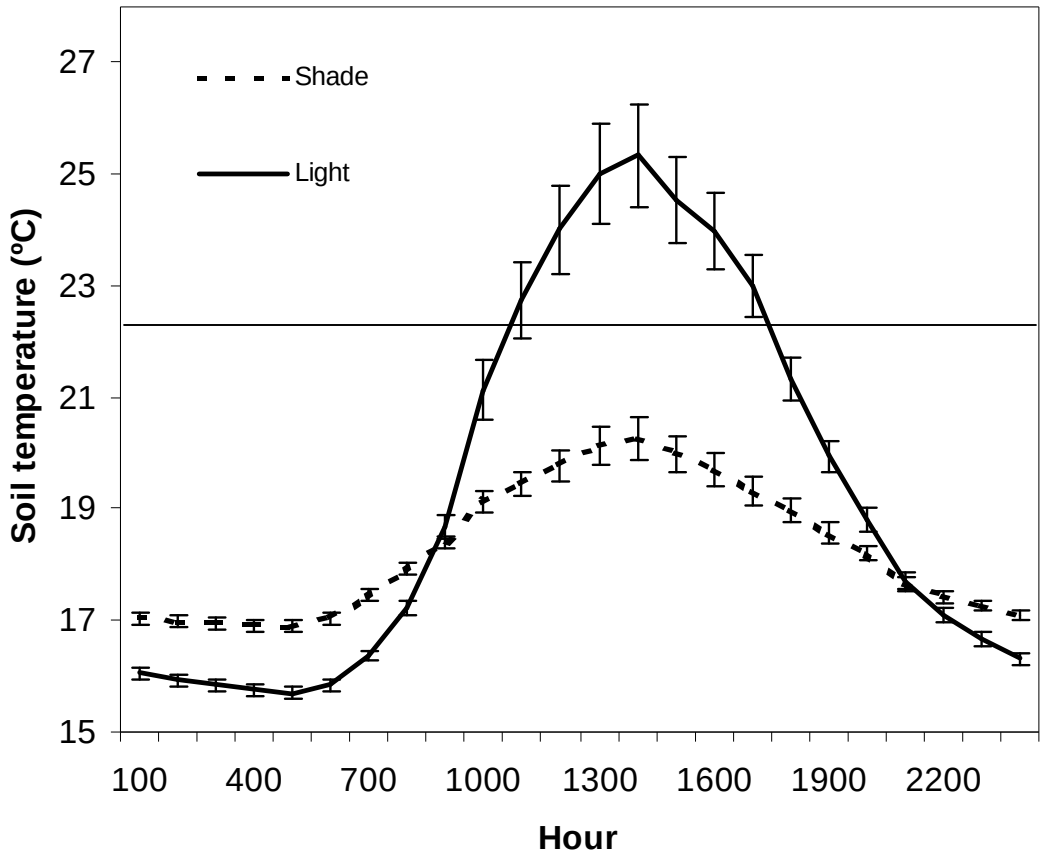

Fig. 8. Mean hourly soil temperature (± 1 SE) from 04/21/06 to 05/31/06 (days 1-40 after seeds were sown) in Experiment 1.

Hemlock can often require from one to two months to reach peak germination rates (Goerlich and Nyland 2000), so it is not surprising that it germinated later than the other species (Fig. 5). But why the stark differences between the two light environments? According to Olson et al. (1959), sustained temperatures above 21˚ C can inhibit hemlock germination. During the first 40 days of Experiment 1 (the main germination period for most species—Fig. 2), the soil temperature in the high-light environment was, on average, above 21˚ C from approximately 1000 to 1800 hours, while the mean soil temperature in the shade environment was below 21˚ C throughout the day (Fig. 8). It therefore seems likely that hemlock germination in the high-light environment was simply inhibited by higher soil temperatures.

Hemlock is a late successional species whose regeneration is generally most successful in the relatively cool, moist conditions under established canopies (Goerlich and Nyland 2000). So, perhaps hemlock's more rapid and higher percent germination in the shade environment relates to its habitat preference (Michael Day, personal communication). That is, hemlock germinates relatively poorly in the warmer high-light environment where it is unlikely to become established and survive to maturity, but it germinates relatively well in the cooler shade environment where it is most likely to establish and survive to maturity. These observations fit with hemlock's classification as a late successional, shade tolerant species.

Again, the germination dynamics of red spruce, black spruce, and, to a lesser extent, balsam fir were relatively insensitive to light environment (Fig. 4 and 5).

Based on these characteristics, the species can be grouped as follows:

1) The three spruce species, which had the smallest seeds (Table 6), germinated rapidly, and had high percent germination. The germination rates and percentages of the spruces appeared to be relatively insensitive to the temperature regimes imposed in this experiment and past experiments (Greenwood et al. in preparation).
2) White pine and balsam fir, which had the largest seeds (Table 6) and, relative to group 1, had lower percent germination and had a more-drawn-out germination pattern. Both species germinated more rapidly in warmer conditions in either this experiment (in the case of white pine) or in previous experiments in which temperature differences between warm/cool treatments were greater (in the case of balsam fir; Greenwood et al. in preparation).
3) Hemlock, whose seeds were slightly more massive than those of the spruces (Table 6) and which germinated relatively late in the growing season and exhibited a strong negative response to high temperatures.

Species	Seed mass (mg)
Black spruce	1.5
Red spruce	2.8
White spruce	2.6
White pine	15.3
Balsam fir	8.6
Hemlock	3.0

Table 6. Average seed masses of the seeds planted in Experiment 1. Seeds were acquired from the National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada). n=50 seeds, from which mean seed mass was calculated.

Clearly these three groups of species employ different germination strategies. The spruces employ a rapid all-at-once germination strategy with very high percent germination (Fig. 3 and 5). In contrast are the less prolific and more deliberate germination patterns of white pine and balsam fir (Fig. 3 and 5). Greenwood et al. (in preparation) hypothesize that such deliberate germination patterns could represent a short-term seed-banking strategy. Extended dormancy and long-term seed banking are means by which species hedge their bets in highly variable or stressful environments (Sarukhan 1974; Brown and Venable 1986; Venable and Brown 1988). By lying dormant in an unpredictable environment, a species can increase its reproductive efficiency by germinating in response to conditions favorable for establishment (Sarukhan 1974; Brown and Venable 1986; Venable and Brown 1988). Such dormancy and seed banking can last for several years, especially for herbaceous species (Brown and Venable 1986), but the same bet-hedging principles should logically hold for shorter time scales as well.

For our species, extending the germination of their seed crops over longer periods of time in a single growing season should increase the chances that at least some white pine and balsam fir germinants will encounter favorable conditions for establishment (Greenwood et al. in preparation). For example, if the spruces undergo their rapid germination pulse during a drought, that year's crop of seedlings could endure heavy losses. White pine and balsam fir would also presumably lose a fair proportion of their seedling crops as a result of such a drought, but their more-extended germination phenology would allow at least some of their seeds to germinate after the drought when conditions may be more favorable for germinant establishment and survival.

Such germination patterns may be analogous to capital investment strategies. Spruces tend to invest most of their seed resources into one germination period, while white pine and balsam fir invest smaller amounts of seed resources into a more temporally diverse germination portfolio. The all-eggs-in-one-basket approach of the spruces is riskier; but if successful, it stands to yield very large crops of seedlings that can become established early in the growing season. In contrast, the more conservative, temporally-diverse approach of pine and fir is more likely to weather temporary unfavorable conditions but could be greatly outgained (i.e. outcompeted) by the spruces if the riskier approach proves successful.

So, in moist, favorable conditions, the rapid and highly complete germination of the spruces probably provides a consistently large crop of seedlings that can become established relatively early in the growing season. In poorer and/or more erratic environments, however, the rapid, all-at-once germination strategy of the spruces could make them vulnerable to periods of poor conditions. That is, if the spruces undergo their single, rapid pulse of germination during unfavorable conditions, a large proportion of that season's germinants could die. Predictions of increasingly erratic weather patterns in the future (Easterling et al. 2000; Houghton et al. 2001; but see Bengtsson et al. 2006) thus do not seem to favor the germination strategy of the spruces, but may give a competitive advantage to the more conservative germination strategies of balsam fir and white pine. The relative seed sizes of the two groups of species lend further support to this hypothesis. The larger seeds of fir and particularly pine (Table 6) should make their germinants better at enduring environmental variability and unfavorable conditions (this seed size hypothesis is discussed by Brown and Venable 1988; Leishman et al. 2000).

1.4.2. Seedling Growth and Morphology

1.4.2.1. Height, Dry Mass, Seed Size, and Seedling Development Patterns

At Harvest 1, white pine was by far the tallest and most massive species in either light environment (Fig. 6A-B). This is almost certainly related to the fact that white pine seeds are much larger than the seeds of the other five study species (Table 6). In the shade, balsam fir was about twice as massive as hemlock or the three spruces (Fig. 6A-B), which corresponds well with the seed size differences between fir, hemlock, and the spruces (Table 6).

A cursory examination of the data reveals two exceptions to the positive relationship between seed-size and Harvest 1 seedling dry mass. In the light, the three spruces were similar in height and mass to balsam fir (Fig. 6A-B) despite the fact that the spruces have smaller seeds than balsam fir (Table 6). And despite its slightly larger seeds (Table 6), hemlock seedlings were somewhat shorter and less massive than the spruces in the shade (Fig. 6A-B). But of course, traits other than seed size influence seedling growth. The spruces, for instance, have been found to have higher growth potential than balsam fir in high light conditions (Greenwood et al. in preparation). As such, perhaps the higher growth potential of the spruces in the light allowed them to overcome the nutritive boost provided by balsam fir's larger seed reserves (Table 6).

The second exception, hemlock, germinated later than the spruces and is known to be a slow-growing species (Goerlich and Nyland 2000). Both factors may have contributed to the small size of hemlock seedlings at Harvest 1, but one seems likely to have made a bigger contribution than the other. By Harvest 3, hemlock and the spruces had similar masses in the shade (Fig. 7B). So, hemlock apparently caught up to the

spruces in size, which suggests that growth rate did not differ greatly between the shade-grown spruces and hemlock. This leaves the relatively late germination of hemlock to explain the relationship between seed size and seedling size among hemlock and the spruces.

In summary, initial seedling sizes seem to be positively related to seed size, but various aspects of germination (e.g. rate and timing of germination) and seedling traits (e.g. growth potential) can have an overriding influence. In the shade, the different growth potentials of the six species seemed to be similarly inhibited, and initial seedling sizes largely reflected seed size and germination timing. Germination timing affected the relative sizes of seedlings in the high-light environment, too, as is evident with the late-germinating (Fig. 5) and very-small (Fig. 7A-B) hemlock. But in the high-light environment, the different growth potentials of the six species were fed by more abundant resources, thus causing those different species to diverge more in size. So compared to the shade environment, species growth rate seems to play a relatively large role in determining the early size of seedlings in the high-light environment. And obviously, the apparent effects of seed size on seedling traits will fade with time. That is, seedling growth characteristics will play a larger role in determining seedling size as seedlings grow. Our conclusions are in agreement with many other studies that have found a positive relationship between seed size and initial seedling size, both within and among species (reviewed by Leishman et al. 2000).

At Harvest 1 in the high-light environment, the small-seeded spruces were only about $^1/_3$ the mass of white pine (Fig. 6B). But by Harvest 3 in the high-light environment, the spruces were about $^2/_3$ the mass of white pine and had actually

overtaken white pine in terms of height (Fig. 7A-B), belying the spruces' diminutive seed size (Table 6). White pine was still the most massive species in either light environment, but the spruces demonstrated their growth potential by closing the initially-large size-gap between them and white pine (Fig. 7B).

So, white pine and the spruces clearly have high growth potential in high-light environments. When compared to balsam fir, the spruces again demonstrated their ability to respond to high light conditions. At Harvest 1 in the high-light environment, balsam fir was similar in height and biomass to the three spruces and was actually significantly more massive than red spruce (Fig. 6A-B). By Harvest 3, however, in the high-light environment the spruces were 2-3x taller and more massive than balsam fir (Fig. 7A-B). There are two major reasons for the different growth rates of the spruces and fir in the high-light environment:

1) The spruces demonstrated the capacity for neoformed shoot growth, which is the continuous formation of stem units without an intervening dormant period (Greenwood et al. in preparation). In other words, as long as conditions are favorable for growth, the spruces can continue shoot growth for the entire growing season. In contrast, even under favorable growing conditions, balsam fir sets bud relatively early in the growing season, which restricts its shoot growth potential relative to that of the spruces (Greenwood et al. in preparation).
2) Compared to balsam fir, the spruces allocated a relatively high proportion of their biomass to leaves (Fig. 7H). Assuming that soil resources are not limiting (they were abundant in our study), higher leaf allocation in high-light environments is

generally rewarded with higher growth rates (Mooney 1972; Walters and Reich 1993).

In the shade there was much more convergence among the heights and dry masses of the six species at Harvest 3. As discussed previously, at Harvest 1 the different growth potentials of the six species appeared similarly inhibited in the shade, and seedling sizes largely reflected seed size. By Harvest 3, only white pine differed substantially from the other species in terms of height and dry mass (Fig. 7A-B). The other five species were similar in height and were virtually identical in dry mass (Fig. 7A-B), which again suggests that all species were similarly light-limited in the shade. And in fact, in the shade the species all had relatively similar RGRs (Fig. 7C). Perhaps the larger dry mass and height of white pine in the shade (Fig. 7A-B) were simply related to pine's initial seed-size advantage (Table 6). Various other studies have also found that the growth rates of species with very different growth potentials can converge in very light-limited environments (reviewed by Walters and Reich 1999).

Perhaps the most interesting result is that the growth of the spruces was so strongly spurred by high-light conditions (Table 5). In terms of both dry mass and height, the spruces responded significantly more positively than fir or pine to higher light (Table 5). The high growth potential of the spruces has been noted in other studies that compared the growth of red spruce and balsam fir (O'Brien 2005; Greenwood et al. in preparation). So the spruces are clearly capable of responding vigorously to high light. In the field, however, spruce seedlings are generally not known as particularly rapid growers (Place 1955; Greenwood et al. in preparation). Their neoformed shoot growth is

probably limited by the variable and often suboptimal conditions they encounter in forests. Red spruce, for instance, is often most successful in shady, moderately poor sites because it is unable to compete with hardwoods and other species that are better able to capitalize on the resources of richer sites (Meng and Seymour 1992). This is an excellent illustration of the fact that optimal growth conditions do not always lead to the greatest selective advantage for a given species. This is an important principle to bear in mind when considering the implications of the results presented here.

1.4.2.2. Carbon Allocation

Biomass allocation within each light environment differed greatly among the study species. In the high-light environment, pine and fir had the highest R:S mass ratios; in the shade, fir, white spruce, and hemlock had the highest R:S mass ratios (Fig. 6C; 7E). So, balsam fir is the only species whose R:S mass ratios were consistently among the highest of any species, while red and black spruce were the only species with R:S mass ratios consistently lower than those of any other species, regardless of light environment (Fig. 6C; 7E). Similarly, Greenwood et al. (in preparation) found that the R:S mass ratios of balsam fir seedlings were higher than those of red spruce seedlings in various studies in the greenhouse and in the field.

R:S mass ratios can reveal a great deal about a species' growth strategy. For example, R:S mass ratios can predict the ability of a species to endure dry conditions because R:S mass ratio quantifies the relative amount of tissue involved in gathering water (roots) vs the amount involved in transpiring that water (shoots). FARM ratios may be a more meaningful indicator of a species' ability to endure dry conditions,

however, because R:S mass ratios do not distinguish between stems and leaves, while FARM ratios specifically compare the relative proportion of tissues invested in water-gathering structures (roots) and water-losing structures (foliar surface area). Except for hemlock, in both light environments the FARM ratios of all species were statistically similar, suggesting that the proportion of water uptake to water loss may be similar for all study species (Fig. 7J). Hemlock had a significantly higher FARM ratio than the other species (Fig. 7J), suggesting that it may be less able to endure dry conditions. In the high-light environment, the FARM ratios of the spruces were consistently higher than those of balsam fir, but those differences were not significant (Fig. 7J).

Root length can also reveal a great deal about a species' growth strategy. In general, longer roots allow plants to explore more soil, which improves their chances of encountering and accessing heterogeneous, limiting resources. For instance, longer, deeper roots are typically associated with a greater ability to endure low-water conditions by helping plants access deeper, more reliably-available pools of soil water (Holch 1931; Albertson and Weaver 1945; Bahari et al. 1985; Kozlowski and Pallardy 2002; Ryser 2006). This will be particularly true at the seedling stage when root length is presumably most strongly correlated with root depth. At Harvest 1 in the shade, balsam fir had significantly longer primary roots than the other species (Fig. 6D). But at Harvest 3, despite some statistically significant differences, the primary roots of all species were relatively similar in length, differing from each other by <2 cm (Fig. 7D).

In the high-light environment, balsam fir and white pine had significantly longer primary roots than the three spruces at Harvest 1 (Fig. 6D). It is notable that the average root length of balsam fir was statistically indistinguishable from that of white pine (Fig.

6D), despite the fact that, at Harvest 1, white pine was almost 3x larger than balsam fir (Fig. 6D). This is reflected by fir having a significantly higher R:S length ratio than white pine (Fig. 6E). This, in addition to the facts that, 1) Balsam fir had the highest initial primary root length among shade-grown seedlings, and 2) Balsam fir R:S mass ratios (Fig. 6C), and R:S length ratios (Fig. 6E) were among the highest of any species regardless of light environment, strongly suggests that, relative to the other species, early balsam fir growth was more focused on quickly developing an extensive root system.

At Harvest 3 in the high-light environment, however, balsam fir no longer had the longest primary roots (Fig. 7D). But when considering this, one must bear in mind the relative sizes of the species. By Harvest 3, the three spruces in the high-light environment had grown much larger than balsam fir. This allowed the spruces to close the root-length-gap between themselves and balsam fir without necessarily investing a large proportion of their growth toward lengthening their roots. This observation is important, because in the field, the spruces are generally less able to capitalize on their neoformed shoot growth potential (probably because of the sub-optimal conditions they encounter there), and they are relatively similar in size to balsam fir (Greenwood et al. in preparation). As such, the relative R:S length ratios of fir and the spruces may be the most relevant comparison of their primary root growth and penetration, because the ratios take seedling size into account. And at Harvest 3, fir had a significantly higher R:S length ratio than the spruces (Fig. 7K), indicating that, in field conditions where the species are relatively similar in size (Greenwood et al. in preparation), fir will be capable of the greatest root penetration.

Other seedling traits certainly affect the ability of seedlings to endure dry conditions (Kozlowski and Pallardy 2002), but based solely on our results, it appears that any interspecific differences in the ability to endure low-water conditions will arise primarily due to differences in the root lengths of young seedlings. FARM ratios are not significantly different for most of the species (Fig. 7J), suggesting that the proportion of water uptake to water loss may be similar for all of the species but hemlock, whose relatively high FARM ratios in the high-light environment (Fig. 7J) fit with hemlock's reputation as a drought-sensitive species (Gaerlich and Nyland 2000; Foster et al. 2006; but see Caspersen and Kobe 2001). But in terms of root length, white pine and balsam fir seedlings quickly developed the longest root systems (Fig. 6C), indicating that they will be more capable than the spruces or hemlock of quickly penetrating forest floor litter and reaching deeper, more-reliably-available pools of soil water that could sustain fir and pine seedlings during dry periods that deplete the shallower water sources available to the less-deeply-rooted spruces and hemlock.

1.4.2.3. Seedling Growth and Morphology Summary

In the high-light environment, balsam fir and white pine are dissimilar in dry mass and height but very similar in root length, biomass allocation pattern, leaf morphology, and RGR (Fig. 6A-D; 7A-J). In the shade, however, fir and pine are dissimilar in dry mass, height, and biomass allocation patterns; they resemble each other only in RGR, primary root length, and leaf morphology (Fig. 6A-D; 7A-J), and neither root length nor SLA can distinguish fir and pine from the other species because most species had similar primary root lengths and SLAs in the shade (Fig. 7D; 7J). So in the high-light

environment, fir and pine seem to be a distinct group in terms of biomass allocation patterns and primary root length. But in the shade, the two species differed significantly in those respects, with fir maintaining higher R:S mass ratios (Fig. 6C; 7E) and initially having longer primary roots (Fig. 6D) than white pine.

In both light environments, the three spruce species were very similar to each other in terms of growth rate, height, dry mass, leaf morphology, root length, and carbon allocation (Fig. 6A-D; 7A-J). In terms of growth and carbon allocation, all three species responded similarly to the different light environments (Table 5). So, the three spruces pretty clearly stand together as one group.

Hemlock is somewhat more difficult to categorize, particularly in the high-light environment (Fig. 5). In the shade, it resembled many of the other species in terms of height, dry mass, root length, and tissue allocation (Fig. 7A-H; 7J). However, it is unlike the other species in terms of SLA in either light environment (Fig. 7I). And in the high-light environment, it is distinct from the other species in terms of height, dry mass, root length, and carbon allocation (Fig. 7A-H; 7J). It is difficult to know whether to attribute such similarities and differences to inherent growth patterns or to the much-later germination of hemlock, particularly in the high-light environment (Fig. 5). But regardless of the causes, hemlock appears different enough from the other species to merit its own category.

In summary, hemlock (particularly in the high-light environment) and the spruces form two distinct groups, while fir and pine had notable similarities in the high-light environment, but not the shade environment.

1.4.2.4. Ontogenetic Considerations

In the high-light environment, the spruces were much larger than balsam fir (Fig. 7A-B). Ontogenetic drift tends to cause R:S mass ratios to increase as seedlings grow larger (Poorter and Nagel 2000). So, the fact that the smaller balsam fir had higher R:S mass ratios than the larger spruces (Fig. 7E) further highlights the allocation differences between the species. As such, ontogenetic considerations appear to bolster our conclusions that, relative to one another, early fir growth is more directed toward roots and the early growth of the spruces is more directed toward shoots.

White pine, however, is an exception to this. Its large size relative to the other species (Fig. 6B; 7B) confounds comparisons of its high root allocation with the root allocation of the other species. Again, with increasing size, seedlings typically increase their R:S mass ratios (Poorter and Nagel 2000). So in the case of white pine, it is difficult to say whether its high R:S mass ratios were due to preferential allocation to belowground tissues or if they were simply due to white pine being larger than the other species. However, this distinction may not be particularly important in this case. Two things seem suggest that, at least early in its development (particularly in high-light environments), white pine will consistently have greater root allocation than the spruces:

1) White pine has larger seeds than the other species. Larger seeds tend to produce larger seedlings (Walters and Reich 2000), and the larger white pine seedlings should have greater root allocation than the spruces regardless of whether it is due to ontogenetic drift, preferential root allocation, or both. These large seedlings also

presumably produce longer primary roots, allowing them to reach deeper water sources.

2) At Harvest 2 (data not shown), in the high-light environment the spruces were about two times greater in mass than white pine was at Harvest 1, yet the R:S mass ratios of the Harvest 2 spruces were still slightly lower than those of Harvest 1 pine. If the root allocation of the spruces and white pine were equal, ontogenetic drift should have caused the larger Harvest 2 spruces to have greater R:S mass ratios than the smaller Harvest 1 white pine. But the opposite is true, indicating that, relative to the spruces, high-light-grown pine seedlings do have preferential allocation to roots.

In the low-light environment, on the other hand, pine had only slightly greater (Fig. 6C) or approximately equal (Fig. 7E) R:S mass ratios compared to the spruces, despite pine's much larger size (Fig. 6B; 7B). Given that larger seedlings are generally expected to have higher R:S mass ratios due to ontogenetic drift (Poorter and Nagel 2000), it appears that, relative to the spruces, white pine did not have preferential root allocation to roots in the low-light environment. This indicates that white pine biomass allocation can be highly plastic in response to different light conditions.

1.5. Summary: Experiment 1

The findings of Experiment 1 suggest that there is significant variation among the ecological attributes of these six species. Based on seed size, germination patterns, carbon allocation, and root growth, the six species can be divided into three groups:

1) Hemlock, which had seeds intermediate in mass among the study species, germination that responded negatively to high temperatures, germination that began much later than that of the other species, R:S mass ratios that were moderate among these six species, low growth in high-light conditions, higher SLAs than any other species in both light environments, and significantly higher FARM ratios than the other species in the high-light environment.

2) Black, white, and red spruce, which had the smallest seeds of the study species, germination that was unresponsive to the different light environments, the most rapid and complete germination, the lowest R:S mass and R:S length ratios, and the capacity for vigorous neoformed shoot growth in response to high-light.

3) White pine and balsam fir, which had the largest seeds (particularly white pine) of the study species, had more-gradual and less-complete germination than the spruces, and whose germination rates have been found to respond positively to warmer conditions. Although they differed substantially in size, in high-light conditions, fir and pine both rapidly developed the longest roots and R:S mass ratios of any species. In the shade, however, the two species were less similar, and only fir had relatively higher R:S mass and R:S length ratios than the other species.

Chapter 2: Red Spruce and Balsam Fir Regeneration and Abundance Past and Present: A Brief Review

2.1. Historical Perspective

2.1.1. Paleoecology

Red spruce and balsam fir have not always been abundant in Maine, nor have they always been found in association. Approximately 1000 years ago, black and white spruce, and to a lesser extent, balsam fir, expanded their ranges southward, increasing in abundance in southern Canada and the northern U.S. (Schauffler and Jacobson 2002). This expansion was associated with a shift toward a moister, cooler climate. Recent evidence also indicates that from approximately 1000 to 500 years ago, red spruce expanded its range inland from coastal refugia (Schauffler and Jacobson 2002), an expansion that was also associated with a relatively cool and moist climate (Schauffler and Jacobson 2002; Lindbladh et al. 2003). So clearly the distributions of both spruce and fir are strongly influenced by climate, and the abundance of both species in Maine appears to be positively associated with cooler, wetter climates.

2.1.2. Recent History

By the middle of the 19th century, intensive selection harvesting of white pine had severely depleted pine's availability, making alternative species increasingly attractive to loggers (Whitney 1994). During the period of 1850-1890, red spruce largely replaced white pine as the primary sawlog species in much of New England (Whitney 1994). In the 1880s, red spruce was also adopted as a valuable pulpwood for paper production (Oosting and Reed 1944; Whitney 1994). Today, red spruce remains commercially

valuable. It is a lightweight, straight-grained, resilient wood used for paper, construction lumber, and musical instruments (Blum 1990). In a 1995 inventory of Maine's forests, red spruce was both the leading stock volume species and the leading sawtimber-volume species (Griffith and Alerich 1996).

Balsam fir became a major component of the logging industry in the 1890s, when it joined red spruce as a prominent pulpwood species (Whitney 1994). Today, balsam fir remains commercially important. Its wood is relatively lightweight and soft and is used primarily for pulpwood and light frame construction (Frank 1990). But in general, balsam fir is of low timber value, and land managers commonly try to convert stands of balsam fir to other species that are more valuable and less vulnerable to pests and disease (Johnston 1986). In a 1995 inventory of Maine's forest, balsam fir was the third leading species in growing-stock volume (Griffith and Alerich 1996).

2.1.3. Current Status

Currently, Maine's forests comprise nearly 7.1 million hectares, 2.4 million hectares of which is classified as spruce-fir, which is a forest type dominated by red spruce and balsam fir (Griffith and Alerich 1996). Red spruce and balsam fir are sympatric in much of Maine's forestlands. Balsam fir extends from Newfoundland west to northwestern Alberta, south to northern Minnesota and Wisconsin, and east to New England, nearing its southern limit in southern Maine (Frank 1990). Red spruce has a comparatively small, southerly range, extending from Nova Scotia west to southern Quebec, south to New York and Massachusetts, nearing its northern limits in northern Maine; its range also extends southward within the Appalachian Mountains (Blum 1990).

Balsam fir grows and regenerates robustly throughout Maine's forests, being seemingly well adapted to the moist, cool winters and moist, warm summers therein (DeHayes et al. 1990; Brissette 1996). Since the early 20th century, however, researchers have reported red spruce to be in decline, primarily in high-elevation stands (Korstian 1937; DeHayes et al. 1990; Klein et al. 1991). During this apparent decline of red spruce, some formerly abundant populations have dwindled, many existing populations appear to be ailing, and replacement populations often fail to regenerate (Korstian 1937; Randall 1976; DeHayes et al. 1990; Klein et al. 1991; Gordon 1996; Mosseler et al. 2000). There is also some concern regarding genetic quality in some increasingly isolated spruce populations (Mosseler et al. 2000). Much of this decline has been attributed to the sensitivity of high-elevation red spruce to frost damage (Lazarus et al. 2006). In Maine's low-elevation spruce-fir forests, red spruce appears much less vulnerable to the factors contributing to the decline of high-elevation populations (Johnson et al. 1992).

But throughout the common range of red spruce and balsam fir, post-harvest regeneration in spruce-fir stands is typically dominated by balsam fir (Westveld 1931; Place 1955; McIntosh and Hurley 1964; Meng and Seymour 1992; Seymour 1992; Brissette 1996; Hughes and Bechtel 1997; Battles and Fahey 2000), even when red spruce seed rain predominates (Randall 1976). In a survey of all harvest treatments in the Penobscot Experimental Forest (PEF) in Bradley, Maine, Brissette (1996) reports that regenerating (i.e. seedlings <15 cm tall) balsam fir outnumbered regenerating spruce species 17,239 to 6,635. Forest managers and ecologists have often expressed concern about the limited regeneration of red spruce (Westveld 1931; Place 1955; Randall 1976; Gordon 1996). At least four major considerations may contribute to this concern.

1) Compared to balsam fir, red spruce is more commercially valuable (Blum 1990; Frank 1990).
2) Red spruce is less susceptible to spruce budworm. Solomon et al. (2003) monitored spruce-budworm-induced mortality in unprotected spruce-fir stands in Maine. Twelve years after the start of the 1971-1980s spruce budworm outbreak, balsam fir reached 92-100% basal area mortality and 84-97% stem density mortality, while red spruce reached only 32-59% basal area mortality and 30-66% stem density mortality (Solomon 2003). Along these same lines, Blais (1983) found that stands with a higher proportion balsam fir were most susceptible to spruce budworm damage. As such, it seems economically desirable to keep the working forest from becoming dominated by the relatively budworm-susceptible balsam fir. And in general, more diverse stands should provide greater community stability (Doak et al. 1998; Tilman et al. 1998).
3) Predicted climatic warming will cause the ranges of many species to shift pole-ward (Parmesan and Yohe 2003), which suggests a potentially greater abundance of red spruce at and beyond its current northern range limit near northern Maine (Mosseler et al. 2000).
4) Ecologically, aesthetically, and historically, red spruce occupies a major niche in Maine's forests.

2.2. Life History Comparison of Red Spruce and Balsam Fir

2.2.1. Introduction

Red spruce and balsam fir have several traits in common. Spruce and fir are considered shade tolerant and very shade tolerant, respectively (Baker 1949; Burns et al. 1998) and both are considered seedling bank species capable of persisting for many years in low-light conditions (Landis and Peart 2005). Both species are sympatric in Maine (Blum 1990; Frank 1990), germinate and establish best on mineral soil (Place 1955), and often grow in association with each other in Maine's extensive spruce-fir stands (Blum 1990; Frank 1990; Seymour 1992; Griffith and Alerich 1996). But despite these basic similarities, there are various ecological, developmental, and life history differences between balsam fir and red spruce that may help to explain the relatively limited regeneration of red spruce. This section will review various factors that may contribute to the different regeneration dynamics of the two species. First I will discuss the two species' early life stages, then their later life histories, and finally the effects of various management practices.

2.2.2. Early Life Stages

2.2.2.1. Seed Production, Dissemination, and Predation

Red spruce produces large seed crops every 3-8 years (Blum 1990), but often does not start producing large seed crops until it reaches 70 years of age (Powell 1975). Balsam fir produces large crops every 2-4 years and starts producing seed relatively early in its life cycle (Frank 1990). Neither species can disperse its seeds very great distances, though spruce can disperse its seeds somewhat farther than balsam fir (Frank 1990; Blum

1990; Hughes and Bechtel 1997). In general, mature spruce-fir stands seem to produce adequate amounts of both red spruce and balsam fir seed such that seed availability should not limit the regeneration of either species (Randall 1974).

Seed predation can significantly impact the availability of viable seed (Gashwiler 1967; Janzen 1971; Peters et al. 2004). Although it is generally acknowledged that predators prefer spruce seed over fir seed (Abbott 1962), few studies have directly compared the seed predation rates of red spruce and balsam fir in the field. Kanoti (2005) found no significant difference between seed predation rates of field-sown red spruce and balsam fir, though he did emphasize that predator avoidance of balsam fir seed was unique among the larger-seeded species. Other studies have reported a preference for white spruce seeds (which are very similar to red spruce seeds) over balsam fir seeds (Simard et al. 2003; Peters et al. 2004). So, while the true effects of seed predation on spruce and fir seed crops are unclear, predation almost certainly plays a role and appears likely to have a more negative impact on spruce than on fir.

2.2.2.2. Seed Germination

Both red spruce and balsam fir germinate best on mineral soil (Westveld 1931; Place 1955). The germination of both species is negatively associated with the amount of leaf litter covering the soil, most likely because leaf litter dries out more quickly than mineral soil (Moore 1926). Several researchers have found that the percent germination of spruce and fir seeds responds negatively to severe moisture deficit (O'Brien 2005; Kanoti 2005; Greenwood unpublished data). Kanoti (2005) found that balsam fir germination is actually more sensitive than red spruce germination to moisture stress, but

other studies have found little difference between the two species in that regard (O'Brien 2005; Greenwood unpublished data).

Balsam fir germination is less-complete and more-drawn-out than red spruce germination in a variety of environmental conditions (Fig. 3 and 5; Place 1955; O'Brien 2005; Kanoti 2005; Greenwood et al. in preparation). Greenwood et al. (in preparation) discuss the possible significance of these patterns. Neither red spruce nor balsam fir create persistent, long-term seedbanks (Frank and Safford 1970; Blum 1990; Frank 1990), but Greenwood et al. (in preparation) hypothesize that balsam fir's slower germination rate may represent a short-term seed-banking strategy. This hypothesis is somewhat analogous to capital investment strategies. Red spruce tends to invest most of its seed capital into one germination period, while balsam fir invests smaller amounts of seed capital into a more temporally diverse germination portfolio. The all-eggs-in-one-basket approach of spruce is riskier; but if successful, it stands to yield very large crops of seedlings that can become established early in the growing season. In contrast, the more conservative, temporally-diverse approach of fir is more likely to weather temporary unfavorable conditions but could be greatly outgained (i.e. outcompeted) by red spruce if the riskier approach proves successful.

2.2.2.3. Germinant Establishment

Both balsam fir and red spruce seedlings can persist for many years in very low light conditions (Baker 1949; Burns et al. 1998; Wu et al. 1999; Parent et al. 2000). However, new germinants are very sensitive to water stress and need reliable access to water in order to become established, making early root growth very important to their

survival (Place 1955; Burdett et al. 1983). Both red spruce and balsam fir germinants establish most successfully on exposed mineral soil (Frank 1990; Blum 1990). The amount of leaf litter covering the soil is negatively related to rates of establishment (Moore 1926; Cornett et al. 1998), which is due to at least three factors:

1) The litter layer has a lower water holding capacity than mineral soil, making it a relatively poor substrate for root growth and establishment (Moore 1926; Ahlgren and Ahlgren 1981).

2) Leaf litter can inhibit root penetration, preventing plants from reaching water and soil nutrients (Moore 1926; Koroleff 1954; Ahlgren and Ahlgren 1981).

3) Leaf litter can be stirred up, "suffocating" new germinants (Koroleff 1954; Ahlgren and Ahlgren 1981).

Balsam fir germinants tend to have longer primary roots and greater root penetration than red spruce seedlings (Fig. 6D-E; Place 1955; Klein et al. 1991; Greenwood et al. in preparation). This presumably gives balsam fir an advantage in drier conditions, particularly when litter covers the mineral soil, while shorter-rooted species like red spruce are probably more susceptible to early moisture scarcity (Holch 1931; Albertson and Weaver 1945; Bahari et al. 1985; Kozlowski and Pallardy 2002; Ryser 2006). Also, balsam fir seeds are larger than red spruce seeds (Table 6). Generally, larger seeds have greater food reserves, which can sustain germinants and allow them to survive for longer periods of time before the germinants can acquire heterogeneous limiting resources (Venable and Brown 1988; Leishman et al. 2000). So, germinants of

the larger seeded fir might be expected to endure unfavorable environmental conditions for longer periods of time than red spruce germinants. For instance, fir's larger seeds might allow its germinants to more rapidly grow long taproots that will aid fir germinants in surviving dry conditions.

Taken together, balsam fir's larger seed size, more-drawn-out germination phenology, and more rapid establishment of deeper root systems suggest that its germinants are less vulnerable than red spruce germinants to variable belowground resource conditions, particularly in terms of water scarcity.

2.2.2.4. Seedling Growth and Development

Balsam fir experiences faster height and diameter growth than red spruce in both shaded and open environments (Oosting and Billings 1951; McIntosh and Hurley 1964; Battles and Fahey 2000), though red spruce has been observed to outgrow balsam fir on poorly drained sites (Meng and Seymour 1992). During its first growing season, however, red spruce can undergo season-long neoformed shoot growth under high-light conditions, while balsam fir sets bud relatively early regardless of conditions (Place 1955; Greenwood and McConville 2002; O'Brien 2005; Greenwood et al. in preparation). The capacity for neoformed shoot growth in spruces is generally lost after 5-10 years (Grossnickle 2000), but red spruce's early shoot growth potential suggests that, under favorable conditions, red spruce seedlings can outgrow balsam fir seedlings. And in fact, various greenhouse experiments have demonstrated that, given abundant light, water, and nutrients, red spruce seedlings can greatly outgrow balsam fir seedlings

(Fig. 7A-B; Greenwood and McConville 2002; O'Brien 2005; Greenwood et al. in preparation).

In the field, however, first year balsam fir seedlings generally grow both taller and more massive than red spruce seedlings. In a survey of red spruce and balsam fir seedlings in an undisturbed spruce-fir stand in Danforth, ME, Greenwood et al. (in preparation) found that balsam fir seedlings from 0-3 years of age grew taller and more massive than red spruce seedlings of the same age class. In the 3-5 year age class, the shoot dry weights of spruce and fir seedlings were not significantly different, but the much greater root mass of balsam fir gave its seedlings a significantly greater total dry mass (Greenwood et al. in preparation).

Carbon allocation patterns are very different for spruce and fir. Compared to balsam fir, red spruce allocates significantly more carbon to photosynthetic tissues (Fig. 7H), less to roots (Fig. 7F; Greenwood et al. in preparation), and can maintain season-long neoformed shoot growth (Greenwood et al. in preparation). This suggests a relatively aggressive first-year growth strategy by which red spruce is capable of significant first-season growth under consistent, high-resource conditions (particularly with respect to light). Balsam fir, on the other hand, allocates less to photosynthetic tissues (Fig. 7H), more to root mass and extension (Fig. 6C; 7F), and sets bud relatively early in its first year (Greenwood et al. in preparation). This suggests that balsam fir seedlings employ a more conservative growth strategy by allocating fewer resources toward growth potential and more toward coping with spatial and temporal belowground-resource heterogeneity.

Given red spruce's much greater first-season growth potential, it may seem paradoxical that field-grown balsam fir seedlings so consistently outgrow red spruce seedlings (Greenwood et al. in preparation). However, this is partially explained by the light-limiting conditions of the understory, which do not allow red spruce to capitalize on its higher growth potential. And if red spruce cannot capitalize on its higher growth potential, the more conservative, stress-tolerating/avoiding developmental traits of balsam fir may be advantageous. Various researchers have found that the species best suited to endure the rigors of forest understories are often those that sacrifice growth potential in favor of allocation to structure, defense, and stress tolerance/avoidance mechanisms like root growth, thicker stems, and higher tissue density (Kitajima 1994, Kobe et al. 1995, Pacala 1996, Walters and Reich 1999; Walters and Reich 2000; Lusk and del Pozo 2002; but see Wyckoff and Clark 2002).

2.3. Later Life Stages

2.3.1. Path to the Canopy

Balsam fir typically grows more rapidly than red spruce, often reaching reproductive maturity at around 20 years of age or 15 feet of shoot length (Bakuzis et al. 1965). The typical lifespan of balsam fir is less than 100 years, due largely to pest susceptibility and to a heart rot fungus that infects over 50% of balsam fir by age 70 (Johnston 1986; Frank 1990; Seymour 1992). As such, successful balsam fir typically reaches the canopy relatively quickly and then dies or is harvested shortly thereafter (Johnston 1986; Battles and Fahey 2000). But despite its limited lifespan, balsam fir often does not follow a direct path to the canopy. Fir can survive understory suppression

for up to 100 years (Parent et al. 2000), and advance growth seems to be very important for fir regeneration (Westveld 1931; Meng and Seymour 1992; Morin and Laprise 1997), though this is not without exception (Hughes and Bechtel 1997).

Although balsam fir can and often does endure suppression, a very long stay in the understory does not necessarily bode well for fir's success. Landis and Peart (2005) found that only 20% of fir that successfully reached the canopy had endured suppression after reaching 50 cm in height. Davis (1990) found that 60% of mature fir in second-growth stands in southeastern Maine arose from very small advance growth (<0.1 m in height), while the remaining 40% arose from larger advance growth. These results suggest that although balsam fir can long endure deep shade, its probability of reaching the canopy may be negatively impacted by suppression during its later, juvenile stages. Nonetheless, advance growth is unquestionably a prominent part of fir regeneration (Davis 1990; Seymour 1992).

As with balsam fir, suppression-tolerance and advance growth are very important to red spruce attaining canopy dominance. Red spruce can survive suppression in deep shade for over 100 years until harvest, death, or damage of overstory trees creates a gap through which the suppressed red spruce can reach the canopy (Blum 1990). Various researchers have found that the majority of red spruce reaching the canopy consists of formerly suppressed trees (Davis 1966; Davis 1990; Meng and Seymour 1992; Wu et al. 1999; Landis and Peart 2005), though this is not without exception (Hughes and Bechtel 1997). In a study in the southern Appalachians, Wu et al. (1999) found that red spruce trees in the canopy had endured an average of 1.73 episodes of suppression averaging 19 years per episode. In other words, spruce seedlings rarely follow a direct path to the

canopy. Beneath dense overstories, new seedlings are typically suppressed until overstory gaps provide light and a path to the canopy. In existing gaps, new spruce seedlings are typically overtopped by faster growing hardwoods, beneath which the spruces are suppressed until new overstory gaps provide light and a path to the canopy (Davis 1966; Powell 1975; Davis 1990).

2.3.2. Lifespan

Mature red spruce can dominate the canopy for a long time, sometimes living for more than 300 years (McIntosh and Hurley 1964). As such, red spruce is generally considered a late-successional species. Red spruce can reach reproductive maturity as early as 15-20 years of age in open areas or after 40-50 years of age beneath dense overstories (Korstian 1937). However, abundant seed production often does not occur until spruce reaches about 70 years of age (Powell 1975).

Presumably, the different life spans of red spruce and balsam fir strongly influence the dynamics of spruce-fir stands. For instance, if disturbances such as clearcutting prevent much of the forest from reaching later stages of succession, slower growing, late-successional species like red spruce may be inhibited by the rapid stand turnover while fast-growing hardwoods and species like balsam fir (which, though not particularly fast-growing, is still faster-growing than red spruce) may not be inhibited. This will particularly be true if red spruce canopy attainment relies heavily on well-established advance growth, which seems to be the case (Davis 1966; Powell 1975; Davis 1990; Meng and Seymour 1992; Wu et al. 1999; Landis and Peart 2005). Along these lines, Seymour (1992) hypothesized that the historical dominance of red spruce in virgin

spruce-fir forests was largely due to spruce's long life span relative to fir. If that longevity advantage is removed by disturbance, red spruce regeneration will presumably suffer.

However, as previously discussed, Schauffler and Jacobson (2002) present palynological evidence indicating that red spruce rapidly expanded its range and became abundant in Maine between 1000 and 500 years ago. So, spruce's long lifespan and persistence in the canopy could not have been the crucial factor mediating spruce's rapid increase in abundance in Maine's forests. Its long lifespan certainly would help it to persist in areas it had already colonized, but the rapid colonization itself must have been mediated by other factors.

Given the life history characteristics of red spruce, it is certainly conceivable that spruce could regenerate and growth robustly under the right conditions. Red spruce has the capacity for abundant seed production (Randall 1974), high percent germination (Fig. 3; Greenwood et al. in preparation), vigorous early growth (Fig. 7A-B; Greenwood et al. in preparation), and rapid attainment of reproductive maturity when grown in open areas (Korstian 1937). If all of these capacities worked in tandem, it is easy to imagine red spruce populations quickly expanding and becoming pervasive in Maine's forest, after which spruce's long lifespan (and resulting canopy dominance) would facilitate red spruce's continued presence, even if conditions were no longer optimal for spruce regeneration relative to that of many competing species (e.g. balsam fir and faster-growing hardwoods). Given red spruce's relatively low R:S mass ratios (Fig. 6C; 7E; Greenwood et al. in preparation) and meager early root development and soil penetration (Fig. 6D-E; Klein et al. 1991) a moister climate would presumably facilitate the success

of spruce's early life stages. And in fact, Schauffler and Jacobson (2002) found that the expansion of red spruce was associated with the climate becoming cooler and moister.

The previous account is speculative, but it certainly fits what we know about red spruce's life history and paleoecology. It does leave some major questions unanswered, however. For instance, how did spruce expand its range so rapidly from coastal refugia (Schauffler and Jacobson 2002) given its relatively short dispersal range (Blum 1990)? Also, what species did spruce displace/replace in the late Holocene forest into which it expanded? The rapid expansion of spruce populations would presumably have required significant growing space into which spruce could disperse and become established as a canopy dominant (Michael E. Day, personal communication). The availability of this growing space may have been mediated by the decline of another forest species (Michael E. Day, personal communication), though I am not aware of any studies that have specifically addressed this.

2.4. Effects of Commercial Harvesting

Several harvesting practices seem to be detrimental to red spruce populations. Extensive diameter limit harvesting of red spruce has been cited as a dysgenic practice that results in a decline in the quality and quantity of remaining red spruce (Gordon 1996; Sokol et al. 2004). Clearcutting has also been implicated in the decline of red spruce (Korstian 1937; Gordon 1996; Mosseler et al. 2000). Mosseler et al. (2000) points out that clearcutting can reduce the high atmospheric moisture conditions that favor red spruce. Also, given red spruce's relatively poor initial regeneration (Korstian 1937; McIntosh and Hurley 1964; Davis 1966; Randall 1976; Brissette 1996; Hughes and

Bechtel 1997), reliance on advance growth and suppressed individuals for attaining canopy (Korstian 1937; McIntosh and Hurley 1964; Davis 1966; Davis 1990; Seymour 1992; Meng and Seymour 1992), and reliance on its long lifespan for maintaining canopy dominance (Seymour 1992), post-harvest population reductions of red spruce relative to balsam fir are not surprising.

In other words, logging seems detrimental to red spruce regeneration while providing a relative boon for balsam fir. In the time between harvest rotations, the shorter-lived, faster-growing fir can reach the overstory and achieve reproductive maturity. Red spruce typically takes much longer to reach the overstory, meaning that under a fairly frequent harvesting rotation, many suppressed, second-growth red spruce will be unable to replace the first-generation canopy by the time the area is harvested again, which will allow relatively few spruces to attain canopy and produce seeds for the next generation of recruits.

Given red spruce's life history characteristics, it almost seems as if any harvesting of spruce stands will be detrimental to spruce populations. However, the regeneration success of spruce and fir is closely related to the amount advance growth left after harvest or disturbance (Davis 1966; Davis 1990; Seymour 1992). As such, harvesting practices that preserve red spruce advance growth will also favor red spruce regeneration (Davis 1990; Seymour 1992). But even in those circumstances, suppressed fir tend to outnumber suppressed spruce (Seymour 1992), and suppressed fir may respond more vigorously to release from suppression (Westveld 1931).

2.5. Summary

The interspecific differences discussed in this section are summarized in Table 7.

Under more scarce or temporally and spatially heterogeneous soil moisture conditions, the early life stages of balsam fir appear to have an advantage over those of red spruce in seed size, germination pattern, biomass allocation pattern, and seedling establishment. Red spruce seedlings have much greater growth potential than balsam fir seedlings, but in the field spruce is rarely able to capitalize on that growth potential, probably due to the highly-heterogeneous light, moisture, and nutrient conditions typical of forests.

In the field, balsam fir seedlings, juveniles, and adults generally grow faster than the same life-stages of red spruce. Fir also appears to have a general advantage over spruce in terms of age of reproductive maturity, seed production frequency, seed predation rates, and response to various harvesting regimes. Relative to balsam fir, red spruce appears to have a general advantage in terms of its higher percent germination, lower susceptibility to pests and pathogens, and longer lifespan (if it is allowed to reach old age). Many of these factors require field studies to assess the true degree to which they affect the relative regeneration success of the two species. Nonetheless, the numerous apparent advantages of balsam fir over red spruce may help to explain the relatively vigorous regeneration of fir often observed in Maine's forests.

Table 7.

Parameter/life stage	Species		Implications & Discussion
	Red spruce	Balsam fir	
Seed production & dissemination	Begins seed production later; less frequent highly productive years	Begins seed production earlier; more frequent highly productive years	Advantage fir, though studies have found that neither species is very limited in this regard (Randall 1974)
Seed size	Smaller	Larger	Fir better at establishing in less favorable/more variable conditions
Seed predation	Higher	Low	Advantage to fir
% Germination	Very high (90%)	Moderate (50%)	Advantage to spruce
Germination pattern	Rapid, all-at-once	Slower, more drawn out	Advantage to spruce in more consistent, high-resource conditions; advantage to fir in more heterogeneous environments
Germinant growth and establishment	Lower root penetration; early growth concentrated more on aboveground tissues	Greater root penetration; early growth concentrated more on roots	Advantage to spruce in more consistent, high-resource conditions; advantage to fir in more heterogeneous environments
Seedling growth	Higher maximum growth potential; grows more slowly than fir in the field	Lower maximum growth potential; grows faster than spruce in the field	Advantage to spruce in more consistent, high-resource conditions; advantage to fir in more heterogeneous environments
Understory suppression tolerance	High tolerance	High tolerance	No large differences
Sapling/adult growth	Slower growth	Faster growth	Advantage to fir

Table 7. Species traits related to regeneration for red spruce and balsam fir and brief discussion of the implications of those traits for the regeneration dynamics of the two species.

Table 7 continued.

Parameter/life stage	Species		Implications & Discussion
	Red spruce	Balsam fir	
Pests & pathogens	Less vulnerable to pests and pathogens (e.g. spruce budworm)	More vulnerable to pests and pathogens (e.g. spruce budworm; heartrot fungus)	Fir much more vulnerable to pests and pathogens. Heartrot fungus, for example, typically limits fir lifespan to 100 years or less
Life span	Up to 300 years	About 100 years	Spruce presumably perists by reaching the canopy &, over its long life, producing enough recruits to replace the long-lived adults. Fir presumably persists by regenerating vigorously in many conditions
Effects of harvesting	Slower, more gradual regeneration	More rapid, aggressive regeneration	Spruce regeneration positively related to length of harvest cycle; fir recruits are much more abundant than spruce under most harvesting regimes

Table 7. Species traits related to regeneration for red spruce and balsam fir and brief discussion of the implications of those traits for the regeneration dynamics of the two species.

Chapter 3. Relative Effects of Light, Soil Moisture, and Belowground Competition on the Growth and Development of Red Spruce and Balsam Fir Seedlings

3.1. Introduction

As discussed in section 5 of Chapter 2, there appears to be a consistent pattern in the early life stage characteristics of red spruce and balsam fir. The seed sizes, germination patterns, germinant growth potentials, early root growth, and early carbon allocation patterns of the two species all suggest that balsam fir will be better than red spruce at establishing and surviving in environments with scarcer and/or more temporally and spatially heterogeneous soil water. Larger seeds (Venable and Brown 1988; Leishman et al. 2000), more drawn out germination phenology (Sarukhan 1974; Brown and Venable 1986; Venable and Brown 1988), deeper roots (Holch 1931; Albertson and Weaver 1945; Bahari et al. 1985; Kozlowski and Pallardy 2002; Ryser 2006), and higher allocation to belowground tissues (Pallardy and Rhoads 1993; Llaret et al. 1999; Kozlowski and Pallardy 2002; but see Engelbrecht et al. 2006) are all positively associated with better seedling establishment and survival in environments with scarce or highly heterogeneous belowground resources—and they are all characteristics of balsam fir relative to red spruce. This suggests that the early life stages of the two species differ in their response to dry conditions, which could be a key factor in the limited regeneration of red spruce relative to balsam fir.

O'Brien (2005) found that drought killed five-month-old red spruce seedlings significantly faster than it killed balsam fir seedlings of the same age. So there is

evidence that spruce is more vulnerable than fir to extended, lethal droughts, but what about the subtler, long-term effects of different belowground resource conditions on seedling growth and development? That is, how does the growth and development of the two species respond to different belowground resource conditions and precipitation patterns?

Red spruce (Westveld 1931; Davis 1966; Davis 1990; Meng and Seymour 1992; Wu et al. 1999; Landis and Peart 2005) and balsam fir (Westveld 1931; Meng and Seymour 1992; Morin and Laprise 1997) regeneration relies heavily on advance growth. As such, few newly germinated seedlings follow a direct path to the overstory. Beneath dense overstories, new seedlings are typically suppressed in the understory until overstory gaps provide light and a path to the canopy. In gaps, new seedlings are typically overtopped by faster growing hardwoods, beneath which the spruce and fir seedlings are suppressed until new overstory gaps provide light and a path to the canopy.

Given the prominence of suppressed advance growth in the lifecycles of spruce and fir, it may seem as if early growth would not be particularly important for the species' long-term success. That is, early growth rates may be of little importance if most seedlings end up being suppressed in the understory. However, early growth rates seem to be important even for suppressed seedlings (Lorimer et al. 1988; Cao and Ohkubo 1999; Wu et al. 1999; Landis and Peart 2005). Individuals with the greatest early growth are most likely to persist in the understory as advance growth, probably because larger, more robust seedlings are more likely to withstand harsh understory conditions and survive to form robust advance growth (Burdett et al. 1983; Kobe et al. 1995; Gilbert et al. 2001; Lin et al. 2002; Wyckoff and Clark 2002)

Given the importance of early growth to regeneration success, understanding the determinants of seedling performance is crucial to gaining a more complete understanding of red spruce and balsam fir regeneration. Of the factors affecting the growth and mortality of young seedlings, light (Kitajima 1994; Canham et al. 1996), moisture (Canham et al. 1996; Davis et al. 1998 and 1999), and competition (Ross and Harper 1972; Cater and Chapin 2000) are among the most important.

3.2. Materials and Methods

3.2.1. Introduction to Experiment 2

We monitored the growth and development of balsam fir and red spruce for one full growing season plus an additional two months of their second growing season under various levels of light, soil moisture, and belowground competition. This experiment will hereafter be referred to as Experiment 2.

The different soil moisture conditions allowed us to observe the hypothesized differences in soil moisture sensitivity of the growth of the two species. The different belowground competition treatments allowed us to monitor the effects of further reductions in water as well as competition for soil nutrients. The different light levels allowed us to study these phenomena in light environments that span the typical range found in northern forests.

Experiment 2 had four overlapping objectives:

1) To test the hypothesis generated by Experiment 1 that red spruce growth is more sensitive than balsam fir growth to dry conditions.

2) To further explain differences in the regeneration success of red spruce and balsam fir.
3) To further describe the early life stages of red spruce and balsam fir.
4) To enhance predictions of the performance of the early life stage of red spruce and balsam fir in various possible future climate scenarios.

3.2.2. Experimental Design and General Procedure

We employed a 2x2x2x2x3 full factorial split-split plot design with ten replications per treatment and three harvests (Fig. 9A). Each replicate was divided between two pots, one containing two seedlings and the other containing one seedling for a total of 320 pots and 480 seedlings (Fig. 9B). 160 seedlings were set aside for each harvest, with half of the seedlings from each two-seedling-pot harvested when they were two-months-old (Harvest 1) and the other half of the seedlings in the two-seedling-pots harvested when they were four-months-old (Harvest 2) (Table 8). The seedlings in the one-seedling-pots were harvested after being grown for two months in addition to their first growing season (Harvest 3) (Table 8).

The experiment was divided into three blocks. Each block was split into two plots, each receiving a different light treatment. Each light-treatment plot was split into subplots, each receiving a different watering treatment (Fig. 9A). Watering treatments were split in this way in order to prevent water from splashing into dry pots while well-watered pots were being watered. Competition treatments and species were randomized within the moisture subplots.

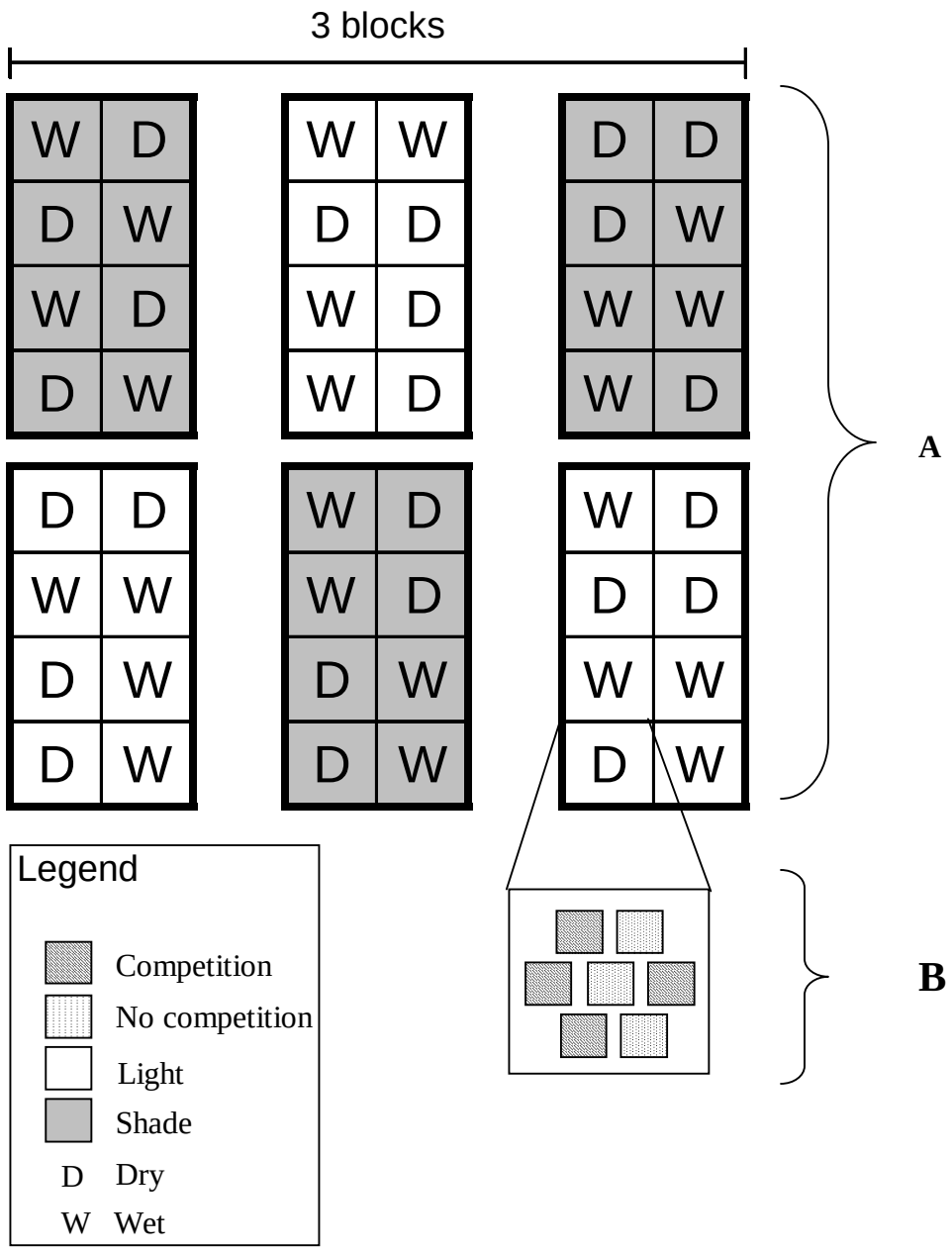

Figure 9. Schematic of Experiment 2, including the main treatment splits (A) and a sample subplot (B). Each subplot contained six or seven pots containing randomly assigned red spruce or balsam fir seedlings treated with randomly assigned competition treatments. Half of the pots contained two seedlings (one for Harvest 1, the other for Harvest 2) and the other half contained one seedling (for Harvest 3). In total, there were 320 pots with a total of 480 seedlings (160 seedlings for each harvest).

	Date	Species	Treatments							
			Light				Shade			
			Wet		Dry		Wet		Dry	
			Comp	No comp	Comp	No comp	Comp	No comp	Comp	No comp
Seeds sown	5/25/2006 5/15/2006	Red spruce Balsam fir								
Harvest 1	**7/31/2006**	**Red spruce** **Balsam fir**	10 10	10 10	9 10	10 10	10 10	10 10	10 10	10 10
Competition sowing	8/1/2006									
Competition clipped	9/1/2006									
Watering treatment initiated	8/31/2006									
Harvest 2	**9/23/2006**	**Red spruce** **Balsam fir**	9 10	10 10	10 10	10 10	10 10	10 10	7 9	10 10
Seedlings moved to greenhouse	1/9/2007									
Harvest 3	**3/21/2007**	**Red spruce** **Balsam fir**	10 10	10 10	8 8	10 10	7 9	9 8	3 9	6 9

Table 8. Sequence of events in Experiment 2, including the number of seedlings harvested in each treatment at the three harvests.

Seedlings were planted in 10x10x35 cm tree pots (Stuewe and Sons Inc. Corvallis, OR USA) filled with a 1:1 mixture of peat and sand and 4 kg/m^3 Osmocote 18-6-12 (Scott-Sierra, Milpitas, CA USA). Nine seeds of either spruce or fir were sown in each pot. As the seeds germinated, target seedlings were randomly chosen and the remaining germinants were discarded. For the first three weeks of their growth, red spruce germinants were covered with 1 cm hardware cloth in order to prevent predation by rodents and birds. Watering-treatment subplots were rotated within each light plot approximately every two weeks in order to minimize edge effects.

3.2.3. Experimental Study Sites

From May 2006 through January 9, 2007 the study was located in an open-air hoophouse in Orono, ME (Table 1). The hoophouse floor was comprised of crushed gravel to facilitate draining.

The climate of Orono is cool and moist, with a 30-year (1971-2000) mean annual temperature of 6.5º C and mean annual precipitation of 1023 mm. May through October (the approximate growing season in Orono) has an average temperature of 14.9º C and average precipitation of 527 mm (Climatography of the United States No. 81).

On January 9, 2007, the study was moved to a nearby temperature-controlled greenhouse where it remained until the conclusion of the study.

3.2.4. Seeds

Red spruce and balsam fir seeds were provided by The National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada). Seed sources were chosen for their proximity to our study site. Five seed sources were used

for each species to minimize site bias (Table 9). For each species, equal weights of seed from each seed source were mixed before sowing.

On May 15, 2006, seeds were shallowly buried within a 1 cm thick layer of peat that overlaid the 1:1 peat and sand mixture in the growth containers. Due to early seed predation, red spruce was resown on May 25, 2006.

Species	Province	Location	Latitude (ºW)	Longitude (ºN)	Elevation (m)
Balsam fir	New Brunswick	Johnson settlement	45.56	67.25	100
	New Brunswick	Kouchibouguac nation	46.49	64.59	20
	New Brunswick	Perth-Andover	46.44	67.39	175
	Nova Scotia	Spencers Island	45.21	64.42	30
	Nova Scotia	Abraham Lake	45.10	62.38	150
Red spruce	Nova Scotia	Bear River	44.35	65.40	125
	New Brunswick	Astle	46.25	66.28	175
	Quebec	Petite Casacpedia	48.34	65.34	500
	Quebec	Petit-lac-ste-anne	47.13	69.38	550
	Quebec	Lac Etchemin	45.20	70.55	800

Table 9. Seed sources for Experiment 2. Seeds were acquired from the National Tree Seed Centre (Natural Resources Canada, PO Box 4000, Fredericton, NB, E3B5P7 Canada).

3.2.5. Treatments

3.2.5.1. Light

Seedlings received either 50-70% or 10-15% of full sunlight, approximating the light conditions in a forest gap and beneath a dense overstory, respectively (Kuppers et al. 1996; Messier et al. 1998). From May 2006 until August 31, 2006, the seedlings were grown in an open-air hoophouse covered by 60% neutral shade cloth, which reduced light levels to approximately 65% of full sun. On September 1, 2006, the 60% neutral shade cloth was replaced by 4 mil polyethylene sheeting in order to exclude rain and manually control watering. The polyethylene sheeting reduced light levels to approximately 50% of full sun. After receiving their chilling requirement outside during the fall and early winter, the seedlings were moved into a nearby greenhouse on January 9, 2007, where they received 70% of full sunlight. Once the seedlings were inside the greenhouse, 16-hour days were provided with overhead lamps to stimulate the breaking of winter dormancy. Red spruce broke bud after an average of 16 days in the greenhouse (i.e. January 25, 2007) and balsam fir broke bud after an average of 18.6 days in the greenhouse (i.e. January 28, 2007) (Table 10). An ANOVA model was used to test for significant species and treatment effects on the rate of budbreak (not shown). Light, water, competition, and block effects were not significant ($\alpha = 0.05$), but species differences were highly significant ($p<0.001$).

Half of the seedlings were provided with additional shade by being housed under 90% neutral shade cloth supported by shelters constructed from ½ inch PVC piping (PVC fittings from A to Z Supply, Grass Valley, CA). Seedlings grown under the 90% shade cloth received approximately 13% of full sun from May 2006 until August 31, 2006,

approximately 10% of full sun after September 1, 2006, when hoophouse shade cloth was replaced by 4 mil polyethylene, and approximately 15% of full sun after January 9, 2007, when seedlings were transferred to the greenhouse.

	Degree days until budbreak
Balsam fir	18.6 ± 0.3 (n=76)
Red spruce	16.0 ± 0.3 (n=64)

Table 10. Number of days (± 1 SE) after moving one-year-old red spruce and balsam fir seedlings into a heated greenhouse before the seedlings broke bud and resumed growth. Seedlings remained outside in ambient winter weather until January 9th, 2006, at which time they were moved inside a greenhouse and provided with 16-hour days using overhead lamps. Species differences were significant ($p<0.001$). Number of replicates (n) is in parentheses.

3.2.5.2. Water

From May 15, 2006 to August 31, 2006, seedlings were well watered to facilitate germination, establishment, and early growth. In addition to ambient rainfall, pots received water from overhead sprinklers for 10 minutes, three times per day.

On September 1, 2006, the experiment was covered by 4 mil clear polyethylene sheeting in order to exclude rainfall. From September 1, 2006 until November 26, 2006, pots were watered manually. Half of the seedlings were watered to field capacity approximately every 2-3 days (hereafter referred to as the wet treatment). The other half of the seedlings were watered to field capacity every 5-14 days (hereafter referred to as the dry treatment). The goal of the dry treatment was to impose a highly-water-limiting but non-lethal soil moisture environment, which is why rewatering time varied, depending on how quickly the soil dried. In general, dry seedlings were rewatered every 7-14 days during fall 2006 and every 5-7 days after being moved into the greenhouse. Wet seedlings were typically watered every 2-3 days during fall 2006 and every-other-day in the greenhouse. Within each watering treatment, all pots were watered on the same schedule.

From the end of November, 2006 until January 9, 2007, the seedlings were dormant and were allowed to receive ambient precipitation. When the seedlings were moved into the greenhouse on January 9, 2007, they were all well watered until January 31, 2007, by which time the vast majority of seedlings had broken bud and resumed growth. On February 1, 2007, the two watering treatments, wet and dry, were resumed and maintained until Harvest 3 on March 21, 2007.

3.2.5.3. Competition

On August 1, 2006 half of the pots were sown with grass seed (Scotts Premium Sun and Shade mixture--contents: 27.57% Abbey Kentucky bluegrass, 25.61% Fenway creeping red fescue, 24.44% Evening Shade perennial ryegrass, and 20.61% Laredo perennial ryegrass) at a density of 0.03 kg/m^2. The pots in the no-competition treatment were kept free of vegetation by hand-weeding as needed.

For the first four weeks after being planted, the grass was allowed to grow freely in order to facilitate establishment and root productivity. As such, there was some early light competition associated with the competition treatments. But on September 1, 2006 the grass was clipped to a height of approximately 2 cm and was kept near that height by trimming two or three times per week. The grass was kept short to prevent it from competing with spruce and fir seedlings for light. By minimizing shoot competition, we were able to specifically monitor the effects of root competition. We focused on root competition for three reasons:

1) Root competition has been found to be highly important in forests (Wilson 1988; Cater and Chapin 2000), particularly on less fertile and/or drier sites (Casper and Jackson 1997; Coomes and Grubb 2000).
2) The effects of different light levels on the growth and development of spruce and fir have already been studied in Experiment 1 and by Greenwood et al. (in preparation). Our knowledge of the effects of root competition on spruce and fir is relatively limited.

3) Root competition can speed soil water depletion (Fig. 10), allowing us to further study the relative sensitivity of spruce and fir to different soil moisture conditions. Root competitors will also compete with spruce and fir for soil nutrients, which, given the growth and root allocation differences between spruce and fir, could reveal important differences between the two species.

3.2.6. Data Collection

3.2.6.1. Environmental Monitoring

Light levels relative to full sunlight were measured using a LI-185B quantum radiometer/photometer (Licor Inc., Lincoln, Nebraska). Light levels were measured from 1100-1300 hours on cloudless days in both light environments (shade and high-light) in each experimental setting (shade-cloth-covered hoophouse, plastic-sheeting-covered hoophouse, and greenhouse). Measurements were taken on three occasions in each experimental setting and are summarized in section 2.5.1 of this chapter.

Using a WET Sensor and HH2 moisture meter (Delta-T Devices, Cambridge, England), percent soil moisture was monitored at three soil depths (6 cm, 18 cm, and 30 cm) by inserting sensor probes horizontally into the soil through pre-made holes in the pots. Measurements were taken during a sample period in September 2006 on six pots in each light-competition-watering treatment combination.

3.2.6.2. Seedling Data

The first harvest of spruce and fir occurred on July 31, 2006 before competition and moisture treatments were initiated (Table 8). Each seedling was removed intact from

its pot. Root and shoot lengths were immediately measured. The dry weight of leaves, stems, and roots were recorded after drying the tissues at 60º C for at least 72 hours.

The second harvest of spruce and fir occurred on September 25, 2006 (Table 8). Each seedling was removed intact from its pot. Root and shoot lengths of the fresh seedlings were immediately measured, as were leaf areas and root areas. To obtain root areas, individual root systems were rinsed thoroughly, detached from the plants, spread in a tray of water, scanned on a flatbed scanner, and analyzed using WinRhizo root analysis software, version 2007a (Regent Instruments Inc., Quebec, Canada). Five seedlings from each species-treatment combination were randomly selected for leaf area measurements. To measure leaf areas, a representative sample of approximately 40 needles per plant were removed from the stem, scanned with a flatbed scanner, and analyzed using WinSEEDLE image analysis software, version 2007a (Regent Instruments Inc., Quebec, Canada). The dry weight of leaves, stems, and roots were recorded after they were dried at 60º C for at least 72 hours.

At Harvest 2, grass roots were harvested from 20 pots, 5 in each light-moisture treatment combination. Roots were weighed after being dried to constant mass at 60º C for 72 h.

The third harvest of spruce and fir occurred on March 21, 2007 (Table 8). The measurements taken on spruce and fir seedlings during Harvest 3 were identical to those taken during Harvest 2 except for primary root length, which was not recorded at Harvest 3, and basal stem diameter, which was recorded at Harvest 3. Also, at Harvest 3 WinRhizo was used to count the number of root tips in each root system.

3.2.7. Statistical Analysis

3.2.7.1. Statistical Software

All analyses were carried out in R (R version 2.4.1 © 2006--The R Foundation for Statistical Computing).

3.2.7.2. Harvest 1

The competition and watering treatments were imposed after Harvest 1, so for the Harvest 1 data, only light treatment, species, and block effects were used to account for variation in height, primary root length, R:S length ratio, plant dry mass, R:S mass ratio, RMR, LMR, SMR, and SSL (acronyms are described in Table 4). Models were assessed for normality and constant variance by examining normal QQ plots and residual plots, respectively. Dependent variables were log- or square-root-transformed as necessary to better approach normality (Appendix). Following transformations, all models appeared to meet assumptions of ANOVA.

For all seedling traits, the following ANOVA model was used:

Y ~ light:block + species + light + block + species:light

The MS of the 'light:block' term was used as the error MS in the F-ratios of the 'light' term in order to account for splitting and block effects (Appendix). Means were separated using Tukey's HSD procedure.

3.2.7.3. Harvests 2 and 3

For the Harvest 2 and 3 data, ANOVAs were performed with species, light treatment, competition treatment, watering treatment, and block effects accounting for variation in height, dry mass, primary root length (Harvest 2 only), R:S length ratio (Harvest 2 only), R:S mass ratio, RMR, SMR, LMR, SLA, SSL, FARM, SRL, root tips per root length (Harvest 3 only), root tips per root mass (Harvest 3 only), and basal stem diameter (Harvest 3 only). (acronyms are described in Table 4). FARM ratios were calculated using the SLAs that were measured for a subset of five seedlings per species in each treatment combination.

For Harvest 3, an additional ANOVA was performed for relative growth rate (RGR). For RGR calculations, the ln-transformed Harvest 1 dry masses were averaged in each species-treatment combination and subtracted from each ln-transformed Harvest 3 dry mass in the same species-treatment combination. The difference was then divided by the number of days between Harvests 1 and 3. The RGR equation can be found in section 2.5.3 of Chapter 1 (equation 1).

Harvest 1 dry masses were averaged across blocks, so RGR was analyzed using an ANOVA with species, light treatment, competition treatment, and watering treatment accounting for variation in RGR. The following model was used for RGR:

RGR ~ sp + light + water + comp + sp:light + sp:water + sp:comp + light:water + light:comp + water:comp + sp:light:water + sp:water:comp + light:water:comp + sp:light:water:comp

For all other traits, the following model was used:

Y ~ block + light + block:light + water + block:water + water:light + block:water:light + comp + sp + comp:sp + light:comp + light:sp + water:comp + water:sp + water:sp:comp + water:light:comp + water:light:sp + water:light:comp:sp

The MS of the 'light:block' term was used as the error MS in the F-ratio of the 'light' term in order to account for splitting and block effects. Similarly, the MS of the 'water:light' and 'block:water:light' terms were summed and used as the error MS for the F-ratios of the 'water' and 'water:light' terms in order to account for splitting and block effects (Appendix).

The different light environments had strong effects on watering treatments (Fig. 10), competition treatments (Table 11), and seedling traits. In order to better discern the effects of the various treatments, additional ANOVAs were performed for the Harvest 2 and 3 data within each light environment for height, dry mass, primary root length (Harvest 2 only), R:S length ratio (Harvest 2 only), R:S mass ratio, RMR, SMR, LMR, SLA, SSL, FARM, SRL, root tips per root length (Harvest 3 only), root tips per root mass (Harvest 3 only), and basal stem diameter (Harvest 3 only) (acronyms described in Table 4) using the following model:

Y ~ block + water + block:water + comp + sp + comp:sp + water:comp + water:sp + water:sp:comp

	Competitor root dry mass (g) at harvest 2
Shade	0.13 ± 0.01 (n=10)
Light	2.38 ± 0.18 (n=9)

Table 11. Mean grass competitor root system dry mass per pot (± 1 SE) in the two light environments at Harvest 2 of Experiment 2. Number of replicates (n) is in parentheses.

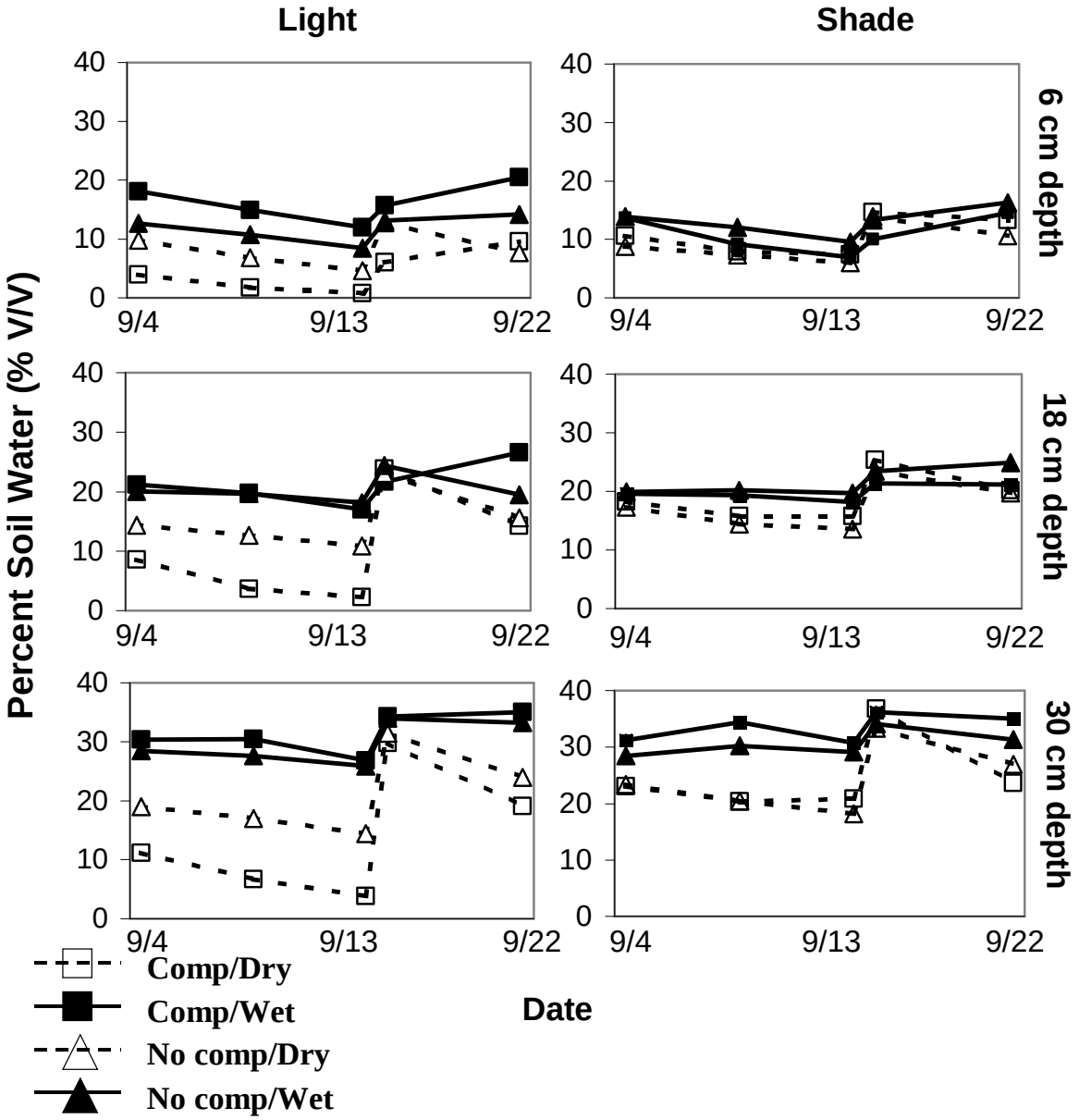

Figure 10. Time series of soil moisture data (percent volume/volume) at three depths in the pots of Experiment 2. Measurements were taken from September 4, 2006 until September 22, 2006 to characterize soil moisture dynamics in each light-competition-moisture treatment combination. Pots were all watered to field capacity on September 1, 2006. Wet seedlings were watered to field capacity every 2-3 days and water was withheld from dry seedlings for 14 days until September 15, whent they were rewatered to field capacity. (n=6 per treatment combination, evenly divided among spruce and fir)

The MS of the 'block:water' term was used as the error MS in the F-ratio of the 'water' term in order to account for splitting and block effects (Appendix). Again, Harvest 1 dry masses were averaged across blocks, so light/shade RGRs were analyzed using the same model as above, but without the 'block' or 'block:water' terms.

For the Harvest 2 and 3 data, species' responses to the two light environments were evaluated by calculating a relative light response (RLR) statistic in each species-treatment combination for root morphology (SRL for Harvest 2; root tips per root length for Harvest 3), seedling size (height and total dry mass), and carbon allocation patterns (R:S mass ratio). These four parameters were selected to give a representative picture of the relative growth and development of the two species in response to the various environmental conditions. RLR calculations are further described in section 2.5.3 of Chapter 1 (equation 2).

Relative responses to competition (RCR) and water (RWR) were similarly calculated for SRL (Harvest 2) root tips per length (Harvest 3), height, seedling dry mass, and R:S mass ratio. RCR was calculated for each seedling trait by averaging the ln-transformed values of a given parameter in the no-competition treatment and subtracting that average from each individual value in the competition treatment of the same species-light-water treatment combination:

$$\text{RCR} = \ln\left(\text{magnitude in comp trt}\right) - \bar{x}\left[\ln\left(\text{magnitudes in no comp trt}\right)\right] \quad (3)$$

RWR was calculated for each seedling trait by averaging the ln-transformed values of a given parameter in the dry treatment and subtracting that average from each individual value in the wet treatment of the same species-light-competition treatment combination:

$$\text{(4)} \qquad \text{RWR} = \ln\left(\text{magnitude in wet trt}\right) - \bar{x}\left[\ln\left(\text{magnitudes in dry trt}\right)\right]$$

A positive RCR indicates that a trait was greater in magnitude in the competition treatment than in the no-competition treatment, while a negative RCR indicates that a trait was lower in magnitude in the competition treatment than in the no-competition treatment. Similarly, a positive RWR indicates that a trait was greater in magnitude in the wet treatment than in the dry treatment, while a negative RWR indicates that a trait was lower in magnitude in the wet treatment than in the dry treatment.

Since the shade, no-competition, and dry treatment values used for RLR, RCR, and RWR calculations, respectively, were averaged across blocks, the three statistics were analyzed using ANOVA models with species and treatment combinations accounting for variation in the three parameters (Appendix). The following models were used for the three statistics:

RLR ~ species + water + comp + species:water + species:comp + water:comp + species:water:comp

RCR ~ species + water + light + species:water + species:light + water:light + species:water:light

RWR ~ species + comp + light + species:comp + comp:light + species:light + species:comp:light

All Experiment 2 models were assessed for normality and constant variance by examining normal QQ plots and residual plots, respectively. Dependent variables for all models were log- or square-root-transformed as necessary to better approach normality. All models appeared to meet assumptions of ANOVA. All models were assessed for significance at $\alpha = 0.05$. Species-treatment combination means for the RLR, RCR, and RWR statistics were compared using Tukey's HSD procedure. For all other Experiment 2 models, Tukey's HSD procedure was used to compare the species-water-competition treatment combination means within each light environment.

3.3. Results

3.3.1. Treatments and Microenvironmental Conditions

Percent soil moisture was monitored at three soil depths (6 cm, 18 cm, and 30 cm). Measurements were taken from September 4, 2006 until September 22, 2006 in order to characterize the soil moisture dynamics in each light-competition-moisture treatment combination. Pots were all watered to field capacity on September 1, 2006, after which the wet pots were watered to field capacity every 2-3 days and water was withheld from the dry pots for 14 days until September 15, 2006 (Fig. 10), at which time they were rewatered to field capacity. So, the data presented in Figure 10 covers about one-and-one half watering cycles for the dry seedlings.

The two watering treatments had very different effects on soil moisture in the different light and competition treatments (Fig. 10). The dry treatment had much stronger negative effects on soil moisture in the high-light environment than it did in the shade environment (Fig. 10). In the high-light environment, soil moisture was depleted from the competition-pots faster than it was in the no-competition-pots (Fig. 10). In the shade, however, root competition had little effect on soil moisture dynamics (Fig. 10). In both light environments, the upper soil maintained lower average soil moisture than the deeper soil (Fig. 10), indicating that the deeper soil layers contained more persistent pools of water.

Competitor productivity was measured at Harvest 2 using the dry masses of the grass roots. In the high-light environment, grass roots had penetrated to the bottom of the 35 cm-deep pots and had an average dry mass of 2.38 g per pot (Table 11). In the shade environment, grass roots appeared to be restricted to the top 5-10 cm of the pots and had an average dry mass of only 0.13 g per pot (Table 11). So, root competition was very low in the shade environment during fall 2006. After the seedlings were moved into the greenhouse on January 9, 2007, the grass competitors in the high-light environment appeared to recover well, but those in the shade environment had mostly died over the winter, and thus were expected to have little if any effect on shade-grown seedlings. So, any effects of competition in the shade environment are almost certainly related to the grass's four-week establishment phase, during which the grass was allowed to grow freely and compete with spruce and fir seedlings for light (see section 2.5.3).

Again, the competition and watering treatments were imposed after Harvest 1 (Table 8), and thus only apply to Harvest 2 and 3 data.

3.3.2. Harvest 1

Species effects were significant ($\alpha = 0.05$) for all traits (Table 12), indicating that spruce and fir differed in all measured morphological and tissue allocation traits. There were significant light:species interactions for height, dry mass, RMR, SMR, and SSL, indicating that the response of those traits to the different light environments differed between spruce and fir (Table 12).

	Height	Dry mass	1° root length	R:S length	R:S mass	RMR	SMR	LMR	SSL
block	**0.014**	0.202	0.369	**0.019**	0.334	0.296	0.395	0.107	**0.000**
sp	**0.003**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.011**	**0.000**	**0.000**
light	**0.049**	**0.014**	**0.015**	0.100	0.056	0.063	**0.027**	0.115	**0.001**
light:sp	**0.008**	**0.000**	0.135	0.429	0.287	**0.013**	**0.002**	0.677	**0.000**

Table 12. P-values for Experiment 2 Harvest 1 ANOVAs for height, dry mass, primary root length, R:S length, R:S mass, RMR, SMR, LMR, and SSL. Acronyms are described in Table 4. Significance assessed at α=0.05. Model details are provided in the appendix.

In the shade environment, balsam fir and red spruce were similar in height, but spruce was significantly taller than balsam fir in the high-light environment (Fig. 11A). In both light environments, balsam fir had significantly longer roots than red spruce (Fig. 11B), which was further reflected in fir having higher R:S length ratios than red spruce in both light environments (Fig. 11C).

In the shade environment, balsam fir was significantly more massive than red spruce (Fig. 11D). Fir was also somewhat more massive than spruce in the high-light environment, though the difference was not significant (Fig. 11D).

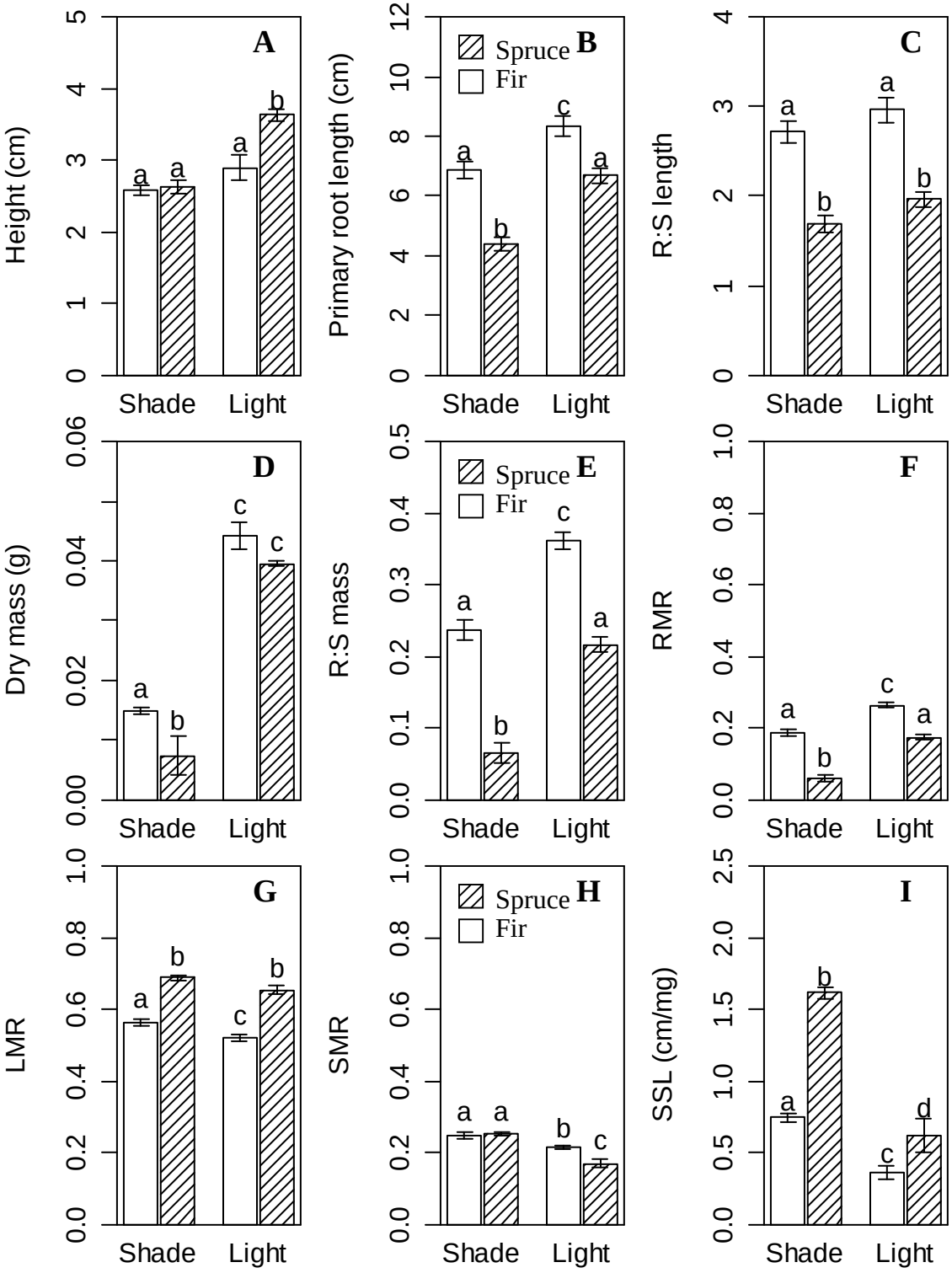

Figure 11A-I: Experiment 2 Harvest 1 means (± 1 SE) for height (A), primary root length (B), R:S length (C), plant dry mass (D), R:S mass (E), RMR (F), LMR (G), SMR (H), and SSL (I). Acronyms are described in Table 4. Different letters indicate significant differences assessed by Tukey's HSD at α=0.05. (n: Balsam fir-light = 40; Balsam fir-shade = 40; Red spruce-light = 38; Red spruce- shade = 40)

Compared to red spruce, balsam fir allocated a significantly higher proportion of its biomass to roots in both light environments (Fig. 11E-F). Both species allocated most of their resources to leaves, but red spruce had a significantly higher LMR than balsam fir in both light environments (Fig. 11G). In the shade environment, the two species had similar SMRs, while balsam fir had a higher SMR than red spruce in the high-light environment (Fig. 11H).

In both light environments, red spruce had a significantly higher SSL than balsam fir (Fig. 11I), indicating that spruce's stems were more elongated than those of fir.

Red spruce was significantly taller in the high-light environment than it was in the shade environment, while the height of balsam fir was not significantly different between the two light environments (Fig. 11A). For both species, compared to seedlings grown in the shade environment, seedlings in the high-light environment had significantly longer roots (Fig. 11B), significantly higher R:S mass ratios (Fig. 11E), significantly higher RMRs (Fig. 11F), significantly (but only slightly) lower SMRs (Fig. 11H), and significantly lower SSLs (Fig. 11I). Light environment did not have a significant effect on the R:S length ratios of either species (Fig. 11C). The LMRs of both species were also relatively consistent between the two light environments, though the LMR of balsam fir was slightly lower in the high-light environment than it was in the shade (Fig. 11G).

3.3.3. Harvest 2

3.3.3.1. Introduction

P-values for the analyses related to all Harvest 2 data can be found in Table 13 for the overall models, Table 14A for the high-light-environment models, and Table 14B for the shade-environment models.

Competition and watering treatments had only been in place for eight and four weeks, respectively, by Harvest 2. The grass competitors spent much of those eight weeks getting established. As such, water and competition treatments were expected to have relatively small effects on Harvest 2 seedling growth and development, and the following discussion will focus primarily on the effects of the different light environments.

	Height	1° root length	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	R:S length	SRL	SSL
block	**0.031**	**0.033**	**0.036**	0.293	0.132	**0.005**	0.558	0.178	0.143	**0.001**	0.993	**0.043**
light	**0.001**	**0.004**	**0.001**	**0.006**	**0.008**	**0.004**	0.472	**0.013**	**0.012**	**0.002**	**0.005**	**0.001**
water	0.890	0.918	0.518	0.948	**0.010**	0.097	**0.003**	0.396	**0.004**	0.815	**0.001**	0.374
comp	0.134	0.162	**0.000**	0.086	**0.001**	0.794	**0.006**	**0.000**	**0.004**	0.333	0.071	**0.000**
sp	**0.000**	**0.000**	**0.000**	0.530	**0.000**	0.259	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
light:water	0.594	0.917	0.713	0.970	0.361	**0.014**	**0.018**	0.520	0.216	0.518	0.179	0.311
comp:sp	0.537	0.120	0.731	0.382	0.563	0.694	0.838	0.087	0.915	0.226	0.304	0.223
light:comp	0.732	0.670	0.190	0.544	0.452	0.170	0.682	0.539	0.443	0.646	0.124	0.685
light:sp	**0.000**	0.877	**0.000**	0.346	**0.000**	**0.044**	0.116	**0.008**	**0.000**	**0.000**	**0.000**	**0.000**
water:comp	0.680	0.451	0.710	0.683	0.814	0.901	0.761	0.607	0.741	0.901	**0.003**	0.910
water:sp	0.619	0.513	0.610	0.337	0.904	0.591	0.755	0.728	0.769	0.599	0.342	0.676
water:comp:sp	0.827	0.637	0.326	0.614	0.908	0.165	0.326	0.889	0.807	0.941	0.793	0.405
light:water:comp	0.816	0.061	0.381	0.561	0.487	0.906	0.602	0.194	0.563	**0.049**	0.851	0.252
light:water:sp	0.504	0.054	0.478	0.339	0.493	0.768	0.404	0.292	0.596	0.105	0.253	0.703
light:water:comp:sp	0.809	0.108	0.236	0.315	0.740	0.313	0.783	0.392	0.810	0.075	0.759	**0.032**

Table 13. P-values for Experiment 2 Harvest 2 ANOVAs height, dry mass, primary root length, SLA, RMR, SMR, LMR, FARM, R:S mass, R:S length, SRL, and SSL. Acronyms are described in Table 4. Significance was assessed at α=0.05. Model details are provided in the appendix.

A - Light	Height	1º root length	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	R:S length	SRL	SSL
block	0.334	**0.037**	0.135	0.384	0.166	**0.015**	0.959	0.208	0.214	**0.008**	0.702	0.080
water	0.995	0.976	0.956	0.877	**0.028**	0.071	**0.004**	0.192	**0.002**	0.902	**0.032**	0.710
comp	0.514	0.314	**0.002**	**0.008**	**0.011**	0.176	0.154	**0.001**	**0.036**	0.349	**0.006**	**0.002**
sp	**0.000**	**0.031**	**0.000**	0.701	**0.000**	**0.009**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.047**
comp:sp	0.728	0.074	0.491	0.087	0.807	0.605	0.574	0.081	0.653	**0.034**	0.407	0.373
water:comp	0.697	0.158	0.475	0.866	0.525	0.986	0.573	0.576	0.564	0.216	0.050	0.496
water:sp	0.474	0.146	0.495	0.924	0.698	0.465	0.404	0.574	0.887	0.434	0.925	0.599
water:comp:sp	0.799	0.447	0.487	**0.032**	0.673	0.883	0.632	0.303	0.870	0.282	0.469	0.498
B - Shade	Height	1º root length	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	R:S length	SRL	SSL
block	0.082	0.255	0.075	0.464	0.628	0.144	0.452	0.230	0.615	0.083	0.536	0.133
water	0.906	0.581	0.525	0.978	0.201	0.119	0.393	0.974	0.198	0.315	**0.011**	0.361
comp	0.117	0.174	**0.015**	0.544	**0.037**	0.520	**0.019**	**0.019**	**0.042**	0.625	0.708	**0.000**
sp	**0.000**	**0.000**	0.924	0.382	**0.000**	0.555	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**
comp:sp	0.468	0.457	**0.026**	0.814	0.684	0.405	0.695	0.342	0.887	0.704	0.236	**0.006**
water:comp	0.909	0.111	0.628	0.572	0.718	0.853	0.885	0.233	0.803	0.126	**0.025**	0.394
water:sp	0.853	0.130	0.997	0.324	0.573	0.987	0.639	0.357	0.534	0.154	0.146	0.816
water:comp:sp	0.503	0.580	0.528	0.625	0.508	0.122	0.416	0.409	0.525	0.283	0.771	0.761

Table 14A-B. P-values for Experiment 2, Harvest 2 ANOVAs in the high-light environment (A) and the shade environment (B) for height, dry mass, primary root length, SLA, RMR, SMR, LMR, FARM, R:S mass, R:S length, SRL, and SSL. Acronyms are described in Table 4. Significance was assessed at α=0.05. Model details are provided in the appendix.

3.3.3.2. Species Trait Comparisons

In both light environments, red spruce was significantly taller than balsam fir (Fig. 12A). In the high-light environment, red spruce was significantly more massive than balsam fir, but there were no interspecific dry mass differences in the shade environment (Fig. 12B). In terms of primary root length, balsam fir had longer roots than red spruce in the shade-environment and the two species had similar root lengths in the high-light environment (Fig. 12C). Given the relative heights and root lengths of the two species, it is not surprising that the R:S length ratio of balsam fir was significantly higher than that of red spruce in both light environments (Fig. 12D).

In both light environments, balsam fir allocated more dry mass than red spruce to roots (Fig. 12E-F), there were no significant interspecific differences in stem allocation (Fig. 12G), and, compared to balsam fir, red spruce allocated a much higher proportion of its dry mass to leaves (Fig 12H). The higher foliar allocation and lower root allocation of red spruce are further reflected in the FARM ratios of the two species, with red spruce's FARM ratios being significantly higher than those of balsam fir in both light environments (Fig. 12K).

In the shade environment, red spruce had much more elongated stems than balsam fir, as reflected by spruce's higher SSLs (Fig. 12J). In the high-light environment, however, there were no significant interspecific differences in SSL, though the stems of spruce were slightly more elongated than those of balsam fir (Fig. 12J). There was also a significant competition effect on SSL (Table 12; 13A-B). Within each water treatment in the low-light environment, spruce SSLs were higher in the competition treatment than they were in the no-competition treatment (Fig. 12J). In the high-light environment,

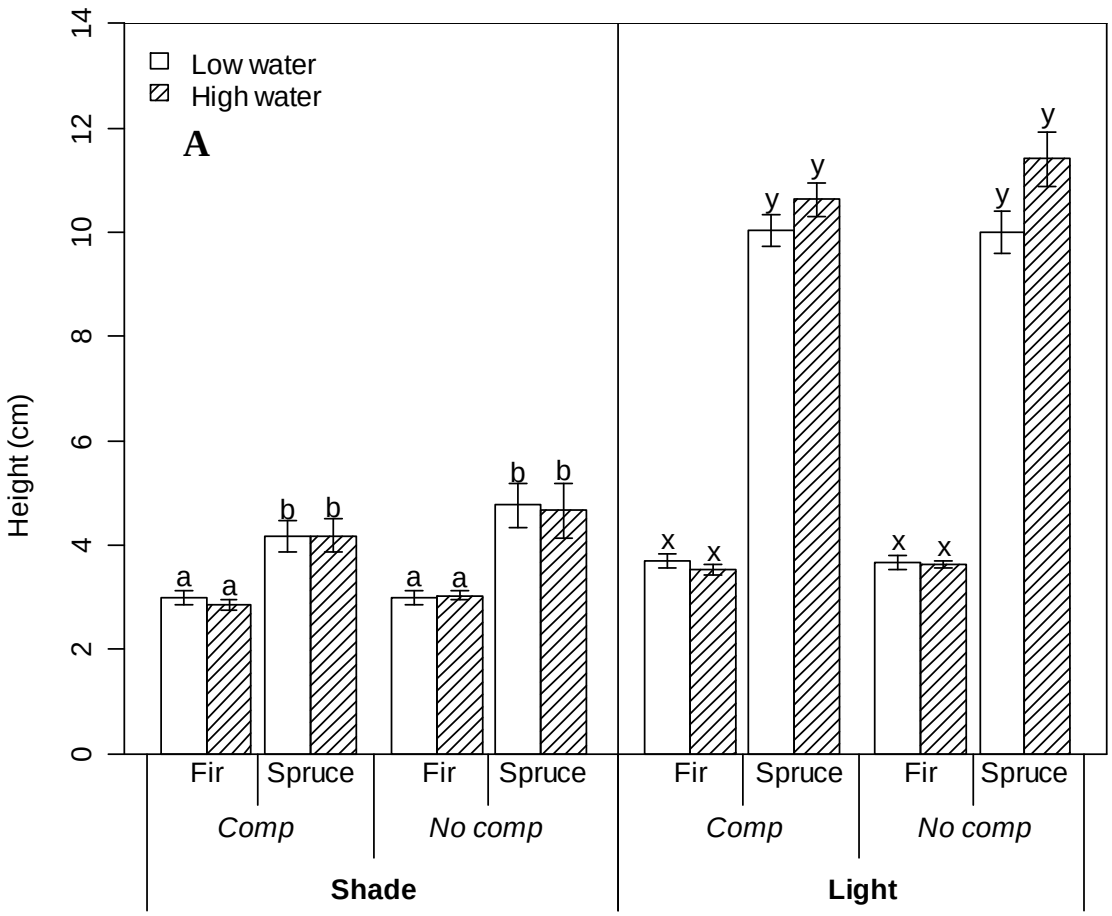

Figure 12A. Experiment 2 Harvest 2 means (± 1 SE) of height. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

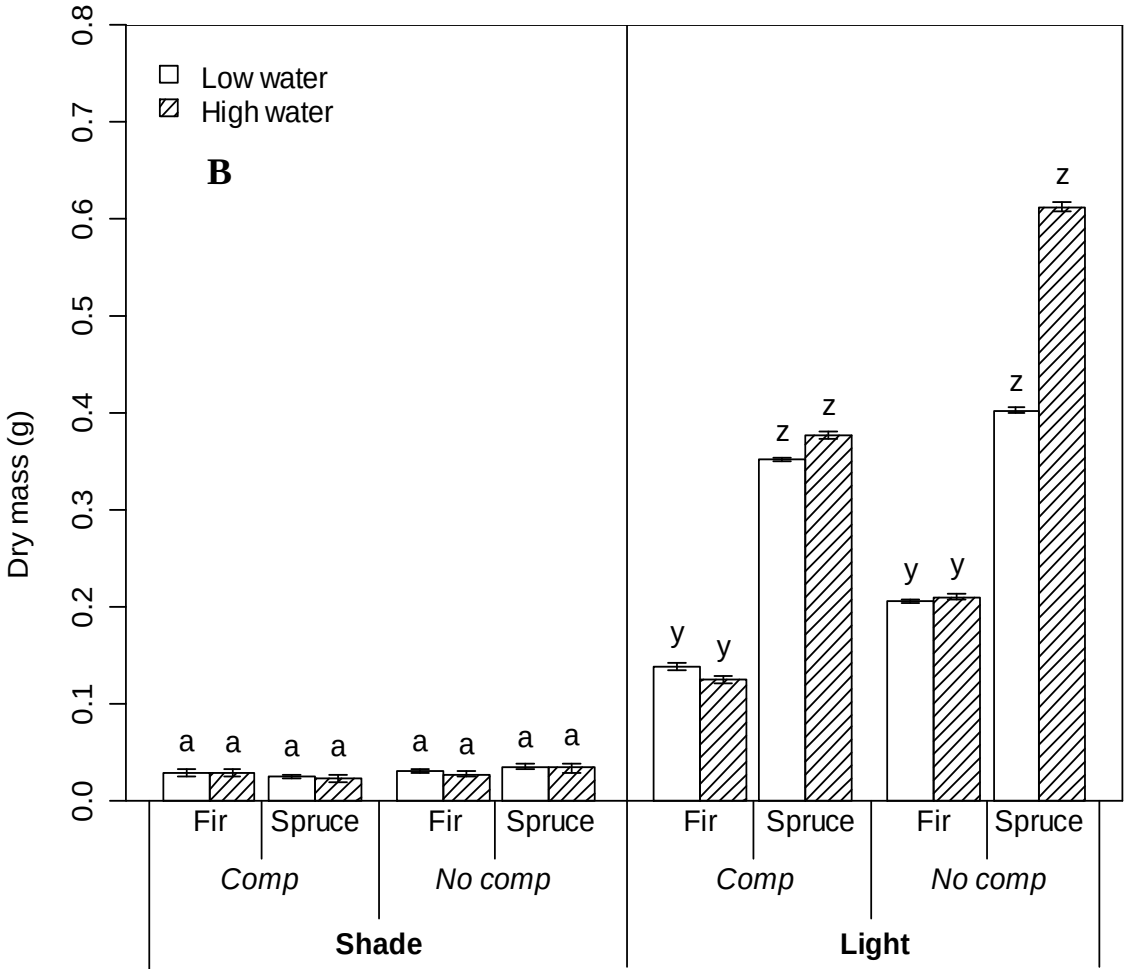

Figure 12B. Experiment 2 Harvest 2 means (± 1 SE) of plant dry mass. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

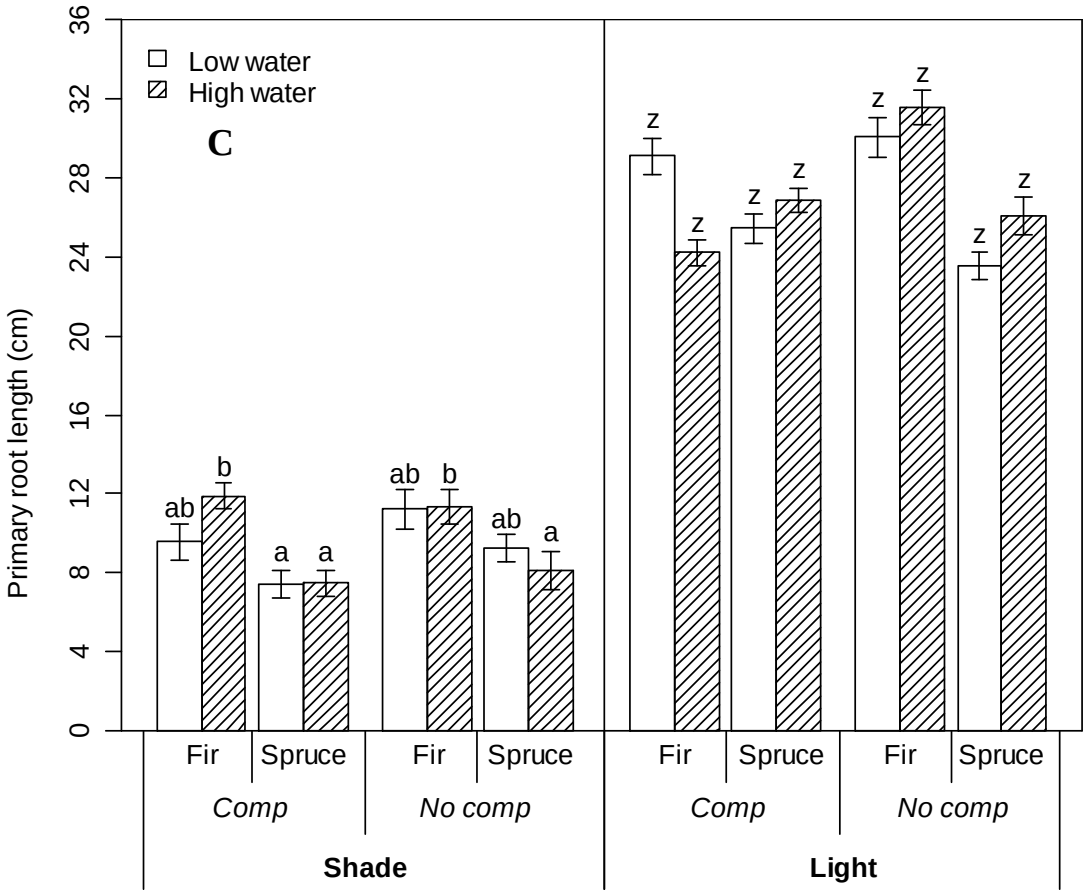

Figure 12C. Experiment 2 Harvest 2 means (± 1 SE) of primary root length. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

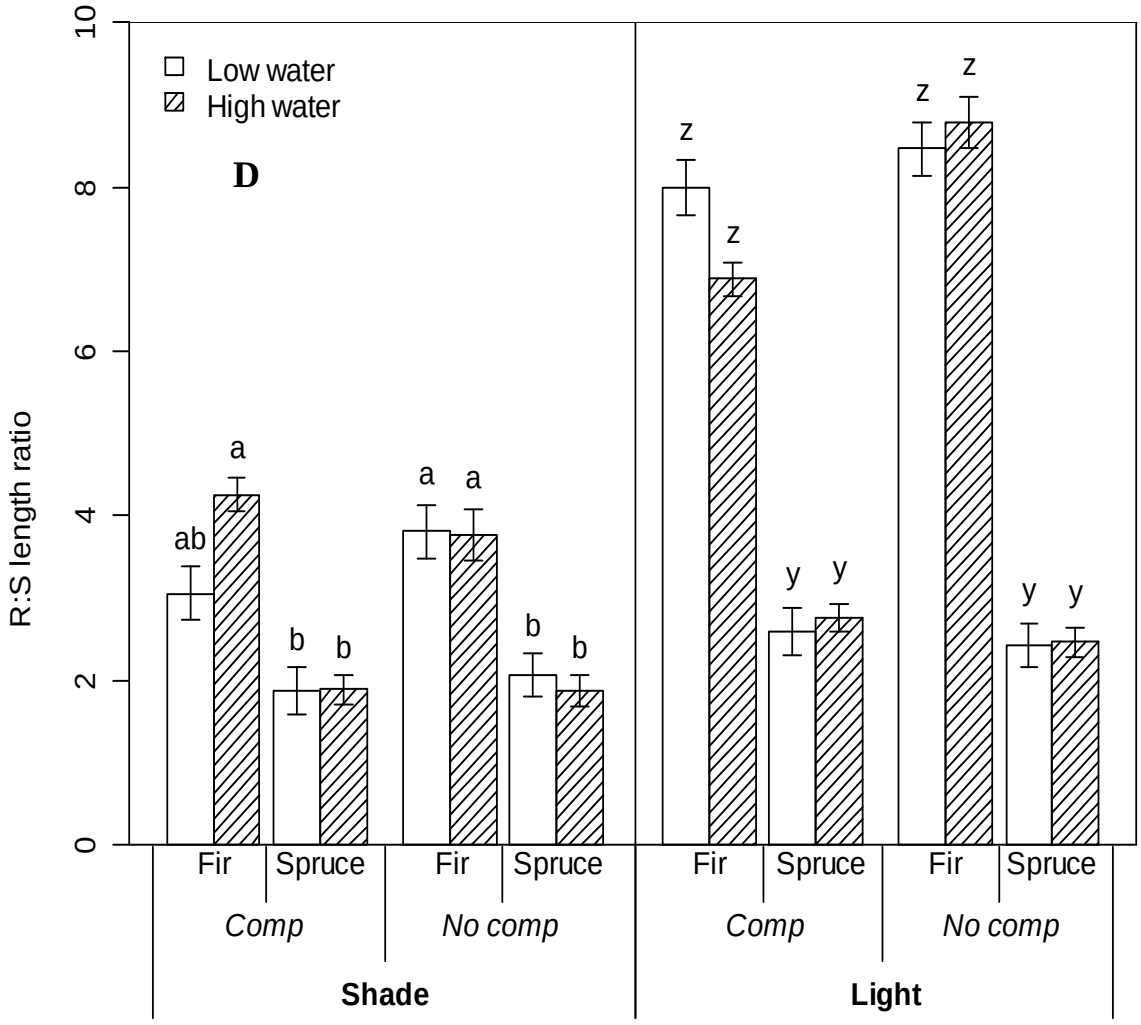

Figure 12D. Experiment 2 Harvest 2 means (± 1 SE) of R:S length ratio (see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

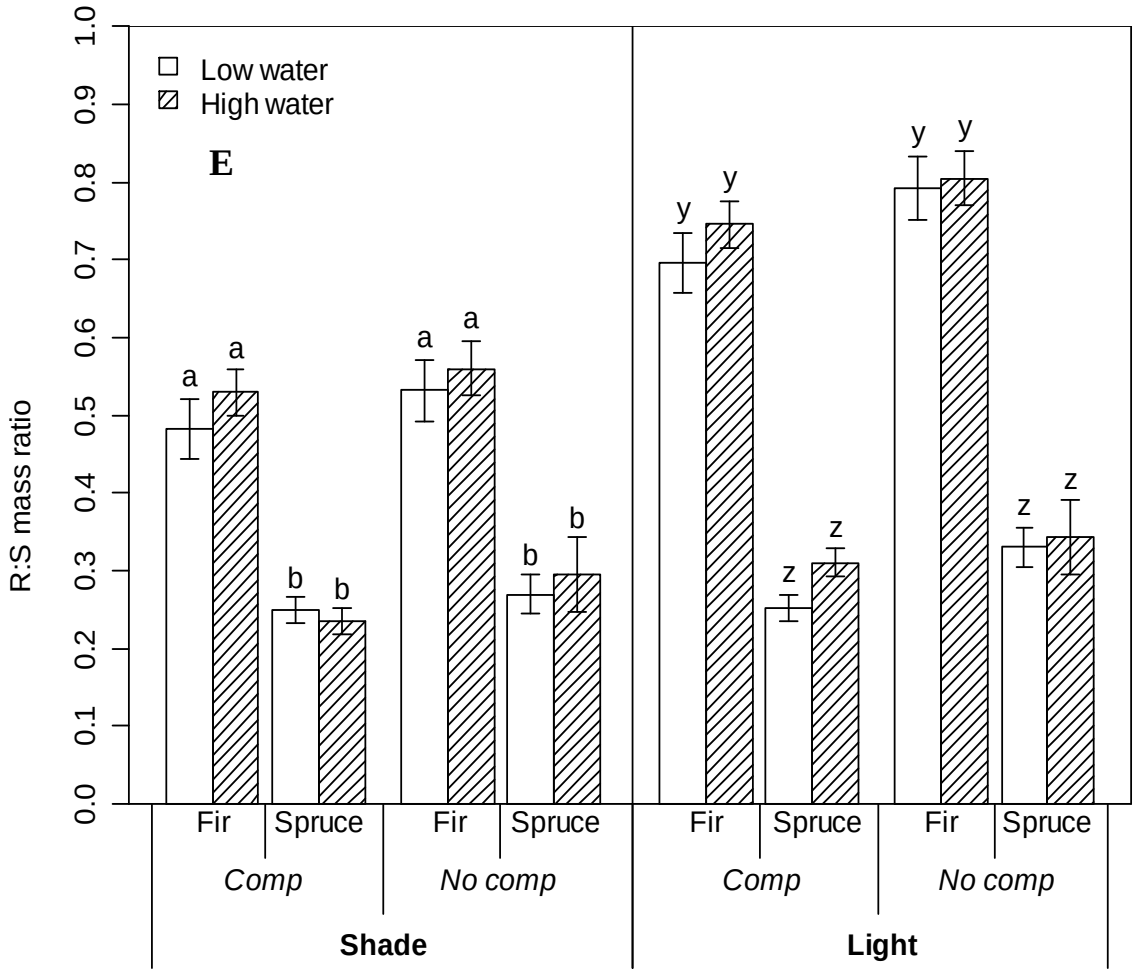

Figure 12E. Experiment 2 Harvest 2 means (± 1 SE) of R:S mass ratio (see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

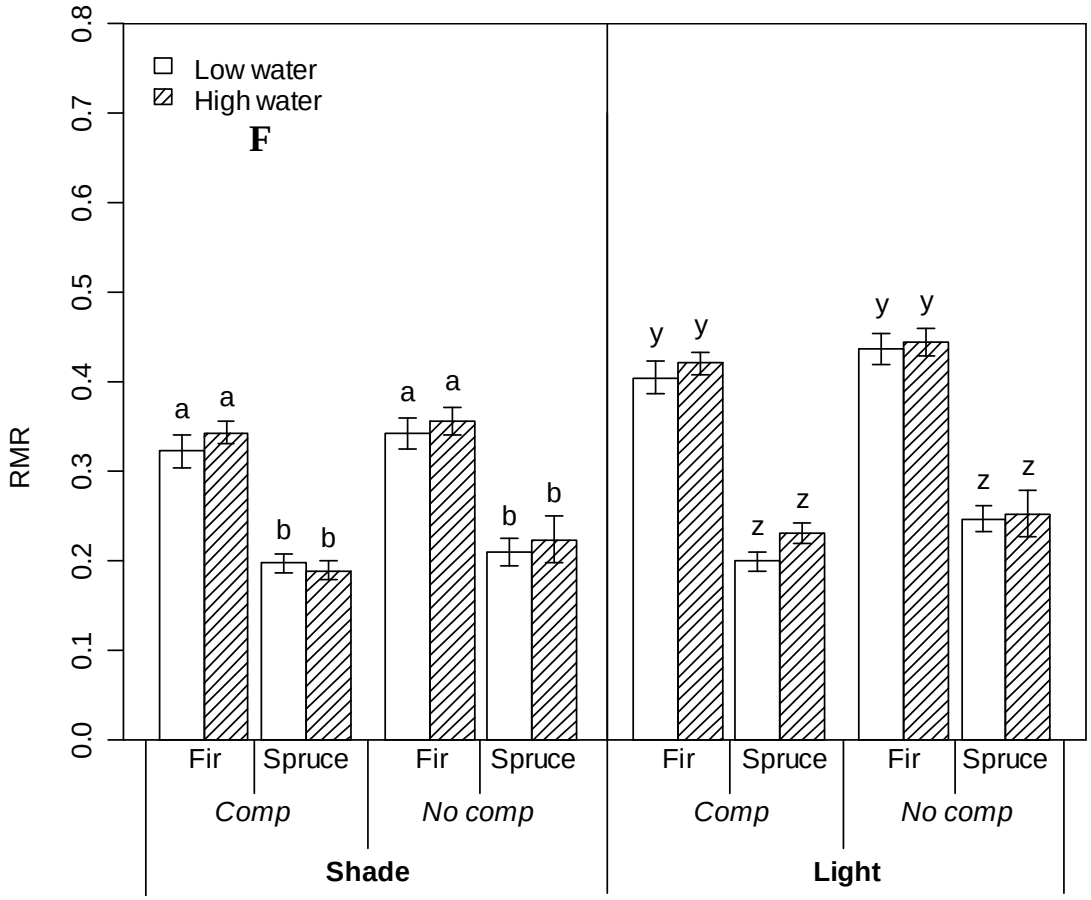

Figure 12F. Experiment 2 Harvest 2 means (± 1 SE) of RMR (root mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

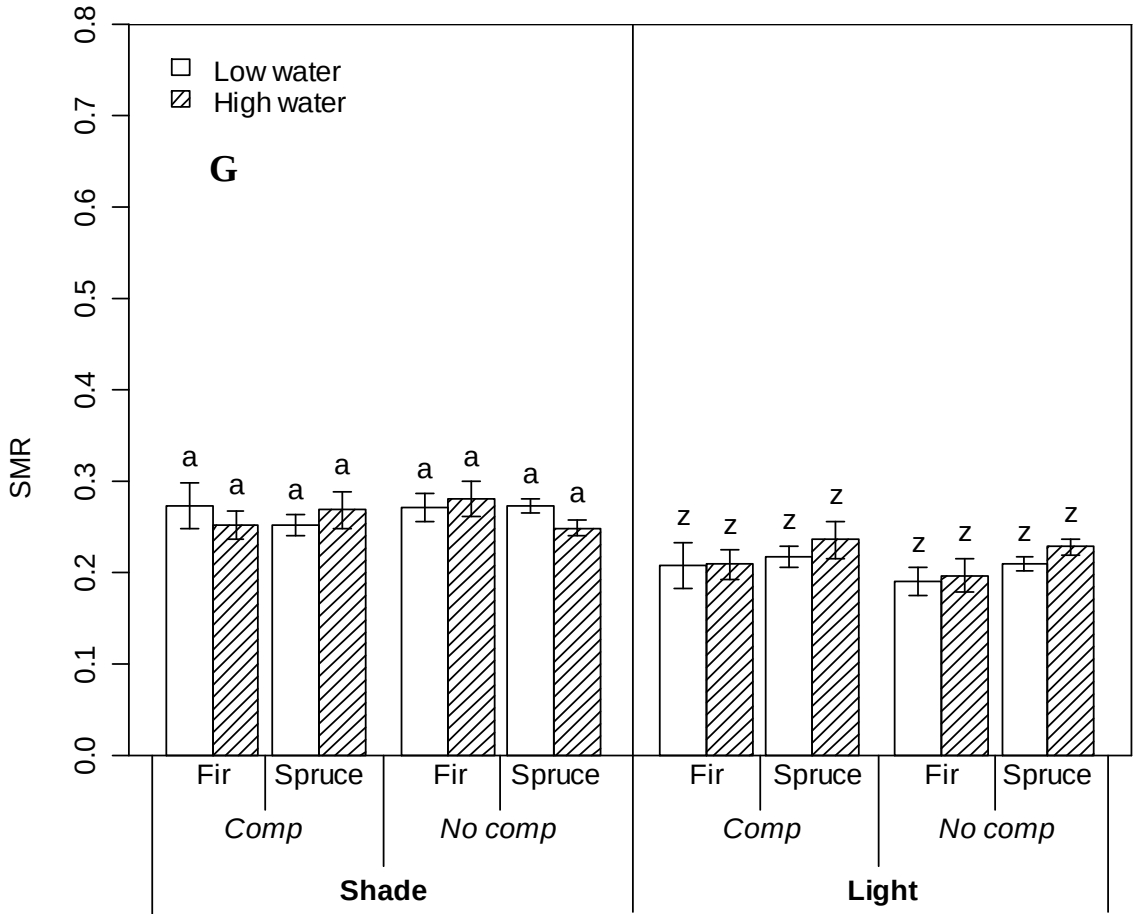

Figure 12G. Experiment 2 Harvest 2 means (± 1 SE) of SMR (stem mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

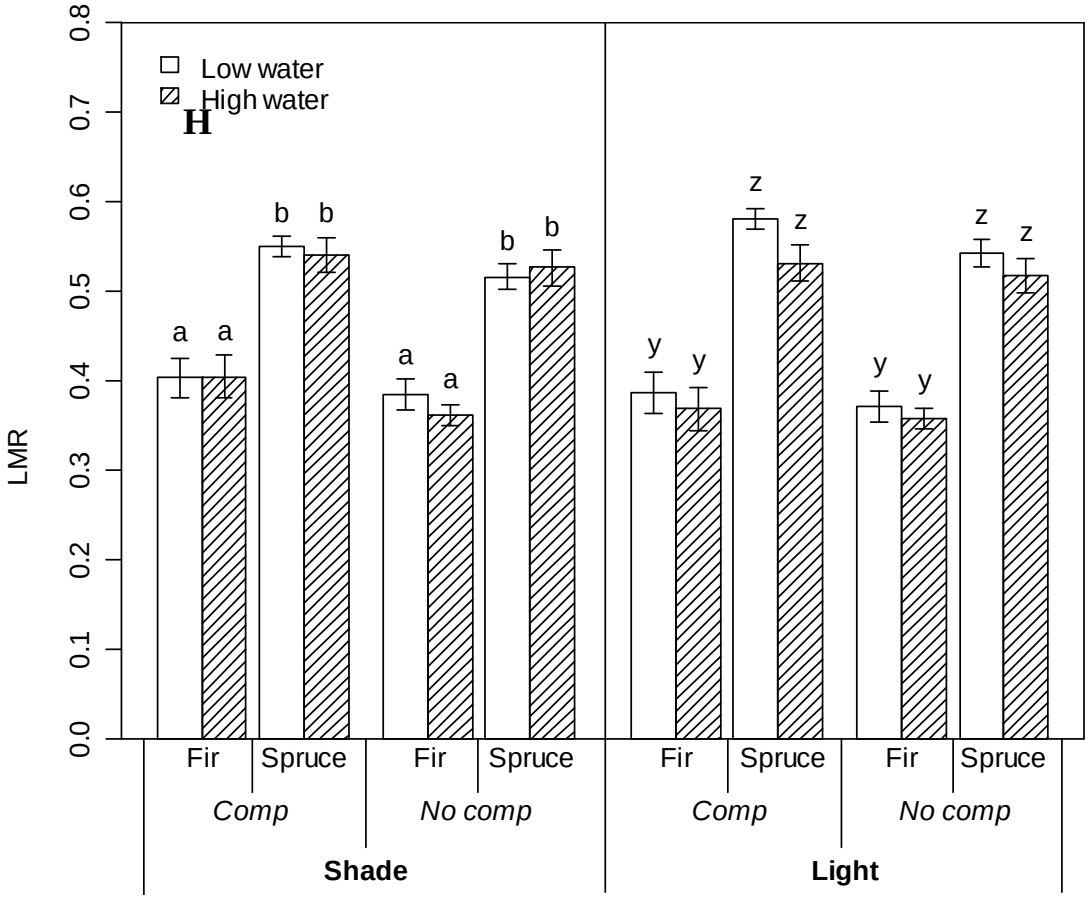

Figure 12H. Experiment 2 Harvest 2 means (± 1 SE) of LMR (leaf mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

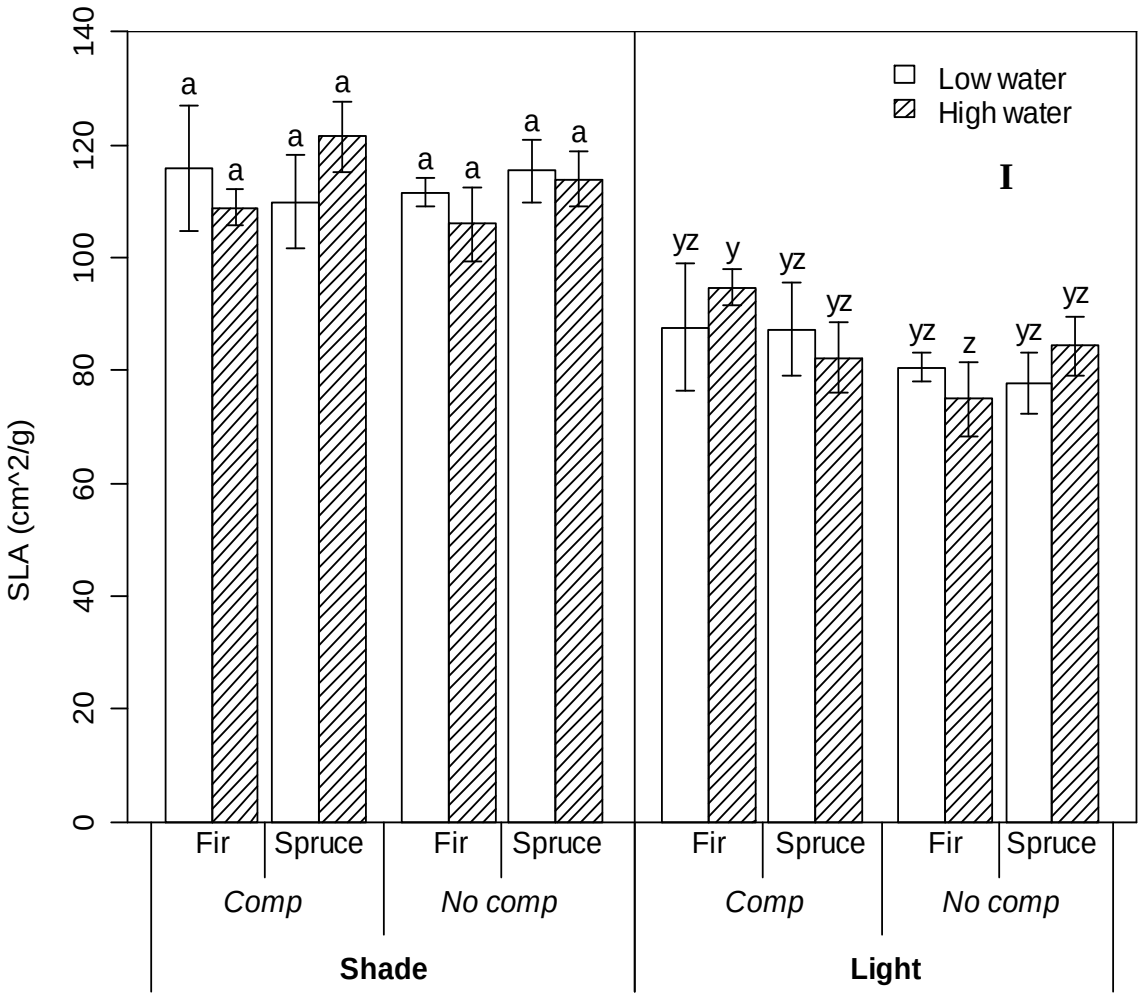

Figure 12I. Experiment 2 Harvest 2 means (± 1 SE) of SLA (specific leaf area—see table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. n=5 for all treatments.

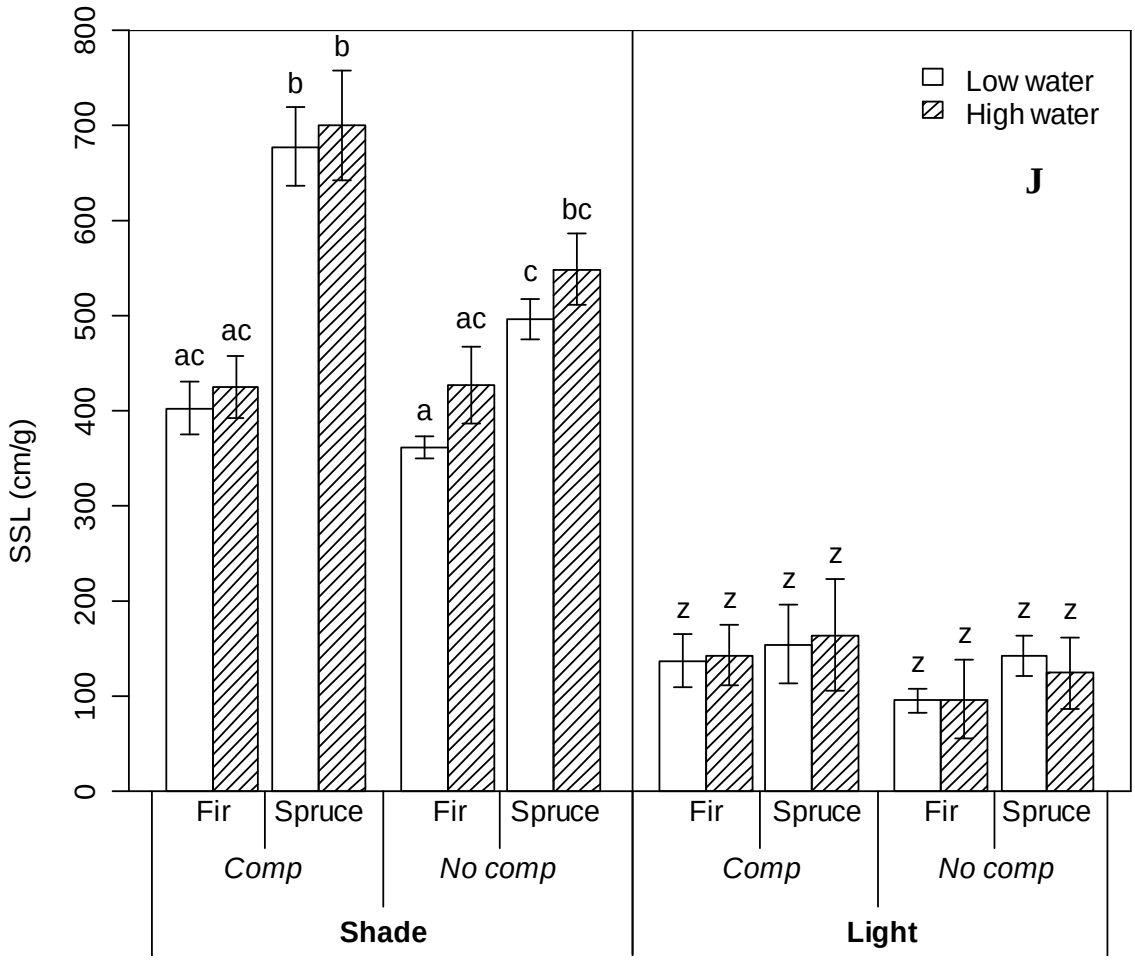

Figure 12J. Experiment 2 Harvest 2 means (± 1 SE) of SSL (specific stem length—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

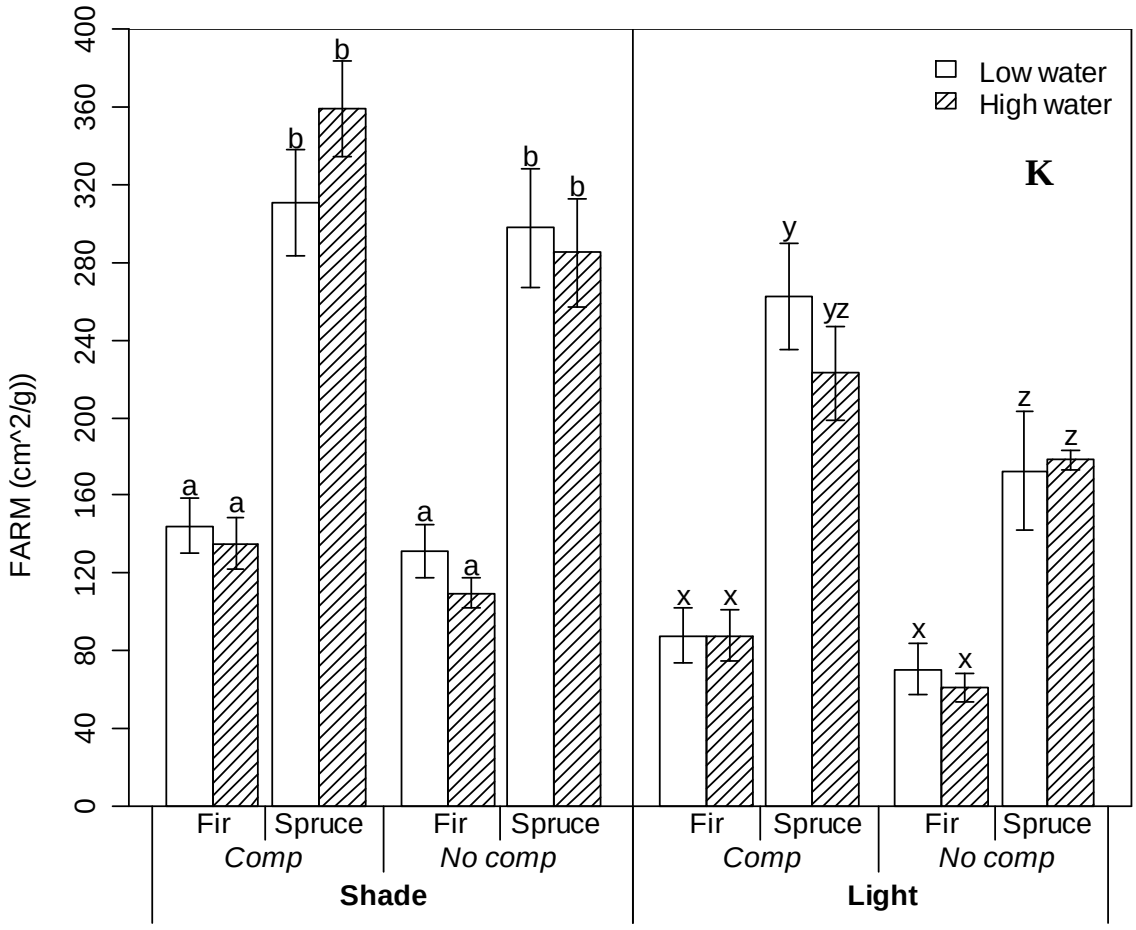

Figure 12K. Experiment 2 Harvest 2 means (± 1 SE) of FARM (foliar-area-to-root-mass-ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	10
			Low water	10				Low water	9
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	10				Low water	10

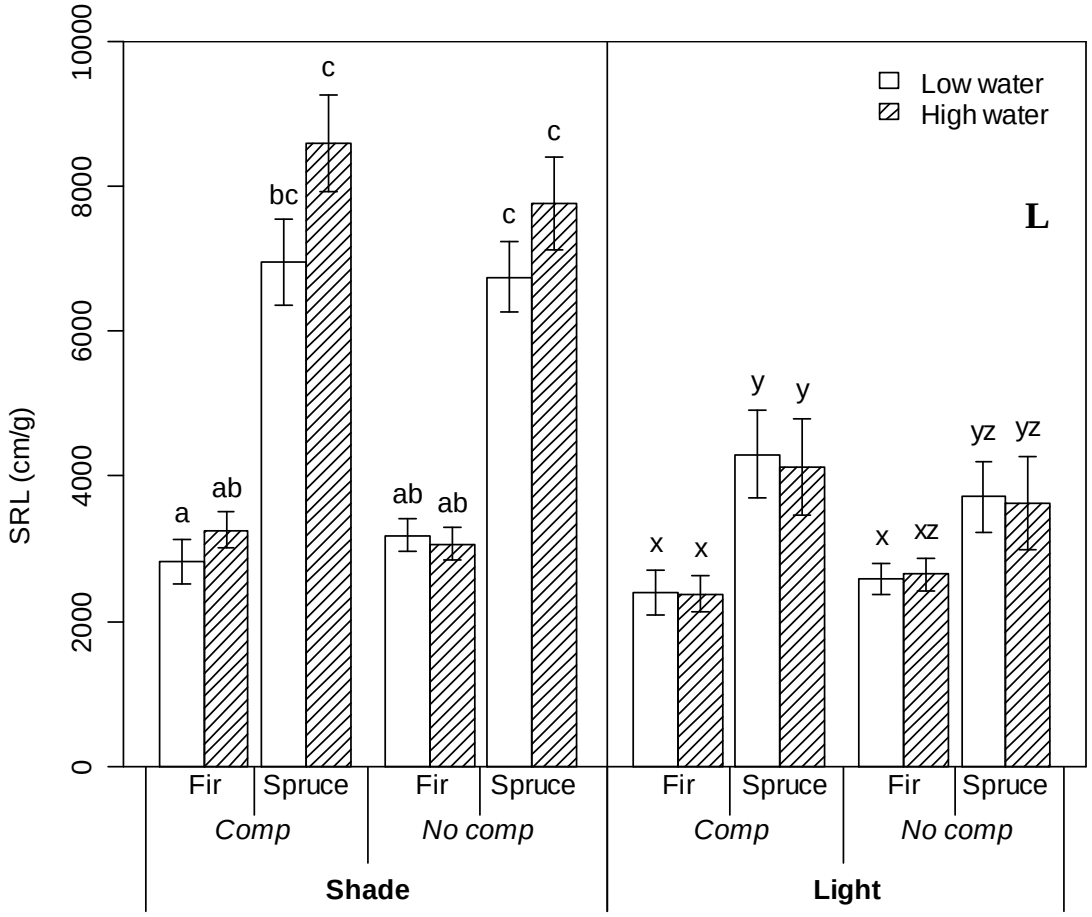

Figure 12L. Experiment 2 Harvest 2 means (± 1 SE) of SRL (specific root length—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	9	Shade	Balsam fir	Comp	High water	9
			Low water	10				Low water	5
		No comp	High water	8			No comp	High water	10
			Low water	9				Low water	10
	Red spruce	Comp	High water	9		Red spruce	Comp	High water	10
			Low water	10				Low water	7
		No comp	High water	10			No comp	High water	10
			Low water	9				Low water	9

both species responded to competition with consistent but non-significant increases in SSL (Fig. 12J).

In both light environments, there were no significant interspecific differences in SLA (Fig 12I). Both species responded to the higher light environment with lower SLAs (Fig. 12I). In the high-light environment, the SLAs of both species increased slightly in response to the competition treatment (Fig. 12I).

In terms of root morphology, red spruce had a higher SRL than balsam fir in all environments, though differences were not always significant in the high-light environment (Fig. 12L)

3.3.3.3. Effects of Light, Water, & Competition

3.3.3.3.1. Effects of Light

In terms of seedling size, $RLR_{dry\ mass}$ was higher than RLR_{height} for both species, indicating that seedling dry mass was more responsive than seedling height to light (Table 15). The heights and dry masses of both species responded positively to the higher-light environment (Table 15). Both overall and within each water-competition treatment combination, red spruce had a significantly higher RLR_{height} than balsam fir (Table 15), indicating that spruce height growth is more responsive than that of balsam fir to light. Overall, spruce had a significantly higher $RLR_{dry\ mass}$ than balsam fir (Table 15). Within each water-competition treatment combination, interspecific differences were not always significant, but spruce still had consistently higher $RLR_{dry\ masses}$ than balsam fir (Table 15).

			Height	Dry mass	R:S mass ratio	SRL
Comp	High water	Balsam fir	0.21 ± 0.06 a (10/10)	1.45 ± 0.12 a (10/10)	0.31 ± 0.09 a (10/10)	-0.16 ± 0.05 a (9/9)
		Red spruce	0.86 ± 0.14 b (9/10)	2.50 ± 0.27 b (9/10)	0.22 ± 0.14 a (9/10)	-0.50 ± 0.07 b (9/10)
	Low water	Balsam fir	0.21 ± 0.04 a (10/9)	1.52 ± 0.12 a (10/9)	0.35 ± 0.08 a (10/9)	-0.13 ± 0.06 a (10/5)
		Red spruce	0.83 ± 0.11 b (10/7)	2.43 ± 0.18 b (10/7)	0.02 ± 0.08 a (10/7)	-0.42 ± 0.06 b (10/7)
No comp	High water	Balsam fir	0.16 ± 0.06 a (10/10)	1.92 ± 0.15 ab (10/10)	0.36 ± 0.04 a (10/10)	-0.06 ± 0.06 a (8/10)
		Red spruce	0.87 ± 0.11 b (10/10)	2.58 ± 0.26 b (10/10)	0.17 ± 0.09 a (10/10)	-0.45 ± 0.08 b (10/10)
	Low water	Balsam fir	0.19 ± 0.05 a (10/10)	1.83 ± 0.06 ab (10/10)	0.40 ± 0.08 a (10/10)	-0.14 ± 0.03 a (9/10)
		Red spruce	0.71 ± 0.08 b (10/10)	2.26 ± 0.16 ab (10/10)	0.22 ± 0.05 a (10/10)	-0.33 ± 0.04 ab (9/9)
		Mean fir	0.19 ± 0.03 **x** (40/39)	1.68 ± 0.06 **x** (40/39)	0.35 ± 0.04 **x** (40/39)	-0.12 ± 0.02 **x** (36/34)
		Mean spruce	0.82 ± 0.05 **z** (39/37)	2.44 ± 0.11 **z** (39/37)	0.16 ± 0.04 **z** (39/37)	-0.43 ± 0.03 **z** (38/36)
		Overall mean	0.50 ± 0.03 (79/76)	2.06 ± 0.06 (79/76)	0.26 ± 0.04 (79/76)	-0.28 ± 0.03 (74/70)

Table 15. Experiment 2, Harvest 2 mean RLRs (relative light responses) (± 1 SE) of height, plant dry mass, R:S mass, and SRL. Acronyms are further described in Table 4. RLR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'light' seedlings (first number) and the number of 'shade' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example, a height mean with a primary root length mean.

The R:S mass ratios of both species were higher in the high-light environment (Table 15). Within each water-competition treatment combination, $RLR_{R:S\ mass}$ was higher for fir than for spruce, though the differences were non-significant (Table 15). Overall, mean fir $RLR_{R:S\ mass}$ was significantly higher than that of red spruce (Table 15).

The SRLs of both species were lower in the high-light environment (Table 15). Overall, mean spruce RLR_{SRL} was significantly more negative than mean fir RLR_{SRL} (Table 15).

3.3.3.3.2. Effects of Water

The RWRs of height, dry mass, R:S mass ratio, and SRL were generally <0.1 units from zero, with standard errors that were equal or greater in magnitude than the quantities themselves (Table 16). This indicates that the watering treatments had relatively minor effects on seedling growth and development at Harvest 2, by which time the watering treatments had only been in place for four weeks (Table 8).

			Height	Dry mass	R:S mass ratio	SRL
Light	Comp	Balsam fir	-0.05 ± 0.04 a (10/10)	-0.10 ± 0.09 a (10/10)	0.07 ± 0.07 a (10/10)	0.14 ± 0.05 a (9/10)
		Red spruce	0.02 ± 0.14 a (9/10)	-0.22 ± 0.24 a (9/10)	0.14 ± 0.14 a (9/10)	0.18 ± 0.06 a (9/10)
	No comp	Balsam fir	-0.01 ± 0.05 a (10/10)	-0.06 ± 0.14 a (10/10)	0.02 ± 0.05 a (10/10)	0.05 ± 0.05 a (8/9)
		Red spruce	0.10 ± 0.12 a (10/10)	0.23 ± 0.26 a (10/10)	0.02 ± 0.08 a (10/10)	-0.03 ± 0.07 a (10/9)
Shade	Comp	Balsam fir	-0.05 ± 0.06 a (10/9)	-0.02 ± 0.11 a (10/9)	0.11 ± 0.07 a (10/9)	0.17 ± 0.07 a (9/5)
		Red spruce	0.01 ± 0.09 a (10/7)	-0.09 ± 0.15 a (10/7)	-0.05 ± 0.08 a (10/7)	0.25 ± 0.04 a (10/7)
	No comp	Balsam fir	0.02 ± 0.03 a (10/10)	-0.15 ± 0.10 a (10/10)	0.06 ± 0.07 a (10/10)	-0.04 ± 0.05 a (10/10)
		Red spruce	-0.05 ± 0.10 a (10/10)	-0.08 ± 0.12 a (10/10)	0.06 ± 0.11 a (10/10)	0.10 ± 0.06 a (10/9)
		Mean fir	-0.02 ± 0.02 z (40/39)	-0.08 ± 0.06 z (40/39)	0.07 ± 0.03 z (40/39)	0.08 ± 0.03 z (36/34)
		Mean spruce	0.02 ± 0.06 z (39/37)	-0.04 ± 0.10 z (39/37)	0.04 ± 0.05 z (39/37)	0.12 ± 0.03 z (39/35)
		Overall mean	0.00 ± 0.03 (79/76)	-0.06 ± 0.07 (79/76)	0.05 ± 0.04 (79/76)	0.10 ± 0.03 (75/69)

Table 16. Experiment 2, Harvest 2 mean RWRs (relative water responses) (± 1 SE) of height, plant dry mass, R:S mass, and SRL. Acronyms are described in Table 4. RWR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'wet' seedlings (first number) and the number of 'dry' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example a height mean with a primary root length mean.

3.3.3.3.3. Effects of Competition

The RCRs of height were very small and did not appear strongly affected by competition treatment for either species (Table 17).

The overall RCRs of dry mass were negative for both species (Table 17), indicating that the dry masses of both species were generally lower in the competition treatment than in the no-competition treatment ($p<0.001$; Table 13). Interspecific differences were not significant overall or within any particular light-water treatment combination (Table 17). There were some non-significant trends, however. In the high-light environment, there were no significant species:competition interactions (Table 14A). But in the shade environment, there were significant species:competition interactions ($p<0.05$; Table 14B), and fir dry mass appeared less responsive than red spruce dry mass to competition treatment. But again, none of these interspecific differences were significant within any particular watering treatment in the shade environment (Table 17).

The RCRs of R:S mass ratio were small but consistently negative for both species in all light-water treatment combinations (Table 17), indicating that both species responded to competition by lowering their R:S mass ratios (i.e. lower allocation to roots). There were no large or consistent interspecific differences in $RCR_{R:S\ mass}$ overall or in any of the light-water treatment combinations (Table 17).

The RCRs of SRL were small and did not appear strongly affected by competition treatment for either species (Table 17).

			Height	Dry mass	R:S mass ratio	SRL
Light	High water	Balsam fir	-0.03 ± 0.06 a (10/10)	-0.49 ± 0.15 a (10/10)	-0.10 ± 0.09 a (10/10)	-0.08 ± 0.06 a (9/8)
		Red spruce	-0.08 ± 0.14 a (9/10)	-0.46 ± 0.25 a (9/10)	-0.16 ± 0.14 a (9/10)	0.04 ± 0.06 a (9/10)
	Low water	Balsam fir	0.01 ± 0.06 a (10/10)	-0.44 ± 0.12 a (10/10)	-0.14 ± 0.08 a (10/10)	-0.18 ± 0.05 a (10/9)
		Red spruce	0.00 ± 0.09 a (10/10)	-0.13 ± 0.17 a (10/10)	-0.28 ± 0.07 a (10/10)	-0.20 ± 0.06 a (10/9)
Shade	High water	Balsam fir	-0.07 ± 0.05 a (10/10)	0.03 ± 0.13 a (10/10)	-0.06 ± 0.06 a (10/10)	0.02 ± 0.05 a (9/10)
		Red spruce	-0.09 ± 0.09 a (10/10)	-0.30 ± 0.14 a (10/10)	-0.20 ± 0.08 a (10/10)	0.08 ± 0.04 a (10/10)
	Low water	Balsam fir	0.01 ± 0.05 a (9/10)	-0.10 ± 0.16 a (9/10)	-0.10 ± 0.12 a (9/10)	-0.18 ± 0.11 a (5/10)
		Red spruce	-0.12 ± 0.09 a (7/10)	-0.33 ± 0.13 a (7/10)	-0.08 ± 0.09 a (7/10)	-0.08 ± 0.07 a (7/9)
		Mean fir	-0.02 ± 0.03 z (39/40)	-0.25 ± 0.07 z (39/40)	-0.10 ± 0.04 z (39/40)	-0.11 ± 0.03 z (33/37)
		Mean spruce	-0.07 ± 0.05 z (36/40)	-0.30 ± 0.09 z (36/40)	-0.18 ± 0.05 z (36/40)	-0.04 ± 0.03 z (36/38)
		Overall mean	-0.05 ± 0.03 (75/80)	-0.28 ± 0.08 (75/80)	-0.14 ± 0.05 (75/80)	-0.07 ± 0.04 (69/75)

Table 17. Experiment 2, Harvest 2 mean RCRs (relative competition responses) (± 1 SE) of height, plant dry mass, R:S mass ratio, and SRL. Acronym details are provided in Table 4. RCR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'competition' seedlings (first number) and the number of 'no competition' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example, a height mean with a primary root length mean.

3.3.4. Harvest 3

3.3.4.1. Introduction

P-values for the analyses of all Harvest 3 data can be found in Table 18 for the overall models, Table 19A for the high-light-environment models, and Table 19B for the shade-environment models. As shown in previous harvests, both across light environments and within each light environment, there were significant species differences in virtually every size, allocation, and morphological trait measured (Table 18; 19A-B). There were also significant species:light interactions for seedling mass and various allocation traits, indicating that the size and allocation of spruce and fir responded differently to different light environments (Table 18). And in the high-light environment, there were significant species:competition interactions for dry mass, root allocation (RMR and R:S mass), and SRL (Table 19A), indicating that those traits of the two species may respond differently to competition. These differences will be presented in detail in the following sections.

	Height	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	Root tips/root length	Root tips/root mass	SRL	SSL	RGR	Stem diameter
block	0.559	0.498	0.350	**0.032**	0.113	0.295	**0.014**	**0.041**	0.508	0.370	0.246	0.113	-	0.724
light	**0.006**	**0.000**	**0.007**	**0.006**	0.070	**0.016**	**0.008**	**0.007**	0.895	**0.015**	**0.017**	**0.000**	**0.000**	**0.001**
water	0.967	0.744	0.251	0.188	**0.048**	**0.020**	0.182	0.191	0.919	0.060	**0.030**	0.673	0.434	0.368
comp	**0.003**	**0.000**	**0.036**	0.993	0.872	0.927	0.291	0.865	0.134	**0.002**	**0.002**	**0.000**	**0.000**	**0.000**
sp	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	0.572	**0.000**	**0.000**
light:water	0.692	0.531	0.183	0.533	0.619	0.531	0.601	0.723	0.302	0.795	0.355	0.923	0.667	0.396
comp:sp	**0.050**	**0.007**	0.578	0.248	0.532	0.587	0.668	0.286	0.799	**0.042**	**0.002**	**0.033**	**0.014**	0.612
light:comp	0.613	**0.015**	0.116	0.819	0.295	0.602	0.359	0.983	**0.006**	**0.039**	0.369	0.304	0.818	0.340
light:sp	0.971	**0.005**	**0.030**	**0.005**	**0.000**	**0.000**	**0.000**	**0.002**	0.101	**0.006**	**0.008**	**0.044**	0.243	0.140
water:comp	0.129	0.245	0.113	0.552	**0.025**	0.284	0.843	0.605	0.749	0.866	0.845	**0.049**	**0.019**	0.312
water:sp	0.819	0.755	0.525	0.424	0.698	0.338	0.395	0.681	0.646	0.905	0.738	0.256	0.196	0.911
water:comp:sp	0.117	0.397	**0.022**	0.173	0.718	0.155	**0.001**	0.243	0.937	0.988	0.810	0.307	0.339	0.311
light:water:comp	0.925	0.501	0.060	0.607	0.567	0.397	0.504	0.597	0.259	0.630	0.721	0.057	0.697	0.903
light:water:sp	0.292	0.364	0.832	0.051	0.445	0.255	0.424	0.065	0.302	0.858	0.694	0.196	0.113	0.341
light:water:comp:sp	0.424	0.216	0.429	0.069	0.819	0.092	0.071	0.084	0.339	0.648	0.769	0.120	0.082	0.118

Table 18. P-values for Experiment 2 Harvest 3 ANOVAs height, dry mass, SLA, RMR, SMR, LMR, FARM, R:S mass, root tips per root length, root tips per root mass, SRL, and SSL. Acronyms are described in Table 4. Significance was assessed at $\alpha=0.05$. Model details are provided in the appendix.

A - Light	Height	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	Root tips/root length	Root tips/root mass	SRL	SSL	RGR	Stem diameter
block	0.842	0.860	0.471	0.604	0.894	0.849	0.583	0.541	0.885	0.803	0.373	0.956	-	0.980
water	0.735	0.275	**0.003**	0.186	0.259	**0.001**	**0.008**	0.209	0.965	0.492	0.171	0.457	0.755	0.120
comp	**0.038**	**0.000**	**0.001**	0.590	0.365	0.869	0.133	0.836	**0.002**	**0.001**	**0.005**	**0.000**	**0.000**	**0.002**
sp	**0.000**	**0.000**	**0.008**	**0.000**	0.638	**0.000**	**0.000**	**0.000**	**0.000**	**0.000**	**0.043**	**0.020**	**0.000**	**0.000**
comp:sp	0.079	**0.050**	0.728	**0.029**	0.636	0.147	0.151	**0.046**	0.283	0.072	**0.021**	0.317	0.096	0.148
water:comp	0.209	0.629	0.807	0.762	0.063	0.300	0.404	0.843	0.316	0.687	0.736	0.700	0.941	0.362
water:sp	0.443	0.807	0.691	0.604	0.422	0.891	0.802	0.467	0.424	0.904	0.694	0.795	0.294	0.652
water:comp:sp	0.102	0.123	0.207	0.176	0.532	0.128	**0.005**	0.282	0.875	0.993	0.859	0.470	**0.044**	0.174

B - Shade	Height	Dry mass	SLA	RMR	SMR	LMR	FARM	R:S mass	Root tips/root length	Root tips/root mass	SRL	SSL	RGR	Stem diameter
block	**0.011**	0.414	0.132	**0.023**	**0.009**	0.273	**0.033**	**0.033**	0.422	**0.010**	**0.003**	0.529	-	0.146
water	0.834	0.905	0.666	0.499	0.173	0.217	0.793	0.539	0.916	**0.043**	**0.001**	0.815	0.315	0.855
comp	**0.037**	**0.046**	0.653	0.506	0.367	0.982	0.911	0.555	0.135	0.993	0.208	0.204	**0.004**	**0.021**
sp	**0.000**	**0.006**	**0.000**	**0.000**	**0.000**	0.510	0.884	**0.000**	**0.000**	**0.000**	**0.000**	0.339	**0.000**	**0.010**
comp:sp	0.516	0.072	0.589	0.147	0.678	0.089	0.060	0.111	0.259	0.451	**0.050**	0.064	0.055	0.272
water:comp	0.175	0.086	0.056	0.626	0.186	0.608	0.371	0.592	0.639	0.852	0.805	**0.036**	**0.033**	0.423
water:sp	0.748	0.204	0.536	0.060	0.729	0.114	0.548	0.093	0.611	0.985	0.804	0.157	0.258	0.442
water:comp:sp	0.502	0.444	0.066	0.712	0.778	0.881	0.118	0.690	0.662	0.990	0.684	0.128	0.680	0.945

Table 19A-B. P-values for Experiment 2, Harvest 3 ANOVAs in the high-light environment (A) and the shade environment (B) for height, dry mass, SLA, RMR, SMR, LMR, FARM, R:S mass, root tips per root length, root tips per root mass, SRL, and SSL. Acronyms are described in Table 4. Significance was assessed at α=0.05. Model details are provided in the appendix.

3.3.4.2. Species Trait Comparisons

Spruce was significantly taller than balsam fir in all treatments and light environments, with high-water/no-competition spruce being the tallest of any species-treatment (Fig. 13A). The basal stem diameters of spruce and fir were similar in the low-light environment, and spruce had consistently higher stem diameters than fir in the high-light environment, though differences were not always significant (Fig. 13B). High-water/no-competition spruce had the greatest stem diameter (Fig. 13B).

There were no consistent or significant differences between the two species in terms of SSL in any treatment in either light environment (Fig. 13C).

In the low-light environment, spruce had significantly greater RGRs than fir in all treatments (except no-competition fir, whose RGR was non-significantly lower than that of competition-spruce) (Fig. 13D). This no doubt reflects the fact that fir seedlings were more massive than spruce seedlings at Harvest 1 in the low-light environment (Fig 11D), a difference that red spruce closed by Harvest 2 (Fig. 12B) by achieving a higher growth rate (not shown). In the high-light environment, spruce RGRs were consistently higher than those of balsam fir, though only the spruces in the no-competition treatment had significantly higher RGRs than the firs (Fig. 13D). High-water/no-competition spruce had the highest RGRs, which were significantly higher than those of fir in all treatments and of spruce in the no-competition treatment (Fig. 13D).

In the low-light environment, the dry masses of spruce and fir were similar, though spruce had slightly greater dry masses than fir in the no-competition treatment (Fig. 13E). In the high-light environment, spruce was consistently more massive than fir (Fig. 13E). Differences were particularly large in the no-competition treatment in which

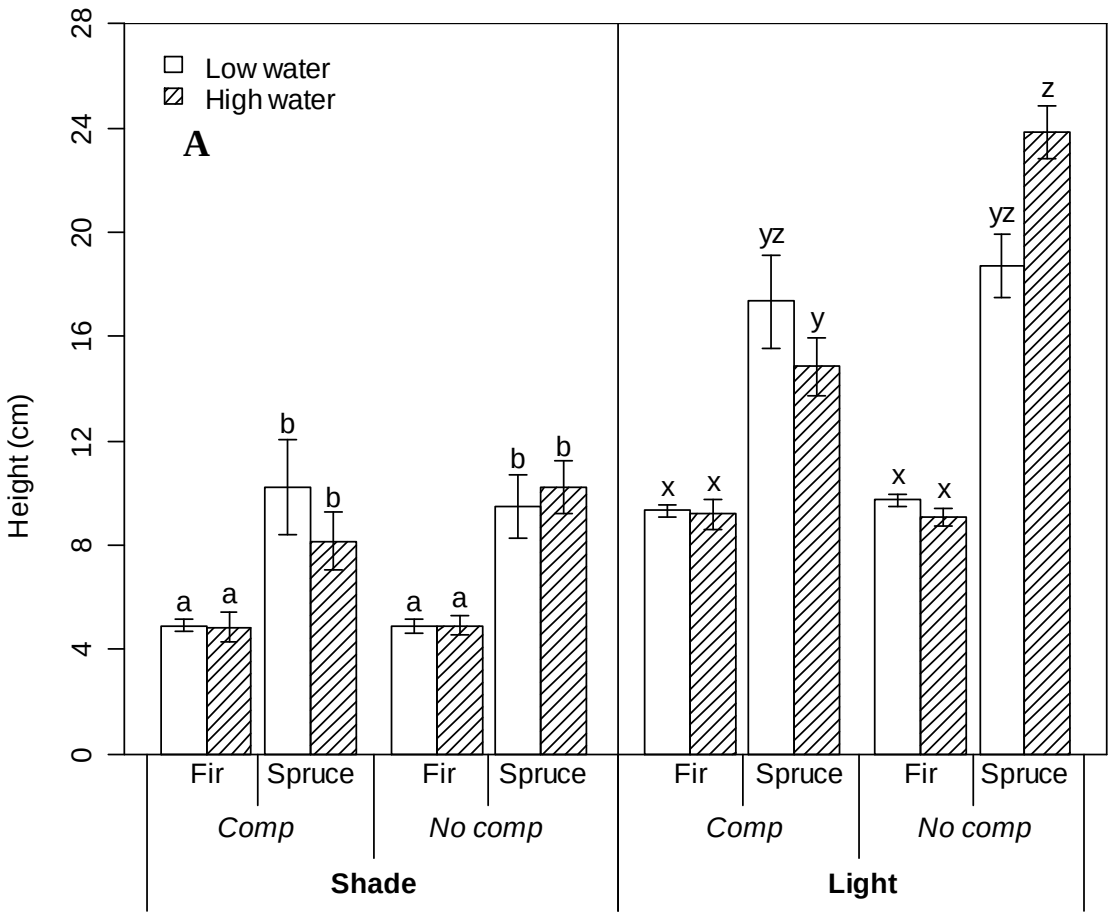

Figure 13A. Experiment 2 Harvest 3 means (± 1 SE) of height. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

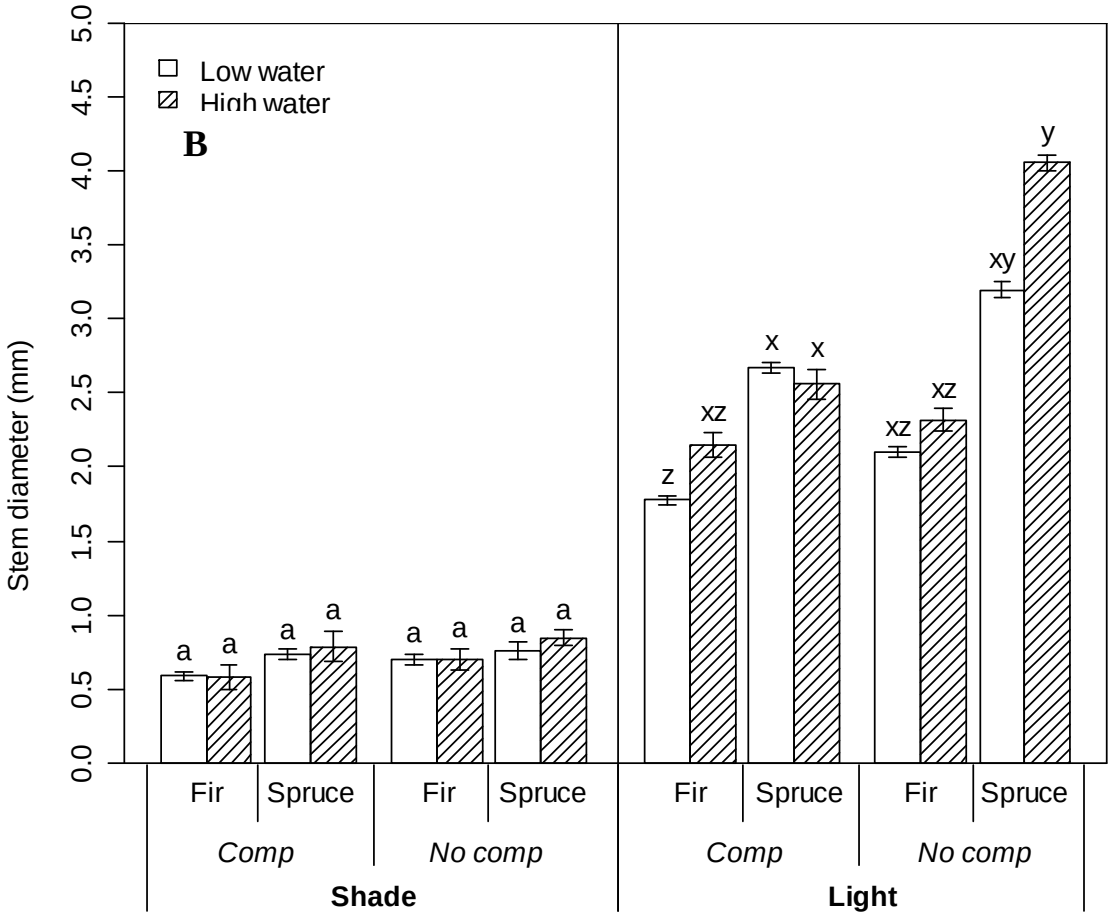

Figure 13B. Experiment 2 Harvest 3 means (± 1 SE) of basal stem diameter. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

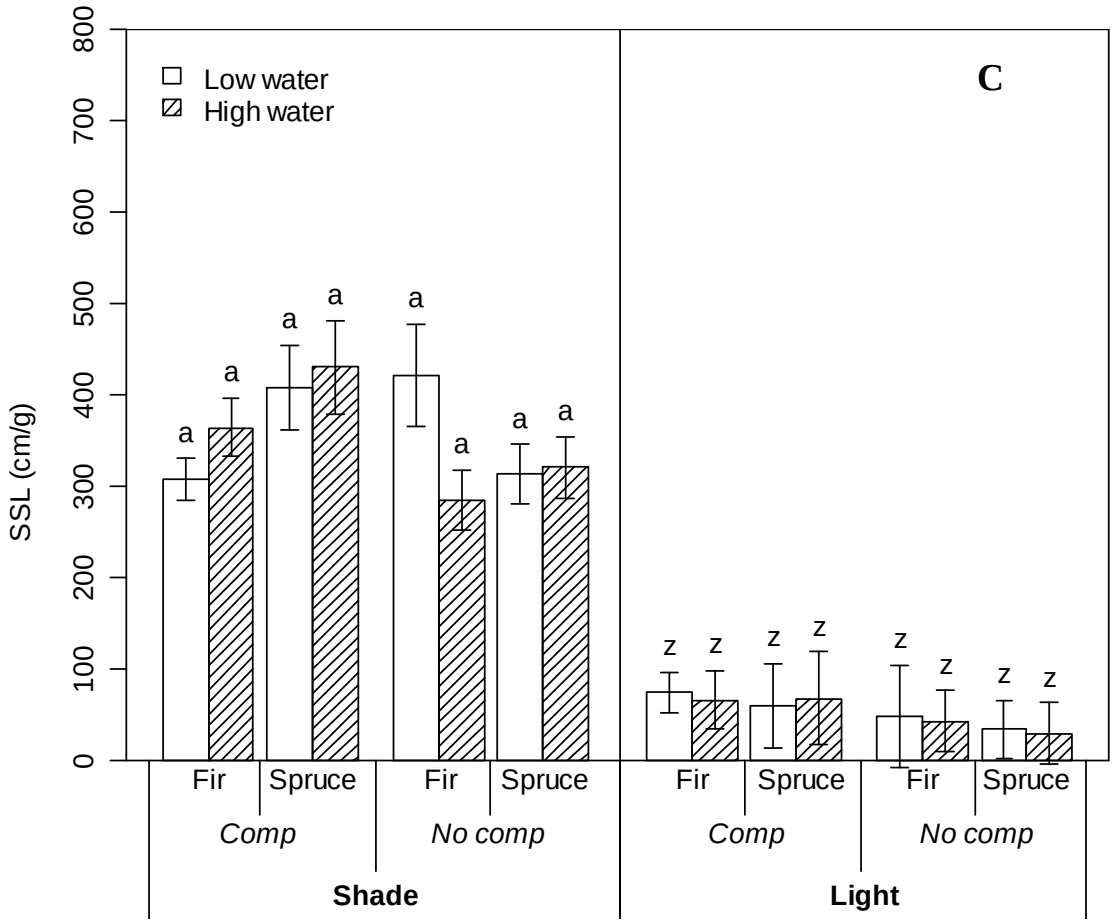

Figure 13C. Experiment 2 Harvest 3 means (± 1 SE) of SSL (specific stem length—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

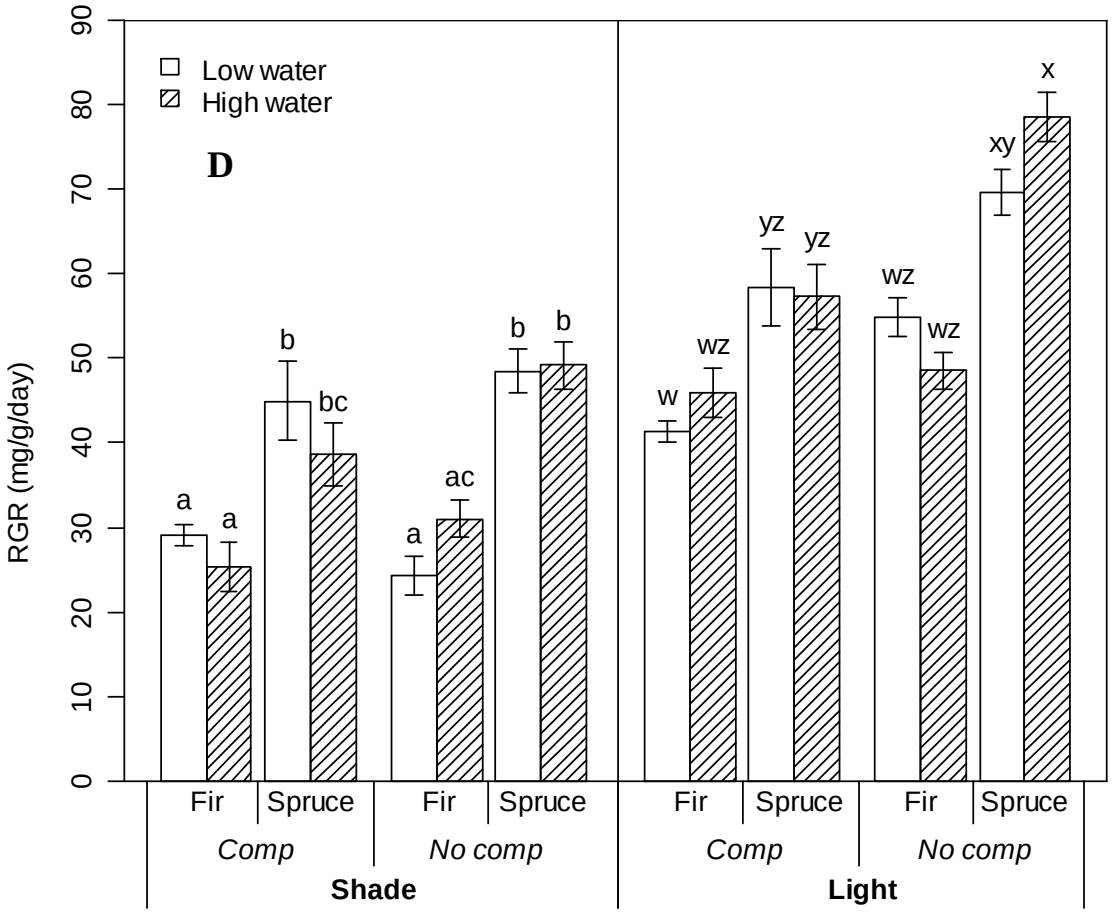

Figure 13D. Experiment 2 means (± 1 SE) of Harvest 1 to Harvest 3 RGR (relative growth rate—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates per treatment, where the first number indicates the number of Harvest 3 seedlings and the second number indicates the number of Harvest 1 seedlings on which calculations were based:

Light	Balsam fir	Comp	High water	(10/40)	Shade	Balsam fir	Comp	High water	(9/38)
			Low water	(8/40)				Low water	(9/38)
		No comp	High water	(10/40)			No comp	High water	(9/38)
			Low water	(10/40)				Low water	(8/38)
	Red spruce	Comp	High water	(10/40)		Red spruce	Comp	High water	(7/40)
			Low water	(8/40)				Low water	(3/40)
		No comp	High water	(10/40)			No comp	High water	(9/40)
			Low water	(10/40)				Low water	(6/40)

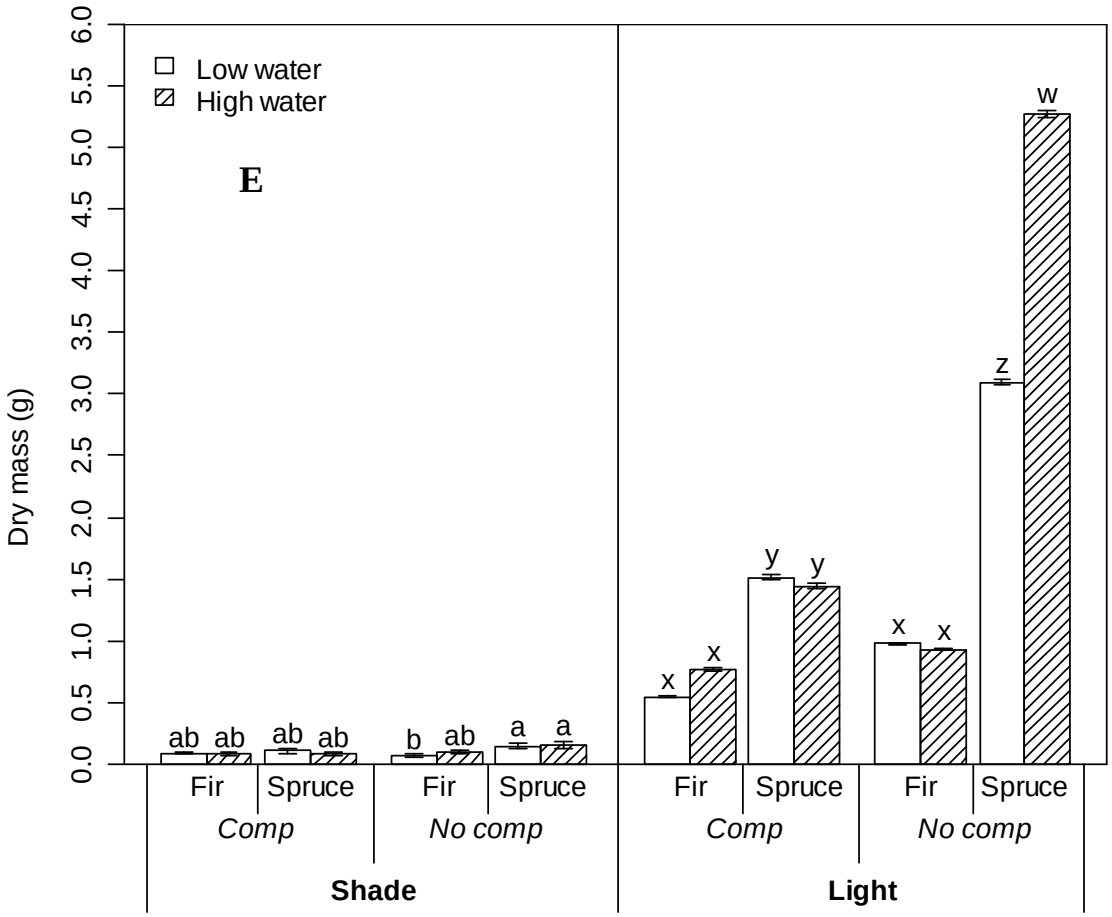

Figure 13E. Experiment 2 Harvest 3 means (± 1 SE) of plant dry mass. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

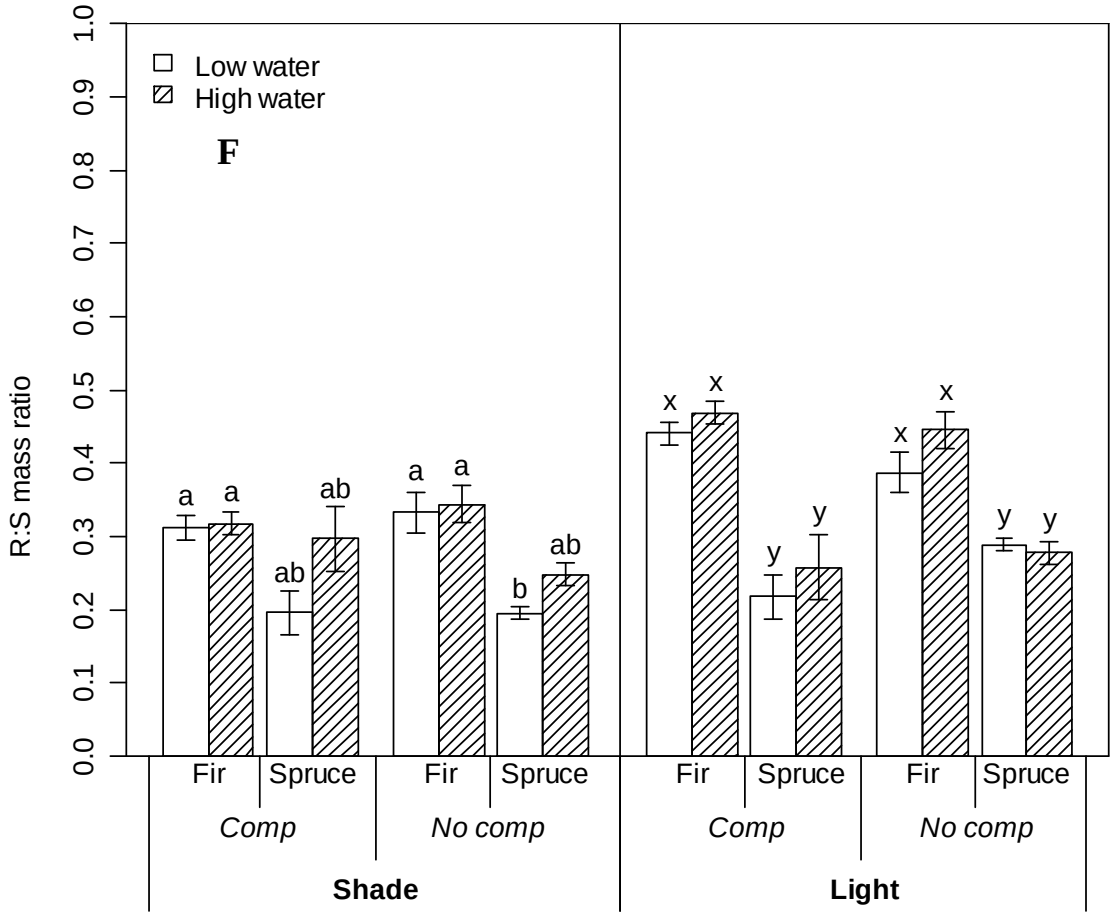

Figure 13F. Experiment 2 Harvest 3 means (± 1 SE) of R:S mass ratio (see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

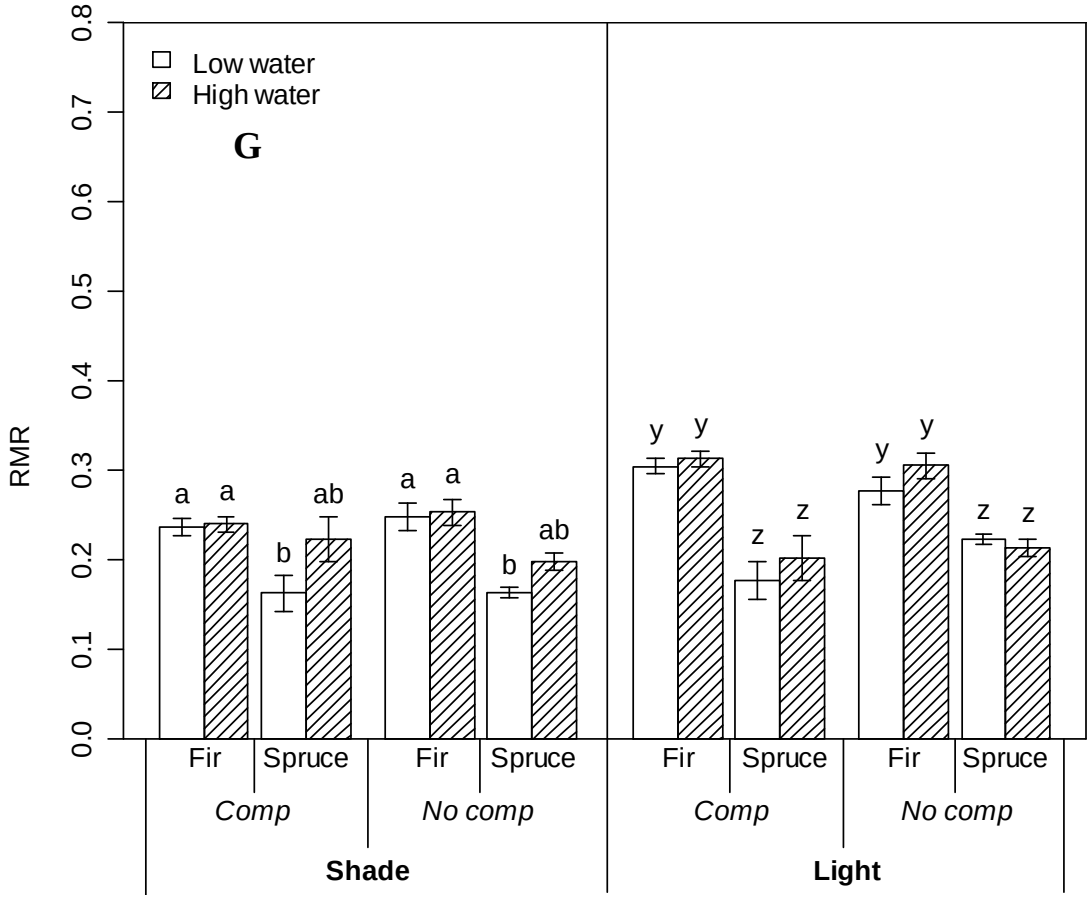

Figure 13G. Experiment 2 Harvest 3 means (± 1 SE) of RMR (root mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

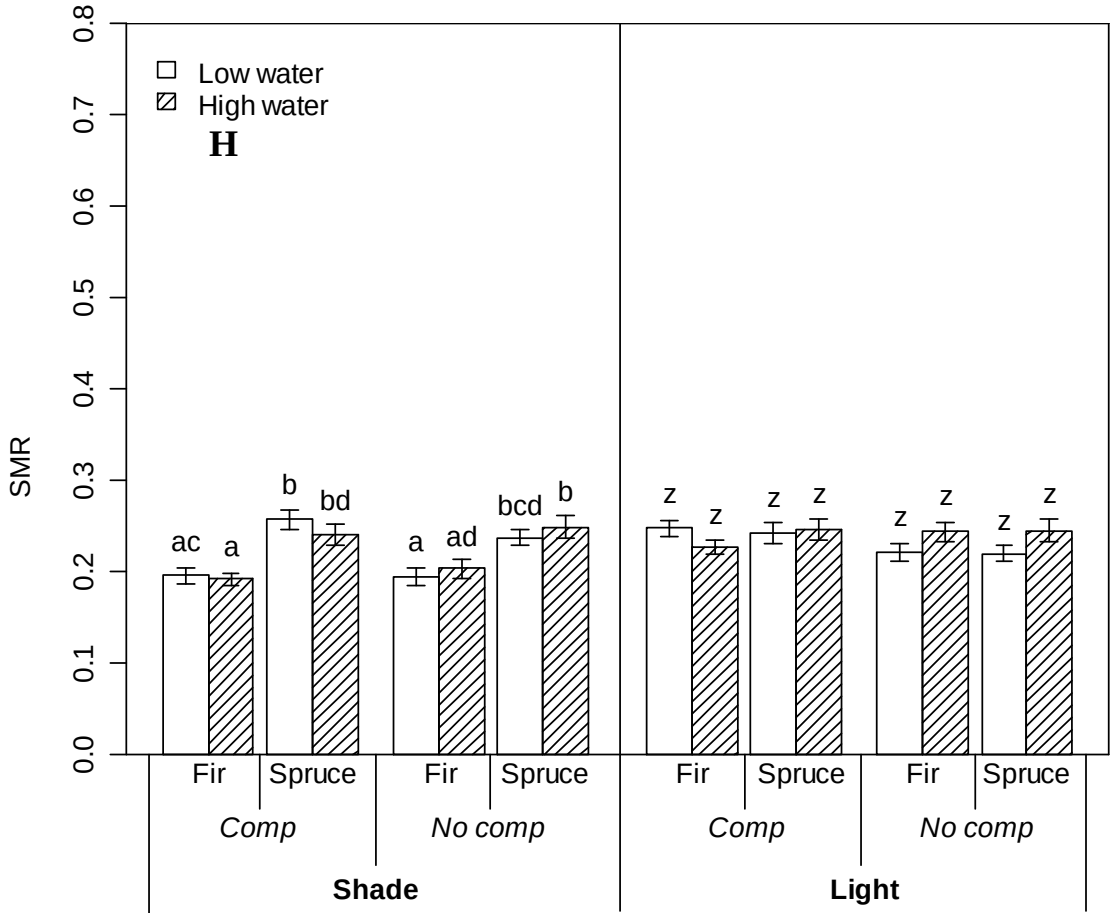

Figure 13H. Experiment 2 Harvest 3 means (± 1 SE) of SMR (stem mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

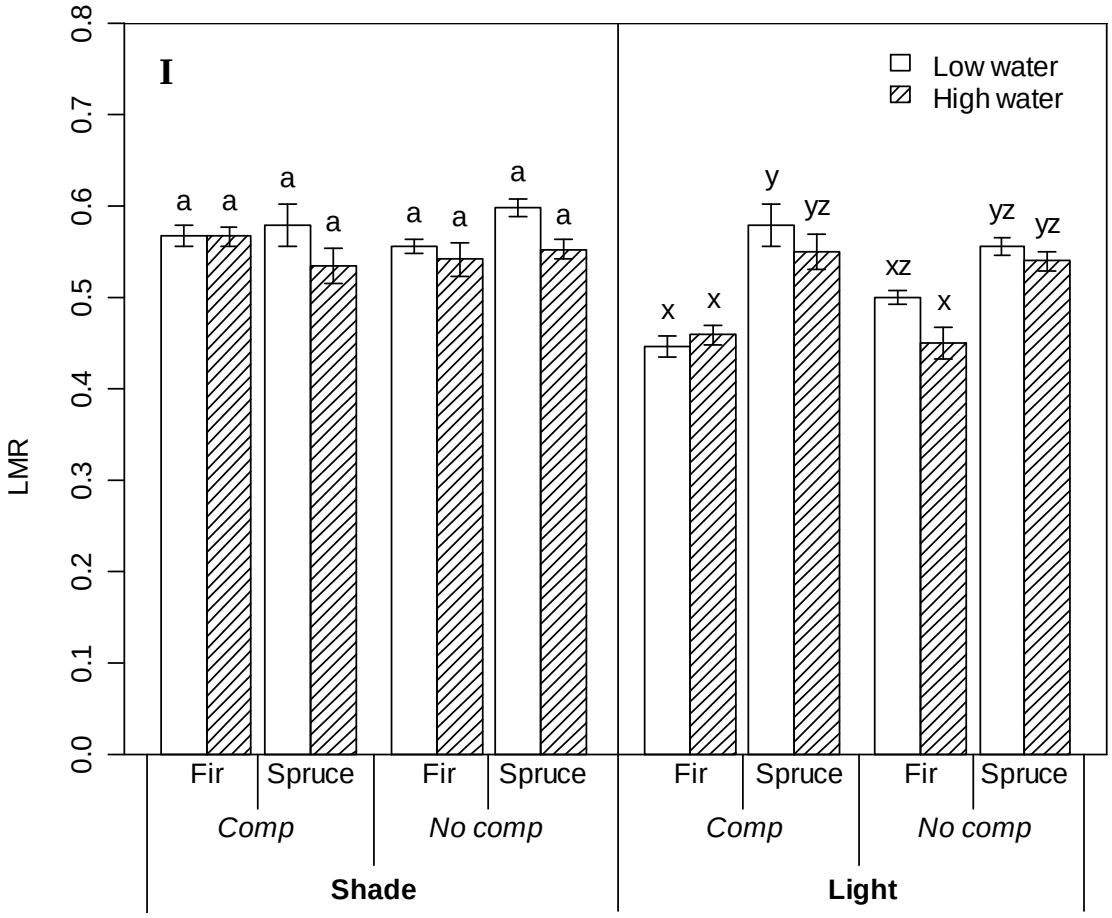

Figure 13I. Experiment 2 Harvest 3 means (± 1 SE) of LMR (leaf mass ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

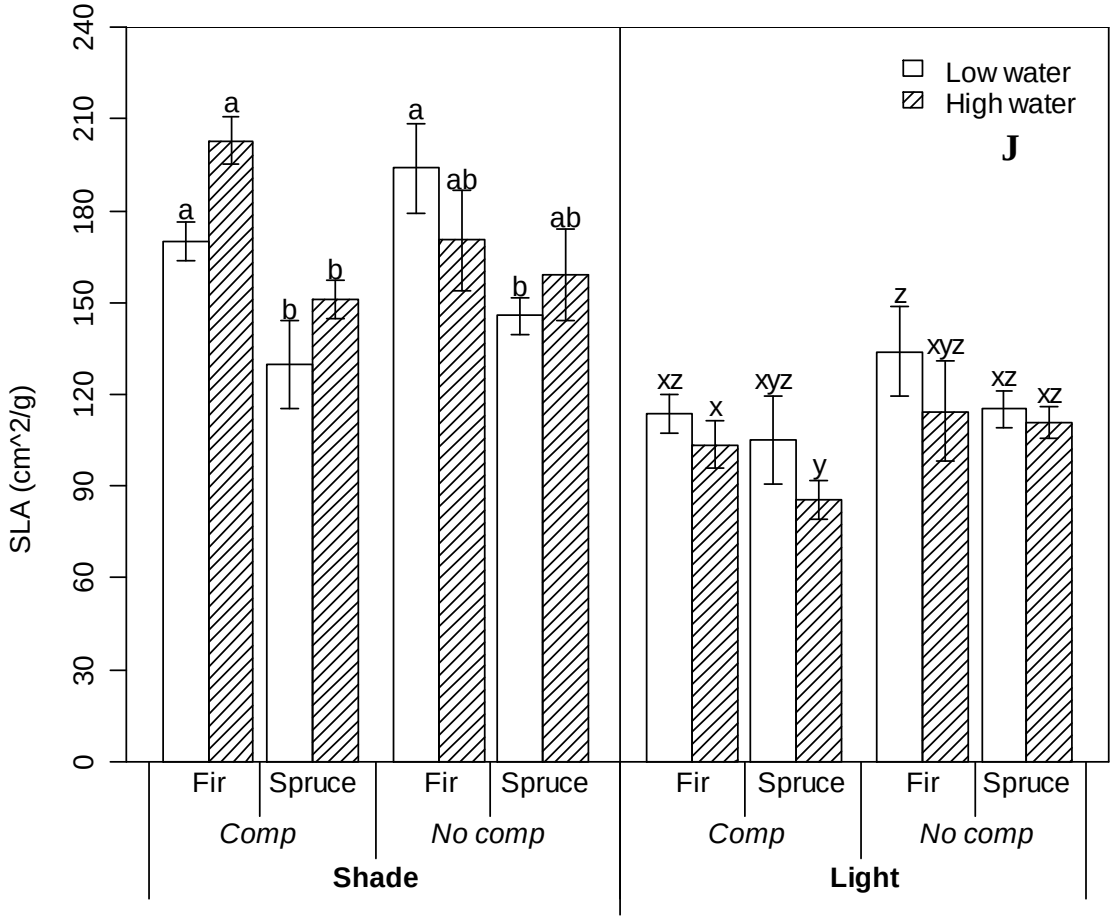

Figure 13J. Experiment 2 Harvest 3 means (± 1 SE) of SLA (specific leaf area—see table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. n=5 for all treatments. n=5 for all treatments except spruce-shade-competition-low-water, where n=3.

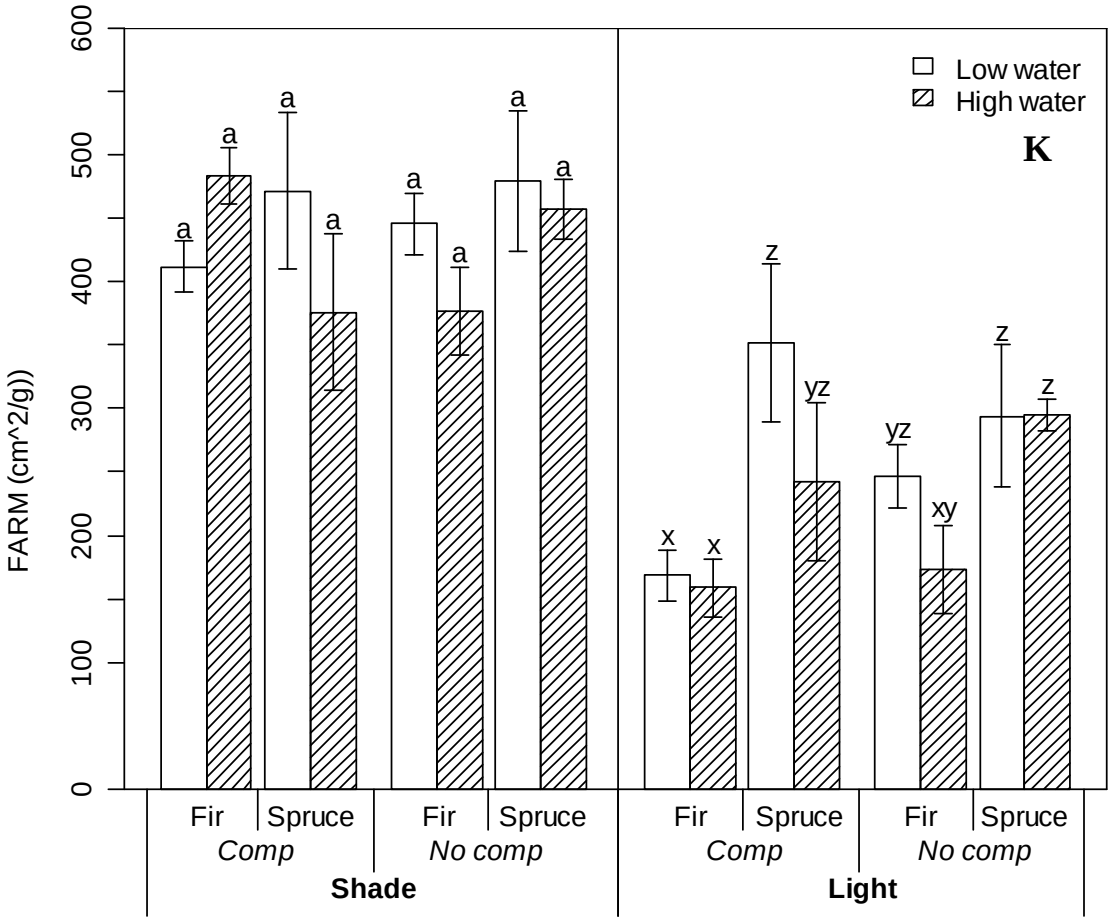

Figure 13K. Experiment 2 Harvest 3 means (± 1 SE) of FARM (foliar-area-to-root-mass-ratio—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

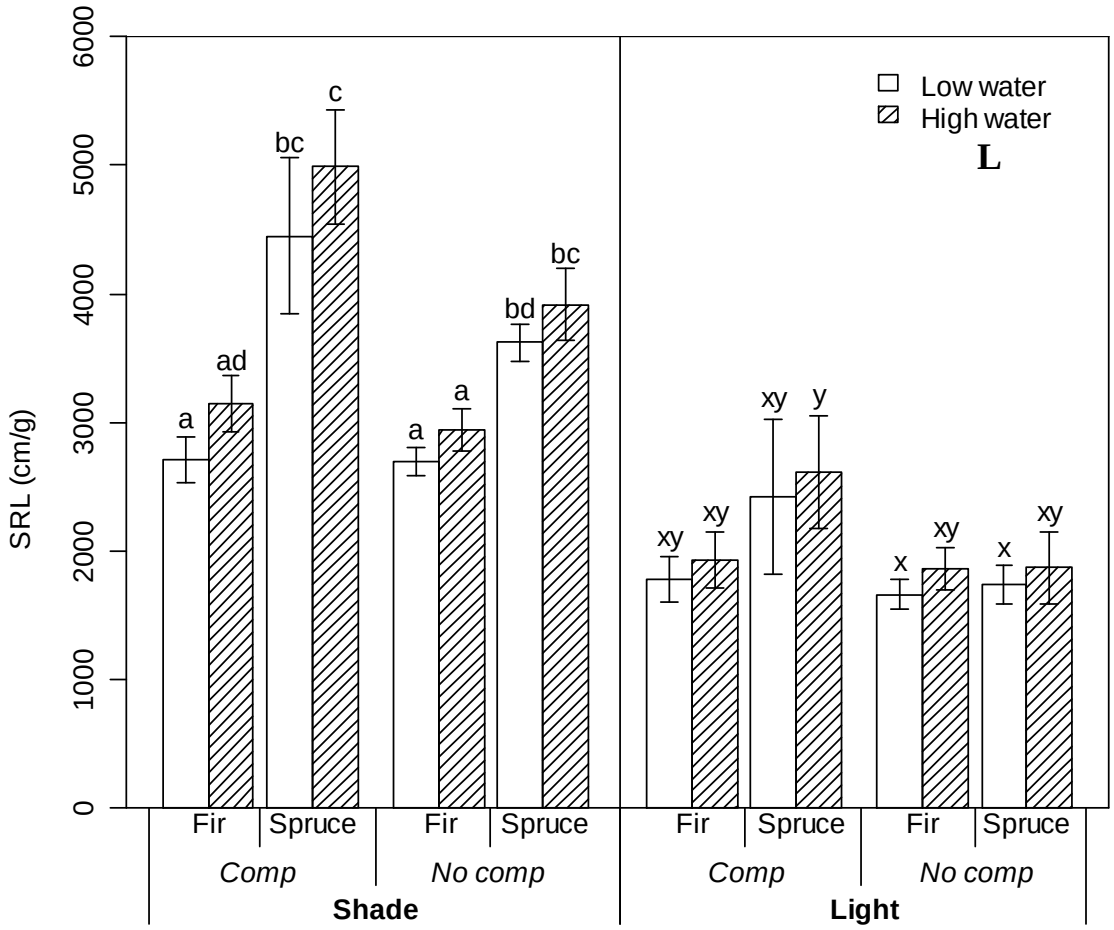

Figure 13L. Experiment 2 Harvest 3 means (± 1 SE) of SRL (specific root length—see Table 4). Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

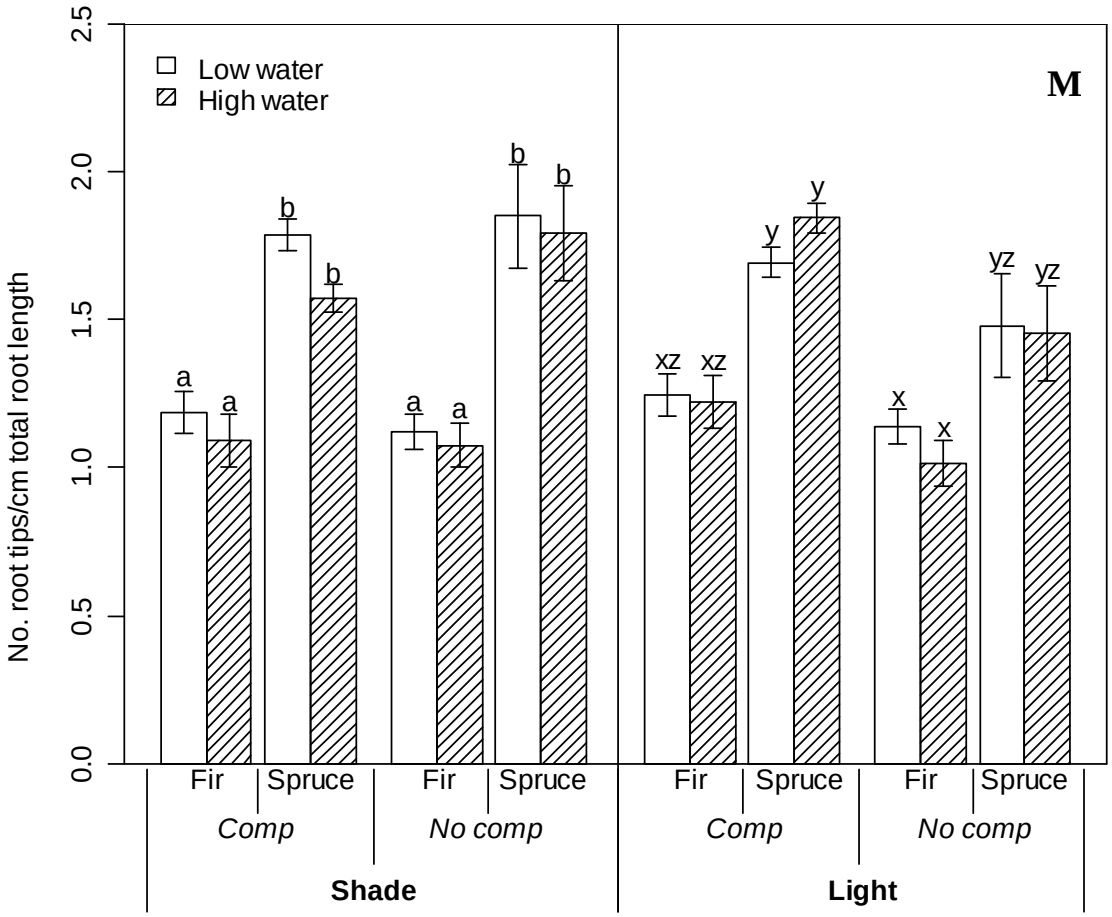

Figure 13M. Experiment 2 Harvest 3 means (± 1 SE) of root tips per cm of root length. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

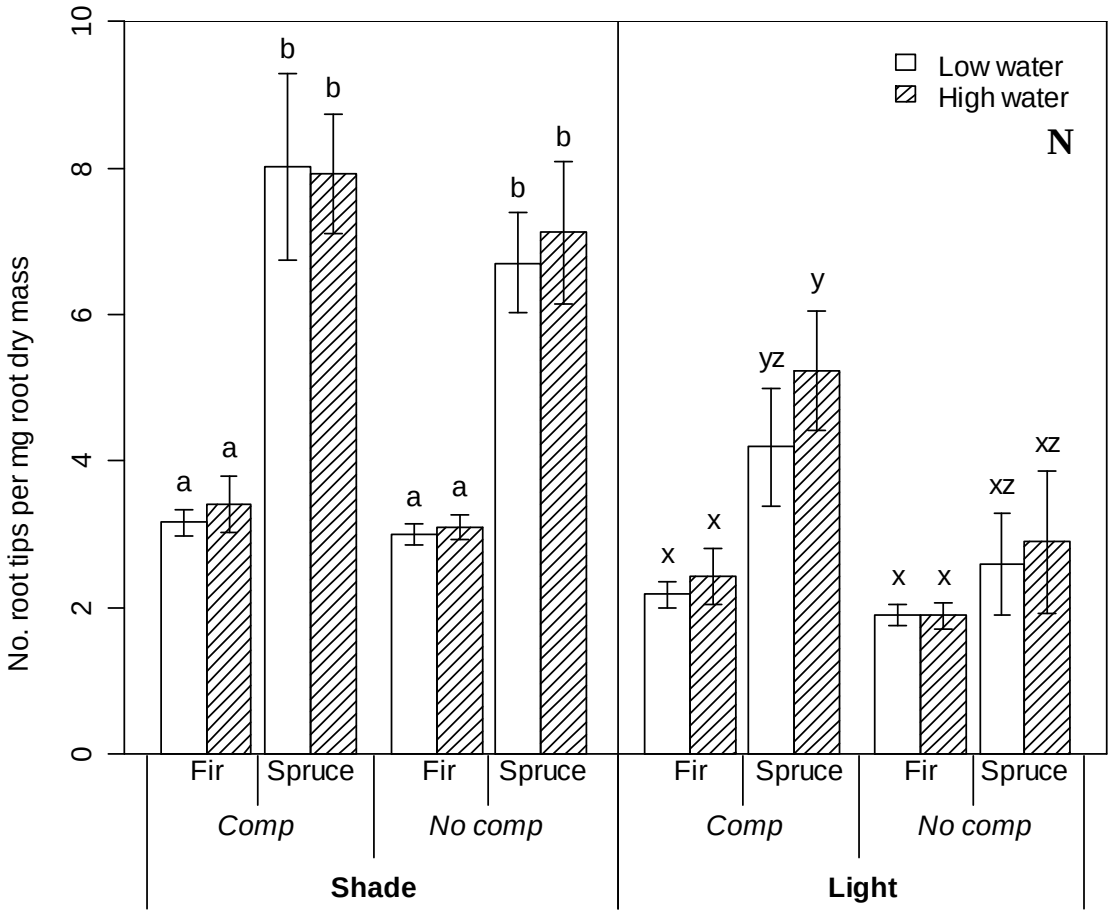

Figure 13N. Experiment 2 Harvest 3 means (± 1 SE) of root tips per gram of root mass. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD test. Different sets of letters are used for shade (a-c) than for light (x-z), because light and shade means were analyzed separately. The two sets of letters do not refer to each other, meaning that one cannot make comparisons of a light mean with a shade mean. Comp = competition; No comp = no competition. Number of replicates in each treatment:

Light	Balsam fir	Comp	High water	10	Shade	Balsam fir	Comp	High water	9
			Low water	8				Low water	9
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	8
	Red spruce	Comp	High water	10		Red spruce	Comp	High water	7
			Low water	8				Low water	3
		No comp	High water	10			No comp	High water	9
			Low water	10				Low water	6

high-water/no-competition spruce had by far the greatest dry masses of any species-treatment (Fig. 13E).

In the low-light environment, fir had higher R:S mass ratios than red spruce in most treatments, though differences were not always significant (Fig. 13F). Interestingly, high-water/competition spruce actually had R:S mass ratios similar to those of fir in the low-light environment (Fig. 13F), which is the only instance of spruce R:S mass ratios approaching those of fir. In the high-light environment, fir had significantly higher R:S mass ratios than spruce in all treatments (Fig. 13F). The related quantity RMR showed the same patterns as R:S mass ratio across species and treatments (Fig. 13G).

In the low-light environment, spruce had consistently higher SMRs than fir, though differences were no always significant (Fig. 13H). In the high-light environment, there were no significant differences or consistent trends in SMR for the two species in any treatment (Fig. 13H).

In the low-light environment, there were no significant differences or consistent trends in LMR for the two species in any treatment (Fig. 13I). In the high-light environment, spruce consistently allocated more to leaves relative to fir, though these differences were not significant in all species-treatment comparisons (Fig. 13I).

In terms of leaf morphology, in the low-light environment, fir had consistently higher SLAs than spruce, though these differences were not always significant (Fig. 13J). In the high-light environment, the SLAs of the two species were relatively similar (Fig. 13J).

In the low-light environment, there were no significant differences or consistent trends in FARM ratios for the two species in any treatment (Fig. 13K). In the high-light environment, spruce generally had higher FARM ratios than balsam fir (Fig. 13K), though differences were not always significant and were somewhat less consistent than they were at Harvest 2 (Fig. 12K).

In the low-light environment, spruce had significantly higher SRLs than fir with one exception; the SRLs of high-water/competition fir were non-significantly lower than those of low-water/no-competition spruce (Fig. 13L). In the high-light environment, interspecific differences were much smaller and less consistent (Fig. 13L).

In the low-light environment, red spruce had significantly higher root-tip-density than balsam fir on both a root length and root mass basis, indicating that spruce root systems were more highly-branched with greater root-tip density relative to those of fir (Fig. 13M-N). In the high-light environment, red spruce also had more root tips than balsam fir on both a root length and root mass basis (Fig. 13M-N); these differences were consistent in all treatments but were not always significant.

3.3.4.3. Effects of Light, Water, and Competition

3.3.4.3.1. Effects of Light

In the competition treatment, fir $RLR_{heights}$ were consistently but non-significantly higher than those of spruce, though these differences were not very large and did not occur in the no-competition treatment (Table 20).

The $RLR_{dry\ masses}$ of spruce were significantly higher than those of fir, though differences were only significant between high-water/no-competition spruce and both high-water/no-competition fir and low-water/competition fir (Table 20).

The $RLR_{R:S\ masses}$ were generally more positive for fir than for spruce except in the low-water/no-competition treatment, where the R:S mass ratios of spruce increased more than those of fir in response to higher light (Table 20).

There were no large or consistent responses of root tips per root length to higher light levels (Table 20).

			Height	Dry mass	R:S mass ratio	Root tips/length	Reps
Comp	High water	Balsam fir	0.66 ± 0.09 a	2.27 ± 0.17 ab	0.37 ± 0.10 a	0.13 ± 0.05 a	(8/9)
		Red spruce	0.52 ± 0.15 a	2.58 ± 0.31 ab	-0.11 ± 0.07 bc	0.13 ± 0.08 a	(10/7)
	Low water	Balsam fir	0.63 ± 0.06 a	1.86 ± 0.09 a	0.33 ± 0.04 a	0.03 ± 0.08 a	(10/9)
		Red spruce	0.30 ± 0.14 a	2.56 ± 0.27 ab	0.11 ± 0.07 abc	-0.07 ± 0.07 ab	(8/3)
No comp	High water	Balsam fir	0.61 ± 0.07 a	2.27 ± 0.14 ac	0.26 ± 0.07 ad	-0.06 ± 0.08 ab	(10/8)
		Red spruce	0.83 ± 0.11 a	3.37 ± 0.28 b	0.09 ± 0.09 bcd	-0.20 ± 0.08 b	(10/7)
	Low water	Balsam fir	0.68 ± 0.05 a	2.70 ± 0.10 ab	0.16 ± 0.05 ac	0.01 ± 0.05 ab	(10/9)
		Red spruce	0.58 ± 0.13 a	2.92 ± 0.22 bc	0.38 ± 0.06 a	-0.21 ± 0.05 b	(10/9)
Mean fir -comp			0.64 ± 0.05 z	2.06 ± 0.10 y	0.35 ± 0.05 y	0.08 ± 0.05 y	(18/18)
Mean spruce-comp			0.41 ± 0.10 z	2.57 ± 0.20 y	0.00 ± 0.05 z	0.03 ± 0.05 y	(18/10)
Mean fir-no comp			0.65 ± 0.04 z	2.48 ± 0.09 y	0.21 ± 0.04 y	-0.03 ± 0.04 y	(20/17)
Mean spruce-no comp			0.71 ± 0.08 z	3.14 ± 0.18 z	0.23 ± 0.05 y	-0.21 ± 0.04 z	(20/16)
Overall mean			0.60 ± 0.04	2.56 ± 0.07	0.20 ± 0.02	-0.03 ± 0.02	(76/61)

Table 20. Experiment 2, Harvest 3 mean RLRs (relative light responses) (± 1 SE) of height, plant dry mass, R:S mass, and root tips per root length. Acronyms are further described in Table 4. RLR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'light' seedlings (first number) and the number of 'shade' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example, a height mean with a primary root length mean.

3.3.4.3.2. Effects of Water

There were no consistently-significant interspecific differences or trends in the RWRs of height, dry mass, R:S mass ratio, or root tips per root length in any treatment (Table 21), indicating that the watering treatments had little effect on the growth and development of most of these seedlings. Only in the case of no-competition spruce did watering treatment have a negative effect on seedling dry mass (Table 21).

			Height	Dry mass	R:S mass ratio	Root tips/length	Reps
Light	Comp	Balsam fir	-0.03 ± 0.09 ab	0.23 ± 0.17 a	0.04 ± 0.10 ab	0.00 ± 0.05 a	(8/10)
		Red spruce	-0.18 ± 0.14 a	-0.21 ± 0.31 a	0.16 ± 0.07 ab	0.07 ± 0.08 a	(8/10)
	No comp	Balsam fir	-0.10 ± 0.07 ab	-0.18 ± 0.14 a	0.12 ± 0.07 ab	-0.10 ± 0.08 a	(10/10)
		Red spruce	0.26 ± 0.11 b	0.41 ± 0.28 a	-0.06 ± 0.09 a	-0.03 ± 0.08 a	(10/10)
Shade	Comp	Balsam fir	-0.05 ± 0.11 ab	-0.19 ± 0.17 a	0.02 ± 0.05 ab	-0.10 ± 0.09 a	(9/9)
		Red spruce	-0.26 ± 0.16 a	-0.22 ± 0.23 a	0.37 ± 0.14 b	-0.13 ± 0.03 a	(3/7)
	No comp	Balsam fir	-0.01 ± 0.08 ab	0.33 ± 0.13 a	0.03 ± 0.07 ab	-0.05 ± 0.08 a	(8/9)
		Red spruce	0.00 ± 0.09 ab	-0.03 ± 0.17 a	0.23 ± 0.06 ab	-0.04 ± 0.09 a	(7/9)
		Mean fir-light	-0.07 ± 0.06 z	0.03 ± 0.11 z	0.08 ± 0.06 z	-0.05 ± 0.04 z	(18/20)
		Mean spruce-light	0.04 ± 0.09 z	0.10 ± 0.21 z	0.05 ± 0.06 z	0.02 ± 0.06 z	(18/20)
		Mean fir-shade	-0.03 ± 0.07 z	0.07 ± 0.11 z	0.03 ± 0.04 z	-0.08 ± 0.06 z	(17/18)
		Mean spruce-shade	-0.13 ± 0.09 z	-0.13 ± 0.14 z	0.30 ± 0.07 z	-0.09 ± 0.05 z	(10/16)
		Overall mean	-0.05 ± 0.04	0.02 ± 0.07	0.11 ± 0.03	-0.05 ± 0.03	(63/74)

Table 21. Experiment 2, Harvest 3 mean RWRs (relative water responses) (± 1 SE) of height, plant dry mass, R:S mass, and root tips per root length. Acronyms are described in Table 4. RWR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'wet' seedlings (first number) and the number of 'dry' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example a height mean with a primary root length mean.

3.3.4.3.3. Effects of Competition

$RCR_{heights}$ were close to zero for all species-treatments except high-water spruce, whose heights responded negatively to competition.

In the high-light environment, the $RCR_{dry\ masses}$ of the two species were consistently negative (Table 22), indicating that competition negatively affected the growth of both species. In the high-water treatment, spruce was significantly more negatively impacted than fir by competition, but the two species responded similarly to competition in the low-water treatment (Table 22).

In the high-light environment, there were few large or consistent trends in $RCR_{R:S\ mass}$ (Table 22).

In the high-light environment, both species showed small but consistent increases in root tips per root length in response to competition (Table 22).

In the low-light environment, there were no large, significant, or consistent trends for the RCRs of height, dry mass, R:S mass ratio, or root tips per root length (Table 22). This is probably due to the very low productivity of the grass competitors in the low-light environment (Table 11) and the low survival of grass during the winter (i.e. few if any competitors resumed growth after seedlings were moved into the greenhouse on January 9, 2007). Any effects of competition in the low-light environment were probably due to the several weeks of light competition provided by the grass during its establishment phase (see section 2.5.3 of this chapter).

			Height	Dry mass	R:S mass ratio	Root tips/length	Reps
Light	High water	Balsam fir	0.00 ± 0.09 a	-0.26 ± 0.17 ac	0.05 ± 0.10 a	0.21 ± 0.05 a	(8/10)
		Red spruce	-0.50 ± 0.14 b	-1.33 ± 0.31 b	-0.06 ± 0.07 ab	0.23 ± 0.08 a	(8/10)
	Low water	Balsam fir	-0.06 ± 0.06 a	-0.67 ± 0.09 bc	0.12 ± 0.04 a	0.11 ± 0.08 a	(10/10)
		Red spruce	-0.07 ± 0.14 ab	-0.71 ± 0.27 bc	-0.28 ± 0.07 b	0.13 ± 0.07 a	(10/10)
Shade	High water	Balsam fir	-0.04 ± 0.11 a	-0.26 ± 0.17 ac	-0.07 ± 0.05 ab	0.01 ± 0.09 ab	(9/8)
		Red spruce	-0.26 ± 0.16 ab	-0.54 ± 0.23 abc	0.13 ± 0.14 a	-0.10 ± 0.03 b	(7/9)
	Low water	Balsam fir	0.00 ± 0.05 a	0.27 ± 0.08 a	-0.05 ± 0.05 ab	0.05 ± 0.06 ab	(9/9)
		Red spruce	0.00 ± 0.20 ab	-0.35 ± 0.28 abc	-0.02 ± 0.15 ab	-0.01 ± 0.03 ab	(3/7)
Mean fir-light			-0.03 ± 0.05 y	-0.46 ± 0.10 y	0.09 ± 0.05 y	0.16 ± 0.05 xy	(18/20)
Mean spruce-light			-0.29 ± 0.10 z	-1.02 ± 0.20 z	-0.17 ± 0.05 z	0.18 ± 0.05 x	(18/20)
Mean fir-shade			-0.02 ± 0.05 y	0.01 ± 0.09 y	-0.06 ± 0.03 yz	0.03 ± 0.05 yz	(18/17)
Mean spruce-shade			-0.13 ± 0.12 yz	-0.44 ± 0.17 y	0.06 ± 0.10 y	-0.06 ± 0.02 z	(10/16)
Overall mean			-0.12 ± 0.04	-0.48 ± 0.07	-0.02 ± 0.03	0.08 ± 0.02	(64/73)

Table 22. Experiment 2, Harvest 3 mean RCRs (relative competition responses) (± 1 SE) of height, plant dry mass, R:S mass ratio, and root tips per root length. Acronym details are provided in Table 4. RCR calculations are described in section 2.8.3 of Chapter 3. Number of replicates in parentheses indicate the number of 'competition' seedlings (first number) and the number of 'no competition' seedlings (second number) used to make each calculation. Different letters indicate significant differences (α=0.05) assessed by Tukey's HSD procedure. Letters are specific to each trait, meaning that one cannot compare, for example, a height mean with a primary root length mean.

3.3.4.4. Seedling Mortality

Red spruce had higher overall mortality than balsam fir (Table 23). Much of spruce's mortality was due to an insect herbivore that fed only on spruce in the low-light environment (Table 23). Herbivory also appeared to make low-light spruce less-able to survive the winter, with five lightly-browsed spruce dying after being moved into the greenhouse in January (Table 23). Relatively few fir seedlings died, with only eight seedlings dying due to either winter damage, human damage (accidental clipping during grass cutting), or an unknown cause during the fall (Table 23). Only one spruce seedling and no fir seedlings died as a result of drought (Table 23).

				Cause of mortality						
				Total mortality	Unknown	Drought	Human accident	Herbivory	Winter damage	Herbivory+ winter
Red spruce	Light	Competition	Wet	**1**	1	-	-	-	-	-
			Dry	**3**	1	1	-	-	1	-
		No competition	Wet	**0**	-	-	-	-	-	-
			Dry	**0**	-	-	-	-	-	-
	Shade	Competition	Wet	**3**	-	-	-	2	1	-
			Dry	**10**	-	-	-	6	-	4
		No competition	Wet	**1**	-	-	-	-	1	-
			Dry	**4**	-	-	-	-	3	1
Balsam fir	Light	Competition	Wet	**0**	-	-	-	-	-	-
			Dry	**2**	-	-	2	-	-	-
		No competition	Wet	**0**	-	-	-	-	-	-
			Dry	**0**	-	-	-	-	-	-
	Shade	Competition	Wet	**1**	1	-	-	-	-	-
			Dry	**2**	2	-	-	-	-	-
		No competition	Wet	**1**	-	-	-	-	1	-
			Dry	**2**	-	-	-	-	2	-
Total red spruce				**22**	2	1	0	8	6	5
Total balsam fir				**8**	3	0	2	0	3	0

Table 23. Total mortality by species and treatment over the course of Experiment 2 and the apparent cause of each death. Herbivory deaths were caused in fall 2006 by a pest that appeared to attack only red spruce seedlings. Winter damage indicates that apparently healthy seedlings died sometime during the winter or soon after being brought into the greenhouse, presumably due to damage incurred over the winter. Herbivory+winter indicates that seedlings were subject to non-lethal herbivory in the fall and died after being brought into the greenhouse. (n=30 seedlings originally planted in each species-treatment combination)

3.4. Discussion:

3.4.1. Harvest 1

Harvest 1 of both Experiment 1 and Experiment 2 occurred 70-80 days after seedlings were planted (Table 2; 8), so it is not surprising that the results of Harvest 1, Experiment 2 resembled the results of Harvest 1, Experiment 1.

In the shade environment, fir and spruce were similar in height in both experiments (Fig. 6A; 11A). In the high-light environment, spruce was significantly taller than fir in Experiment 2 (Fig. 11A), and slightly but non-significantly taller than fir in Experiment 1 (Fig. 6A). In terms of dry mass, fir was somewhat more massive than spruce in both light environments in both experiments (Fig. 6B; 11D). And in both light environments in both experiments, fir had higher R:S mass ratios than spruce (Fig. 6C; 11E). In both light environments in both experiments, fir had significantly longer primary roots than spruce (Fig. 6D; 11B). So, the relative developmental characteristics of spruce and fir were consistent across experiments.

In Experiment 2, the early allocation patterns of balsam fir again appeared directed toward quickly establishing an extensive root system. Compared to red spruce, in both light environments balsam fir had longer primary roots (Fig. 11B), longer primary roots relative to its height (Fig. 11C), and a greater proportion of its carbon allocated toward belowground tissues (Fig. 11E-F).

Compared to balsam fir, the development of red spruce appeared to be directed toward achieving relatively high growth potential. Compared to balsam fir, in both light environments red spruce allocated a significantly higher proportion of its carbon toward leaves (Fig. 11G).

Red spruce also had significantly higher SSLs than balsam fir (Fig 11I), which helps to explain why red spruce had similar or greater heights relative to balsam fir (Fig 11A) despite spruce's significantly lower dry masses (Fig. 11D) and similar allocation toward stem tissues (Fig. 11H) relative to balsam fir.

The LMRs of both species were relatively consistent between the two light environments, though the LMR of balsam fir was slightly lower in the high-light environment than it was in the shade (Fig. 11G). In Experiment 1, LMRs were also relatively consistent between the two light environments for all species except white pine (Fig. 7H; Table 5), indicating that, compared to stem and root allocation, LMR is relatively consistent among light environments for these conifer species, at least during the first growing season.

3.4.2. Harvest 2

3.4.2.1. Introduction

Competition and watering treatments had only been in place for eight and four weeks, respectively, by Harvest 2 (Table 8). They appeared to have relatively small effects on Harvest 2 seedling growth and morphology (Table 16; 17), so the following discussion will focus primarily on the effects of light environment.

3.4.2.2. Seedling Traits

As found in Harvest 1, the growth of balsam fir appeared to be directed toward developing an extensive root system. Balsam fir had greater primary root lengths than red spruce in the shade environment (Fig. 12C), and although the two species had similar

root lengths in the high-light environment (Fig. 12C), fir had much longer roots relative to its height (Fig. 12D) and much higher proportional root allocation (Fig. 12E-F) than red spruce.

Interestingly, in Harvest 3 of Experiment 1, the FARM ratios of spruce were somewhat higher than those of fir, but differences were not significant in either light environment (Fig. 7J). In Harvest 2 of Experiment 2, however, red spruce had much higher FARM ratios than fir in both light environments. In other words, spruce had significantly more leaf area per unit root dry mass than balsam fir, suggesting that spruce will use up its water supplies faster than balsam fir at this stage of development (Day et al. 2005).

In the shade environment, the two species had similar dry masses (Fig. 12B), suggesting that they were similarly light-limited. But the positive dry mass response of red spruce to the high-light environment was significantly greater than that of balsam fir (Fig. 12B; Table 15). The higher growth potential of red spruce was probably related to both its higher allocation to leaf tissues relative to balsam fir (Fig. 11G; 12H) and its capacity for neoformed shoot growth in high-light conditions (Greenwood et al. in preparation). In contrast, balsam fir relies on preformed growth and sets bud relatively early in the growing season, making its first-season shoot growth limited relative to that of red spruce (Greenwood et al. in preparation).

Red spruce had significantly more-elongated stems than balsam fir in the shade environment but not in the high-light environment (Fig 12J), which explains how red spruce could have had greater heights than balsam fir in the shade environment (Fig 12A)

despite spruce's similar dry mass (Fig. 12B) and similar allocation toward stem tissues (Fig. 12G) relative to balsam fir.

In the high-light environment, both species responded to competition with consistent but non-significant increases in SSL (Fig. 12J). Red spruce exhibited a similar response in the shade environment (Fig. 12J). SSLs were also higher in the low-light environment than in the high-light environment (Fig. 11I; 12J), so the slight positive effects of competition on SSLs probably reflects the four weeks during which the grass competitors were allowed to grow freely and compete with spruce and fir for light before the grass was clipped (see section 2.5.3 of this chapter). This illustrates that, while there were some early light-competition effects of grass on spruce and fir seedlings, such effects were very small compared to the effects imposed by the different light environments.

Both species responded to the higher-light environment with lower SLAs (Fig. 12I), which is similar to what was found in Experiment 1 (Fig. 7I). In the high-light environment, the SLAs of both species also increased in response to the competition treatment (Fig. 12I). As discussed above regarding SSL, this response probably reflects the four weeks of light competition provided by the grass competitors during their establishment phase and appears to be relatively small compared to the effects imposed by the different light environments (Fig. 12I).

Place (1955) described the root systems of red spruce seedlings as more fibrous than those of balsam fir. Our results confirm the observations of Place (1955). In the shade environment, red spruce had much higher SRLs than balsam fir (Fig. 12L). In the

high-light environment, the SRLs of red spruce were still greater than those of balsam fir, though somewhat less so than they were in the shade (Fig. 12L).

In the high-light environment, interspecific differences in SRL were lower than they were in the low-light environment. This probably occurred because the thickness of the main roots tends to have a strong effect on SRL calculations. For instance, very thick main roots will constitute a relatively high proportion of root mass but a relatively low proportion of root length (Nicotra et al. 2002). Since red spruce growth responded much more positively than balsam fir growth to higher light (Table 15), it stands to reason that the main roots of spruce also increased in thickness much more than those of fir in response to higher light. So, relative to the low-light environment, we would expect a decrease of spruce SRL relative to fir SRL in the high-light environment, which is what our data shows (Fig 12L).

The strong influence of main-root thickness on SRL calculations makes it difficult to use SRL to compare the fine root architecture of seedlings of different sizes. To address this difficulty, Harvest 3 roots were analyzed in terms of number of root tips per root length, which should be much less sensitive than SRL to the potentially dominating effects of thick main roots.

3.4.2.3. Relative Species Responses to Light, Water, and Competition

In terms of seedling size, $RLR_{dry\ mass}$ was higher than RLR_{height} for both species, indicating that seedling dry mass was more responsive than seedling height to light level (Table 15). This is similar to what was found in Harvest 3 of Experiment 1 (Table 5).

Red spruce growth (i.e. height and dry mass) was more responsive than that of balsam fir to different light conditions (Fig. 12A-B; Table 15). This is similar to what was found in Experiment 1 (Table 5).

In terms of R:S mass ratios, balsam fir changed significantly more than red spruce between the different light conditions (Fig. 12E-F; Table 15). This resumbles the results of Experiment 1, where balsam fir root allocation changed more (though, non-significantly so) than that of red spruce in response to different light conditions (Table 5). Again, however, it is important to note the RLRs of R:S mass ratios only represent the actual differences in R:S mass ratios between seedlings in different light conditions and do not distinguish between ontogenetic drift and phenotypic plasticity as the driver of those differences.

In Harvest 2, water had no large or consistent effects on height, dry mass, R:S mass ratio, or SRL (Table 16).

As previously discussed, in Harvest 2, the effects of grass competition appeared to be due primarily to the few weeks of light competition that occurred while the grass remained unclipped during its establishment phase.

3.4.2.4. Harvest 2 Summary

Interspecific differences in growth and allocation were generally consistent with the results of previous experiments and harvests. The major exception to this was FARM ratios, which were non-significantly higher for spruce than for fir in Harvest 3 of Experiment 1 (Fig. 7J), but were significantly higher for spruce than for fir in Harvest 2 of Experiment 2 (Fig. 12K).

The slight effects of competition on seedling growth and development appeared to be due to a brief period of light competition that occurred during the grass's establishment phase. Watering treatments had no apparent effect on seedling growth and development by Harvest 2.

3.4.3. Harvest 3

3.4.3.1. Seedling Traits

As was found in Experiment 1 (Fig. 6C-E; 7E-F; 7J-K) and Harvests 1 (Fig. 11C; 11E-F) and 2 (Fig. 12D-F) of Experiment 2, relative to spruce, fir directed its growth more toward roots in both light environments at Harvest 3 (Fig. 13F-G), indicating that fir is better adapted than spruce to deal with belowground resource scarcity in both high- and low-light environments.

FARM ratios tell a somewhat different story, however. In the low-light environment, the FARM ratios of the two species were similar (Fig. 13K), because fir had higher root allocation (Fig. 13F-G), similar LMRs (Fig. 13I), but higher SLAs (Fig. 13J) than spruce. This differs from Harvest 2, when spruce had much higher FARM ratios than fir in both light environments (Fig. 12K). This inter-harvest difference is due to differences in leaf allocation and leaf morphology between first season and second season seedlings, with fir greatly increasing its SLAs (Fig. 12I vs Fig 13J) and LMRs (Fig. 12H vs Fig. 13I) relative to spruce from Harvest 2 to Harvest 3 in the low-light environment. So, the relative FARM ratios of these two species can clearly change rapidly from one stage of development to another.

In the high-light environment, the relative FARM ratios of spruce and fir resembled the findings of Harvest 2 (Fig. 12K), with spruce having generally higher FARM ratios than fir (Fig. 13K). This difference was driven by fir having similar SLAs (Fig. 13I), higher root allocation (Fig. 13G), and lower leaf allocation (Fig. 13I) relative to spruce.

The FARM ratios of the two species suggest that, at this stage of development, spruce and fir use their soil water supplies at similar rates in low-light environments, but spruce uses its soil water pools more quickly than fir in high-light environments. Root penetration, however, will strongly affect how much water is available to the seedlings. Primary root length was not measured in Harvest 3, but based on the results of Experiment 1 (Fig. 6D; 7K), Harvests 1 (Fig. 11B) and 2 (Fig. 12D) of Experiment 2, and other studies (Klein et al. 1991; Greenwood et al. in preparation), fir still presumably maintained longer primary roots than spruce.

As in Experiment 1 (Fig. 7J) and the other two harvests of Experiment 2 (Fig. 11G; 12H), spruce allocated more to leaves than did balsam fir in the high-light environment at Harvest 3 (Fig. 13I). This suggests that spruce has greater growth potential than fir in high-light environments (Walters et al. 1993), which is confirmed by the greater heights (Fig. 13A), basal-stem diameters (Fig. 13B), dry masses (Fig. 13E), and RGRs (Fig. 13D) of spruce relative to fir in the high-light environment.

But in contrast to Experiment 1 (Fig. 7J) and the other two harvests of Experiment 2 (Fig. 11G; 12H), spruce and fir had similar LMRs in the low-light environment at Harvest 3 (Fig. 13I), suggesting that the two species had similar growth potentials in that environment (Walters et al. 1993). This is confirmed by the similar stem diameters (Fig.

13B) and dry masses (Fig. 13E) of the two species in the low-light environment. Red spruce did have higher RGRs than balsam fir in the low-light environment (Fig. 13D), but that is presumably related to the smaller masses of red spruce relative to fir at Harvest 1 (on which RGR calculations were based) and the higher leaf allocation of spruce relative to fir at Harvests 1 and 2 (Fig. 11G; 12H), which presumably allowed spruce to maintain higher RGRs than balsam fir during that time.

In the low-light environment, spruce tended to allocate more than fir to its stems (Fig. 13H), which is reflected in the significantly greater heights of spruce relative to fir (Fig. 13A) despite the similar dry masses (Fig. 13E) and SSLs (Fig. 13C) of the two species.

In summary, at Harvest 3 in the high-light environment, the primary allocation trade-off between spruce and fir was between leaves and roots, with spruce allocating more to leaves at the expense of roots (relative to fir) and fir allocating more to roots at the expense of leaves (relative to spruce), while stem allocation was similar between the two species (Fig. 13G-I). In the low-light environment, the primary allocation trade-off between spruce and fir was between roots and stems, with spruce allocating more to stems at the expense of roots and fir allocating more to roots at the expense of stems, while leaf allocation was similar between the two species (Fig. 13G-I).

As found in Harvest 2 (Fig. 12L), spruce generally appeared to have a finer and more-highly-branched root system than balsam fir (Fig. 13L-N). This further confirms the observation of Place (1955) that spruce seedlings have a more ‘fibrous’ root system than balsam fir seedlings. Generally (but certainly not always), species with finer and more-highly-branched root systems have higher growth potentials (Ryser 2006). This is

due to the fact that species with high SRLs and root-tip densities have high soil resource uptake capacity per investment in root tissue. Such species can allocate more resources to aboveground (i.e. photosynthetic) tissues while maintaining the ability to absorb large amounts of soil resources (Ryser 2006). As discussed previously, root tips per root length is here considered to be a more reliable measure of overall root architecture than is SRL or root tips per root mass, both of which can be heavily influenced by, for instance, the presence of very thick main roots that would comprise a high proportion of total root mass while accounting for a low proportion of total root length and root tips (Nicotra et al. 2002). So for spruce and fir, the number of root tips per root length further indicates that early fir growth is directed toward root penetration and establishment (via longer, less-branched roots) and early spruce growth is directed toward facilitating its higher growth potential (via lower root allocation and more-highly-branched root systems that presumably have greater uptake capacity per tissue investment compared to balsam fir roots).

The root allocation of both species was generally somewhat lower at Harvest 3 (Fig. 13G) than it was at Harvest 2 (Fig. 12F), which no doubt reflects the fact that Harvest 3 seedlings had just completed flushing out their preformed growth. Flushing out of preformed growth typically leads to strong increases in shoot growth relative to root growth, which decreases R:S mass ratios until the preformed growth is completed (Reich et al. 1980).

3.4.3.2. Relative Species Responses to Light, Water, and Competition

3.4.3.2.1. Effects of Light

As was found in Experiment 1 (Table 5) and Harvest 2 of Experiment 2 (Table 15), relative to balsam fir dry mass, spruce dry mass was more responsive to higher light at Harvest 3 (Table 20). But in contrast to previous harvests, there was no difference in the response of the heights of the two species to light (Table 20). Nonetheless, the stronger biomass response of spruce to high-light conditions reflects the higher growth potential of spruce seedlings, which is most likely due to spruce's neoformed shoot growth (Greenwood et al. in preparation) and greater high-light leaf allocation relative to fir (Fig 13I).

As shown in Harvest 2 (Table 15), R:S mass ratios of fir changed more than those of spruce in response to light, but these differences were not very large (Table 20). And again, $RLR_{R:S\ mass}$ does not distinguish between ontogenetic changes and actual plastic responses to the two light environments.

The length-based root-tip density of neither species responded very strongly to light (Table 20).

3.4.3.2.2. Effects of Water

Interestingly, the watering treatments had no consistent effects on seedling size, allocation, or root morphology of either species (Table 21). This contradicts the hypothesis that spruce growth is more sensitive than fir growth to dry conditions.

The absence of a consistent watering treatment effect may have been due to the design of the watering treatments. The dry treatments were watered to field capacity and

then allowed to dry gradually. This cyclical watering regime may not have brought soil water levels below a critical growth threshold for any extensive period of time, if at all, which suggests that more constant soil moisture levels may have been more effective. However, sustained dry-soil conditions also may not have affected the growth of the two species. O'Brien (2005) found few effects of sustained dry-soil conditions on the growth and allocation of young spruce and fir seedlings, indicating that the growth and development of spruce and fir are relatively insensitive to non-lethal dry conditions.

However, the watering treatments did have an isolated effect on spruce seedlings in the no-competition treatment in the high-light environment (Table 21), which suggests that water did become limiting in that treatment. There were no such watering-treatment effects on competition-spruce or any of the fir (Table 21), indicating that water was not limiting in those treatments. No-competition-spruce were substantially more massive, on average, than the seedlings of any other species-treatment (Fig. 13E), so perhaps the larger size (and presumably greater transpiration) of no-competition-spruce caused them to be more impacted by drought treatments (i.e. a size penalty). All pots in each watering treatment were watered on the same schedule, regardless of species, which presumably kept pots containing the smaller fir and competition-spruce relatively moist compared to pots containing the much larger no-competition-spruce. During the second growing season when spruce seedlings became very large, pots containing the largest spruce seedlings did appear to dry the fastest (Jason Schatz, personal observation).

3.4.3.2.3. Effects of Competition

Competition was not substantial in the low-light environment (Table 11), so any effects of competition on seedling growth and development in the shade (Table 22) were either due to the initial light competition provided by the grass during its establishment phase or some other unknown factor. Unless otherwise noted, the following discussion will deal exclusively with competition in the high-light environment.

In the high-light environment, root competition was robust (Table 11) and had consistently negative effects on the dry masses of both red spruce and balsam fir (Fig. 13E; Table 22). In fact, in the high-light environment, the dry masses of competition-spruce were almost comparable to those of no-competition-fir (Fig. 13E), at least compared to the huge differences between fir and no-competition spruce (Fig. 13E) and the large differences typically found between spruce and fir in high-light environments (Fig. 7B; 12B).

Water supplies in the high-light environment were depleted somewhat faster in the competition treatments than in the no-competition treatments (Fig. 10), but the negative effects of competition on seedling growth did not appear to be due to water competition. If they had been, there should be more-consistently-negative RWRs in the high-light/competition treatment, because more-frequent watering (i.e. the wet treatment) would presumably have had a big impact on seedling growth if water were particularly scarce in that treatment. There was no such effect (Table 21), suggesting that competition was primarily for nutrients.

In the low-water treatment, competition had similar negative effects on the dry masses of both species (Fig. 13E; Table 22). In the high-water treatment, however,

competition had a much greater negative effect on the height and dry mass of spruce relative to fir (Table 22). This suggests that, in the high-water/competition treatment, both spruce and fir had plenty of water but could not reach their maximum size because of nutrient competition from the grass. And in the low-water/no-competition treatment, spruce and fir had plenty of nutrients, but spruce could not reach its maximum size because of inconsistent water supplies, possibly due to the 'size penalty' discussed in section 4.3.2.2. That is, both spruce and fir reached their maximum size in the no-competition treatments (Fig. 13E), probably because the lack of competition made more nutrients available. However, fir's maximum size was smaller than that of any of the spruces (Fig. 13E), which, in tandem with fir's lower FARM ratios (Fig. 13K), presumably kept pots containing the smaller fir relatively moist compared to pots containing the much larger (and presumably more-water-demanding) spruce. So, fir may never have become water-limited even in the relatively nutrient-rich no-competition treatment. And in the competition treatment, nutrient limitation prevented the spruce from growing large enough to use up water as quickly as the no-competition spruce.

So, there appeared to be an interaction between water, competition, and species in determining the growth of seedlings in the high-light environment. In table 19A, the water:comp:sp term was not significant for dry mass but was significant for RGR ($p<0.05$), suggesting that the 'size penalty' effect mediated by nutrient competition may, in fact, explain both the isolated effects of watering treatment on no-competition spruce (Table 21) and the stronger effects of competition on high-water spruce (Table 22).

So, the slightly higher sensitivity of spruce than fir to competition and drought in our experiment simply may have been a consequence of an experimental design in which

seedlings of different sizes within each treatment had access to equivalent amounts of resources (i.e. same pot size, same nutrient supply, and same watering schedule). In terms of applying these results to the field, larger seedlings in the forest are presumably able to draw resources from soil pools that are more proportional to their size, suggesting that the slight interspecific differences we found in competition and/or drought sensitivity would not apply to field-grown seedlings.

The R:S mass ratios of neither species responded strongly or consistently to competition (Table 22). Interestingly, however, the number of root tips per root length of both species increased slightly in response to competition (Table 22). This may suggest that both species increased their nutrient absorption capacity per investment in root tissue in order to better compete for nutrients with the grass roots. The root-tip density response to competition is too small to be definitive, but the presence of a consistent trend is intriguing.

3.4.3.3. Mortality

Overall, survivorship in Experiment 2 was high (Table 8), so the mortality patterns reveal little about spruce and fir. Although spruce experienced higher overall mortality than fir, most of the spruce deaths were related to a single herbivore that found its way to the experimental site and fed only on spruce in the low-light environment (Table 23). Spruce appeared to be more vulnerable than fir seedlings to winter stress, particularly when the spruce seedlings were damaged by herbivores, but not even those interspecific differences were very large (Table 23).

3.5. Summary

Harvests 1 and 2 produced data similar to that of Harvests 1 and 3 of Experiment 1, with fir allocating more to roots and spruce allocating more to leaves in both light environments. Spruce dry mass was significantly more responsive than fir dry mass to higher light, which is similar to what was found in Harvest 3 of Experiment 1. One key difference between Harvest 3 of Experiment 1 and Harvest 2 of Experiment 2 was in the relative FARM ratios of spruce and fir. In Harvest 3 of Experiment 1, spruce FARM ratios were non-significantly higher than those of fir in the high-light environment. In Harvest 2 of Experiment 2, spruce FARM ratios were significantly much higher than those of fir in both light environments, suggesting that, at that stage of development, spruce will use its soil water pools more quickly than fir. Combined with the longer roots of balsam fir, fir seedlings should be able to withstand dry conditions for longer periods of time than spruce seedlings. This fits with the results of O'Brien (2005) who found that, given equal initial water supplies, five-month-old spruce seedlings died more quickly than fir seedlings after watering was ceased.

At Harvest 2, watering treatments had only been in place for four weeks and had no apparent effects on seedling growth and development. At Harvest 3, watering treatments appeared to have little effect on any seedlings except high-light/no-competition spruce, whose growth was negatively affected by the dry treatment. This may have been due to the fact that high-light/no-competition spruce seedlings were the largest of any seedling-treatment (probably because of the higher nutrient availability in the no-competition treatment and the higher growth potential of spruce), suggesting that

high-light/no-competition spruce had the highest demand for water and were thus the most impacted by depletion of that water in the dry treatment (i.e. a 'size penalty' effect).

At Harvest 2, the small effects of competition on seedling growth and development appeared to be related to the few weeks of light competition that occurred during the grass's establishment phase. Competitor productivity was robust in the high-light environment but almost non-existent in the low-light environment, so any effects of competition in the low-light environment were related to the grass's establishment period when it competed with spruce and fir seedlings for light.

At Harvest 3, competition in the high-light environment appeared to be primarily for nutrients and had similar negative effects on both species in the low-water treatment. In the high-water treatment, however, competition had stronger effects on spruce growth than on fir growth, possibly due to the 'size penalty' effect discussed above, which relates to the interaction effect of species, competition, and soil moisture discussed in section 4.3.2.3 of this chapter.

In terms of root morphology, SRL and root tips per root length further indicate that early fir growth was directed toward root penetration and establishment (via longer, less-branched roots) and early spruce growth was directed toward facilitating spurce's higher growth potential (via lower root allocation and more-highly-branched root systems that presumably have greater uptake capacity per unit mass compared to balsam fir roots).

In the high-light environment, both species responded to competition with slight increases in the number of root tips per root length, indicating that both species may have increased their nutrient absorption capacity per investment in root tissue in order to better compete for nutrients with the grass roots.

3.6. Conclusions

Overall, the growth of spruce and fir appeared to be similarly sensitive to belowground nutrient competition and dry soil conditions. So, we reject the hypothesis generated by Experiment 1 that, because of spruce's lower R:S mass ratios, red spruce growth is more sensitive than fir growth to belowground resource scarcity.

In light of this, it seems likely that any interspecific differences in the responses of red spruce and balsam fir seedlings to dry conditions would probably arise due to differences in mortality caused by severely dry conditions rather than long-term growth effects due to non-lethal variation in soil moisture. This will be discussed further in Chapter 4.

Chapter 4: Implications of the Early Life Stage Characteristics of Six Acadian Conifer Species in a Changing Climate

4.1. Introduction

Global climate change could drastically alter regional climates (Houghton et al. 2001). The combination of increased temperatures and altered precipitation patterns could have a significant impact on soil water availability (Aber et al. 2001), which could contribute to large shifts in species distributions and local abundance (Overpeck et al. 1991; Iverson and Prasad 1998; Hansen et al. 2001; Aber et al. 2001).

It will be particularly important to understand the effects of different climate scenarios on trees' early life stages, including seed germination, germinant establishment, and seedling growth, development, and survival, because, 1) early life stage growth and survival strongly influence the overall population of a given species by limiting the number of trees reaching later life stages (Harper 1977) and 2) trees are most sensitive to drought and other environmental stresses during their early life stages (Harper 1977; Schlesinger et al. 1982; Wellington 1984; Hanson et al. 2001), which suggests that tree early life stages will be among the most responsive components of forest communities to climate change (Joslin et al. 2000; Hanson et al. 2001).

Early life stage traits may be able to help us predict local species dynamics under various climate scenarios. For instance, if the early life stages of a given species have traits typically associated with enduring dry conditions, then the early life stages of that species should perform relatively well in a drier climate. Or, if the early life stages of a given species appear adapted for cooler, moister conditions, then the early life stages of

that species would be expected to perform relatively well in a cooler, moister climate and relatively poorly in a warmer, drier climate. This chapter will frame what we know about the early life stages of red spruce, black spruce, white spruce, balsam fir, white pine, and eastern hemlock in terms of those species' probable fitness in different climates.

4.2. Summary Review of Experiments 1 and 2

4.2.1. Experiment 1

Based on the data from Experiment 1, the six species were divided into three groups:

1) Hemlock, which had seeds intermediate in mass among the study species, germination that responded negatively to high temperatures, germination that began much later than that of the other species, R:S mass ratios that were moderate among these six species, low growth in high-light conditions, higher SLAs than any other species in both light environments, and significantly higher FARM ratios than the other species in the high-light environment.

2) Black, white, and red spruce, which had the smallest seeds of the study species, germination that was unresponsive to the different light environments, the most rapid and complete germination, the lowest R:S mass and R:S length ratios, and the capacity for vigorous neoformed shoot growth in response to high-light.

3) White pine and balsam fir, which had the largest seeds (particularly white pine) of the study species, had more-gradual and less-complete germination than the spruces, and whose germination rates have been found to respond positively to warmer conditions. Although they differed substantially in size, in high-light conditions, fir and pine both

rapidly developed the longest roots and R:S mass ratios of any species. In the shade, however, the two species were less similar, and only fir had consistently higher R:S mass and R:S length ratios than the other species.

4.2.2. Experiment 2

In Experiment 2, the growth of red spruce and balsam fir appeared to be similarly sensitive to belowground nutrient competition and dry soil conditions. So, any interspecific differences in the responses of red spruce and balsam fir seedlings to dry conditions would probably arise due to differences in mortality caused by severely dry conditions rather than long-term growth effects due to non-lethal variation in soil moisture.

Spruce was found to have significantly higher FARM ratios than balsam fir, particularly in high-light conditions; in Experiment 1, spruce had higher FARM ratios than fir in the high-light environment, but the differences were not significant.

4.3. Probable Effects of Climate Change

4.3.1. Introduction

In Experiment 1, the species were divided into three groups based on key early life stage characteristics: 1) hemlock; 2) black spruce, white spruce, and red spruce; 3) white pine and balsam fir. Based largely on those groupings, the probable effects of climate change on the early life stages of those six species will be discussed by integrating the results of Experiments 1 and 2 in view of what is already known about these six species in the scientific literature.

4.3.2 Hemlock

Our findings support previous studies that found hemlock to be a slow growing species (Gaerlich and Nyland 2000) whose germination is strongly inhibited by high temperatures (>21º C—Olson et al. 1959). Our observations fit well with hemlock's general classification as a late-successional, shade-tolerant species.

Hemlock seedlings are very sensitive to dry conditions and depend on consistent rainfall for several years after establishment (Gaerlich and Nyland 2000). In Experiment 1 in the high-light environment, hemlock had the lowest R:S mass ratios, shortest roots, and highest FARM ratios of any species (Fig. 7D-E, J). But in the shade, hemlock's R:S mass ratios were similar to those of the three spruces, and its FARM ratios were not significantly different from those of any other species (Fig. 7E). This indicates that in high-light environments, hemlock is less able than the other species to endure dry conditions. But in low-light environments where hemlock regeneration is most successful (Goerlich and Nyland 2000), hemlock seedlings may be no more or less vulnerable than the three spruce species to dry conditions.

When applying these observations to projections of future hemlock success, one must bear in mind the complexities of forest population dynamics. For example, even if hemlock seedlings are negatively impacted by drier conditions, hemlock's superior shade tolerance or some other factor might still allow it to persist throughout its current range if the climate became more drought-prone. Nonetheless, hemlock's reputation as a drought-sensitive species (Gaerlich and Nyland 2000; Foster et al. 2006; but see Caspersen and Kobe 2001) suggest that a drier and/or more erratic climate could

negatively impact the early life stages of hemlock, while a wetter, more consistent climate could favor the early stages of hemlock.

4.3.3. White Spruce, Black Spruce, Red Spruce, White Pine, and Balsam Fir

The rapid and highly complete germination of the spruces might make them relatively vulnerable to highly variable, stressful conditions (e.g. stochastic droughts). If future weather patterns become more erratic, the all-eggs-in-one-basket approach of the spruces would be vulnerable to years in which the germination pulse of spruce seeds coincides with conditions unfavorable enough to kill the sensitive germinants. On the other hand, moister, more consistent environmental conditions might handsomely reward the rapid and robust germination of the spruces.

The less complete, more-drawn-out germination pattern of balsam fir and white pine suggests that annual crops of their germinants will be more resilient to stressful and/or variable environments. That is, extending germination over a longer period of time increases the likelihood that at least some germinants will encounter favorable conditions for establishment and survival (Sarukhan 1974; Venable and Brown 1988; Greenwood et al. in preparation). Predictions of increasingly erratic weather patterns in the future (Easterling et al. 2000; Houghton et al. 2001; but see Bengtsson et al. 2006) thus seem to favor the germination strategies of white pine and balsam fir. But again, the spruces could greatly outgain (i.e. outcompete) fir and pine if the future climate is wetter and/or more consistent, which could reward the spruces' riskier germination approach by facilitating high survival rates for their potentially large germinant crops.

Seed size can also play a role in seedling establishment. Leishman et al. (2000) reviewed several studies that found a positive relationship between seed size and germinant survival rates both within and among different species. Generally, larger seeds have greater food reserves, which 'feed' germinants and help them reach heterogeneous limiting resources (Leishman et al. 2000). For instance, larger seeds might allow germinants to more quickly develop long taproots with which to reach deeper, more-reliable pools of soil water that will help them to survive dry conditions. As such, germinants of the larger-seeded balsam fir and much-larger-seeded white pine should establish and survive better in more variable environmental conditions than the smaller-seeded spruces.

R:S mass ratio (Pallardy & Rhoads 1993; Lloret 1999; Kozlowski and Pallardy 2002; but see Engelbrecht et al. 2006) and root depth (Holch 1931; Coile 1940; Albertson and Weaver 1945; Bahari et al. 1985; Kozlowski and Pallardy 2002; Ryser 2006) are typically positively associated with the ability to cope with dry conditions, while FARM ratios are presumably negatively associated with the ability to endure dry conditions (Day et al. 2005). The Experiment 1, Harvest 3 FARM ratios of the spruces, balsam fir, and white pine were not significantly different from each other in either light environment (Fig. 7J), suggesting that the species all had similar proportions of water-gathering structures (roots) to water-losing structures (foliar surface area). In Harvests 2 and 3 of Experiment 2, however, red spruce had significantly higher FARM ratios than balsam fir, particularly in the high-light environment (Fig. 13K). And on closer examination, despite the lack of significant differences, the Experiment 1, Harvest 3 FARM ratios of the spruces were higher than those of fir and, to a lesser extent, pine in the high-light

environment (Fig. 7J). Taken together, these results indicate that, particularly in high-light environments, fir will deplete its soil water pools less rapidly and survive somewhat longer than the spruces during sustained dry conditions.

The spruces' meager early root development (Fig. 6C-D) further suggests that the spruces are more sensitive to dry conditions than balsam fir and white pine, which generally had longer roots and higher R:S mass ratios than the spruces (Fig. 6C-D; 7D-E). Balsam fir, in particular, had consistently higher R:S mass ratios (Fig. 6C; 7E; 11E; 12D; 13D) and R:S length ratios (Fig. 6E; 7K; 11C; 12E; 13E) than the spruces in both light environments in Experiments 1 and 2.

Other studies support our hypothesis that pine and fir are less sensitive than the spruces to dry conditions. White pine performs relatively well in low-water conditions (Thomas and Wein 1985; Caspersen and Kobe 2001), which is presumably partly due to pine's rapid development of an extensive root system. Red spruce seedlings are considered to be more vulnerable than balsam fir to early water stress because of spruce seedlings' relatively small root systems (Place 1955; Klein et al. 1991; Greenwood et al. in preparation) that have difficulty penetrating forest floor duff to reach deeper, more reliable soil water (Klein et al. 1991). Balsam fir's longer roots (Place 1955; Klein et al. 1991; Greenwood et al. in preparation) allow it to penetrate much deeper through forest floor litter (Klein et al. 1991).

Again, Experiment 2 demonstrated that the growth of red spruce and balsam fir seedlings is not very sensitive to dry conditions. So, any interspecific differences in the response of red spruce and balsam fir to dry conditions would probably arise due to differences in mortality rates under severe water deficit rather than long-term growth

effects of non-lethal dry conditions. Given the interspecific differences in root length (Fig.6D; 11B) and R:S length ratio (Fig. 6E; 11C), these species will not have access to equivalent pools of water. The shorter-rooted spruce may only have access to the relatively fast-drying forest floor litter or upper soil layers, while the longer-rooted fir (and pine) will have access to deeper, more persistent pools of soil water. Ultimately, differences in root penetration may be responsible for any interspecific differences in seedling mortality under severe water deficits. If the higher FARM ratios of the spruces relative to fir (and perhaps pine) are taken into consideration, the spruces seem even more vulnerable to desiccation-related mortality.

O'Brien (2005) studied the mortality of container-grown red spruce and balsam fir seedlings in response to drought and found that two-month-old seedlings of both species responded similarly to drought, but five-month-old seedlings of balsam fir tolerated and recovered from drought much better than red spruce. For both the two-month-old and five-month-old seedlings, balsam fir had higher R:S mass ratios than red spruce, but the interspecific difference between the R:S mass ratios of the five-month-old seedlings were much greater. The fact that the R:S mass ratios of the two species diverged more with age was at least partially due to the neoformed shoot growth of the spruces, which allowed the spruces to continue to build aboveground tissues well after balsam fir had set bud (O'Brien 2005). In the field, this neoformed growth is less common, most likely due to the suboptimal, heterogeneous conditions typical of forests. Nonetheless, even in forests, the R:S mass ratios of balsam fir seedlings are much higher than those of red spruce (Greenwood et al. in preparation), indicating that the relative drought-sensitivity of spruce and fir will hold there as well.

Given that the growth and carbon allocation patterns of black and white spruce are very similar to those of red spruce (Fig. 6A-D; 7A-H), it stands to reason that the moisture-sensitivity of red spruce will also hold for black and white spruce. Thomas and Wein (1985) found that black spruce seedlings were more sensitive than white pine and balsam fir seedlings to dry conditions. In a study of range limits in west-central Canada, the southern range limits of black and white spruce were found to correlate strongly with climatic moisture gradients (Hogg 1994). Although the factors influencing range limits in west-central North America are no doubt different from the factors influencing range limits in eastern North America, the results of Hogg (1994) at least indicate that the distributions of black and white spruce are sensitive to moisture conditions.

However, there is some evidence contradicting this hypothesis. Black spruce can occur on dry and mountainous sites (Viereck and Johnston 1990), where moisture may not be particularly abundant or reliably available. In a study comparing post-fire regeneration of balsam fir and white spruce, Galipeau et al. (1997) hypothesized that initial balsam fir regeneration was limited primarily by water availability, but did not mention whether water availability appeared to limit white spruce regeneration. Of course, that does not necessarily mean that such limitation did not occur, or that white spruce performs better than fir under water-limiting conditions. There were undoubtedly myriad factors influencing the regeneration of both species, but the findings of Galipeau et al. (1997) appear somewhat at odds with our conclusions and are worth noting.

Nonetheless, the early life stage strategies of the spruces are distinct from those of fir and pine in terms of seed sizes, germination patterns, root growth, and carbon allocation. Taken together, these four parameters suggest that the early life stages of the

spruces are more vulnerable than the early life stages of white pine or balsam fir to drought-related mortality. As such, drier and/or more erratic weather patterns in the future could give a competitive advantage to the early life stages of pine and fir and negatively impact the early life stages of the spruces, while more consistent and water-rich weather patterns would help the early life stages of the spruces to continue to thrive in Maine's forests.

4.3.4. Comparison to the Past

When considering the possible implications of these findings, it is crucial to bear in mind the myriad factors affecting species range limits and forest population dynamics, many of which can override the effects of changing temperature and moisture conditions on the success rates of different forest species. In many cases, changes in species distribution are strongly associated with changing disturbance regimes that are mediated by changes in climate (Dale et al. 2001).

Palynological studies provide unique ways to address such issues by studying changes in species distribution over thousands of years of climate change. In Maine, white pine thrived from 9,000 to 5,000 years ago when the climate was considerably warmer and drier than it is today and declined when the climate became cooler and wetter (Jacobson and Dieffenbacher-Krall 1995). This fits well with our hypothesis that the early life stages of white pine have a competitive advantage in warmer, drier climates.

Balsam fir appears to be somewhat less responsive to climate change than our other study species (Schauffler and Jacobson 2002). If anything, the abundance of fir in Maine tended to decrease during warmer, drier periods and increase somewhat when the

climate became cooler and moister during the late Holocene (Schauffler and Jacobson 2002). This is somewhat at odds with our germination- and biomass-allocation-based hypothesis that balsam fir should perform relatively well in warmer, drier climates. However, fires were also more frequent during the warmer, drier mid-Holocene climate in which white pine thrived (Jacobson and Dieffenbacher-Krall 1995). Fires tend to create favorable conditions for white pine regeneration (Wendel and Clay 1990), but balsam fir abundance tends to be negatively impacted by increasing fire frequency (Frank 1990). So, the higher fire frequency associated with warmer, drier climates may partially account for fir's slight decline in Maine during warmer, drier periods, and its increase during cooler, wetter periods. Several researchers have, in fact, attributed species distributions in north-temperate and boreal forests to fire frequency (Suffling 1995; He et al. 2002), highlighting the potential of climate change to alter vegetation distribution by altering disturbance regimes. The models of both Suffling (1995) and He et al. (2002) indicated that increased fire frequency would decrease balsam fir abundance, pushing fir's range north into less-fire-prone locales. Climate warming may indeed increase the risk of fire, but forest managers can, to some extent, influence the degree to which changing climatic conditions will lead to changes in fire regimes.

Foster et al. (2006) found that hemlock thrived primarily during cool, moist periods and that warming and drying of the climate may have played a significant role in hemlock's steep mid-Holocene decline. This fits with our hypothesis that the early life stages of hemlock would be negatively impacted by a warmer, drier climate.

The relatively recent southward expansion of black and white spruce was associated with the climate growing cooler and wetter, as was the inland expansion of red

spruce populations from coastal refugia (Schauffler and Jacobson 2002). These observations fit well with our hypothesis that the early life stages of white, black, and red spruce are positively affected by wetter conditions. The relative scarcity of the spruces during warmer, drier periods fits with our hypothesis that spruce early life stages are negatively affected by drier climates.

4.4. Summary and Conclusions

Based on the results of Experiment 2, non-lethal drought conditions do not seem to have strong effects on the relative growth of red spruce and balsam fir seedlings. Red spruce and balsam fir R:S mass ratios were consistently among the lowest and highest, respectively, of the six study species, so it seems reasonable to assume that the early growth of our other study species is similarly insensitive to non-lethal drought. O'Brien (2005) demonstrated that spruce seedlings are more vulnerable than fir seedlings to lethal drought, however, which she attributed to the biomass allocation and root penetration differences between the two species. This suggests that differences in root penetration and biomass allocation could have strong effects on the relative success of the early life stages of our study species, because the shorter-rooted spruces may only have access to relatively fast-drying forest floor litter or upper soil layers, while the longer-rooted fir and pine will have access to deeper, more persistent pools of soil water. Also, differences in FARM ratios and R:S mass allocation of the species will affect how quickly seedlings deplete those soil-water pools, thus affecting how long seedlings can survive during severe droughts.

Again, Experiment 2 indicated that non-lethal changes in soil moisture have little effect on the relative growth and development of the seedlings of our study species. This suggests that changes in precipitation patterns would most affect the early life stages of these species through changes in drought-related mortality rates. Presumably, a drier climate would increase drought-related seedling mortality and give a competitive advantage to species better suited to endure droughts, while a wetter climate would reduce drought-related seedling mortality and help species poorly suited to endure droughts.

Based on the data gathered in our experiments, a warmer, drier climate appears likely to favor the early life stages of white pine and balsam fir while hindering the early life stages of hemlock, white spruce, black spruce, and red spruce. On the other hand, a cooler, wetter climate would likely facilitate the performance of the early life stages of hemlock, white spruce, black spruce, and red spruce in Maine's forests.

Of course, given the complexity of competitive interactions and seedling survival, the confidence of such predictions is limited. And again, climate-mediated changes in disturbance regimes could have overriding effects on forest communities (Dale et al. 2001), so an integrated view of forest dynamics is essential to accurately predict the effects of different climate scenarios on local species abundance. And despite the importance of early life stages, one must also consider the response of the entire life cycle of a given species if one hopes to predict its response to climate change. Nonetheless, early life stage performance will be highly important in determining future species ranges and local abundance, and the data presented here will contribute to our understanding of the past, present, and future of Maine's forests.

4.5. Future Research

Experiment 1 characterized the early growth and morphology of black spruce, white spruce, red spruce, balsam fir, white pine, and hemlock. The results suggested that some of the species are much more sensitive than others to dry conditions. Experiment 2 demonstrated that the early growth rates of red spruce and balsam fir, whose R:S ratios were consistently among the lowest and highest, respectively, of the six study species, were similarly insensitive to non-lethal soil water deficits and similarly sensitive to nutrient competition. This led to the hypothesis that any interspecific differences in the responses of the seedlings of these species to dry conditions would probably arise due to differences in mortality caused by severely dry conditions rather than long-term growth effects due to non-lethal variation in soil moisture. This hypothesis should be tested.

A field study could be conducted that incorporates different light environments (e.g. gap and understory) and different depths of organic hummus (to test the effects of interspecific differences in root penetration). Rain exclosures could be used to control watering, and at different points during the first growing season (e.g. 1 month, 2 months, 3 months, 4 months, 5 months, and 6 months after germination), water would be cut off from a subset of seedlings for which mortality rates would then be monitored. Immediately prior to each drought event, a subset of seedlings could be harvested in order to characterize the growth, morphology, and development of each species. Those seedling traits could then be correlated with the drought-related mortality rates.

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APPENDIX

EXPERIMENTS 1 AND 2 ANALYSIS OF VARIANCE

Models (Experiment 2 ANOVAs):

Harvest 1 model (H1 model):
Y ~ light:block + sp + light + block + sp:light

Harvest 2 model (H2 model):
Y ~ block + light + block:light + water + block:water + water:light + block:water:light + comp + sp + comp:sp + light:comp + light:sp + water:comp + water:sp + water:sp:comp + water:light:comp + water:light:sp + water:light:comp:sp

Light/Shade model (L/S model):
Y ~ block + water + block:water + comp + sp + comp:sp + water:comp + water:sp + water:sp:comp

Harvest 3 model (H3 model):
Identical to H2 model

RLR model:
Y ~ sp + comp + water + sp:comp + sp:water + comp:water + sp:comp:water

RWR model:
Y ~ sp + comp + light + sp:comp + sp:light + comp:light + sp:comp:light

RCR model:
Y ~ sp + light + water + sp:light + sp:water + light:water + sp:light:water

Table A1. Exp. 1 Germination initiation: initiation ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	1669.310	333.860	203.841	**< 2.2e-16 *** **	
trt	1	11.000	11.000	1697.877	**0.015***	(using error a)
block	1	4.490	4.490	2.742	0.101	
trt:block (error a)	1	0.010	0.010	0.004	0.9499941	
trt:sp	5	42.700	8.540	5.215	**<3.3e-3*** **	
Residuals	94	144.130	1.531			

Table A2. Exp. 1 Germination completion: completion ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	41920	8384	145.836	**< 2.2e-16 *** **	
trt	1	382	382	3.548	0.311	(using error a)
block	1	72	72	1.252	0.266	
trt:block (error a)	1	108	108	1.871	0.17464	
trt:sp	5	2567	513	8.932	**5.715e-07 *** **	
Residuals	94	5404	57			

Table A3. Exp 1. Germination rate: rate ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	127.945	25.589	102.014	**< 2.2e-16 *** **	
trt	1	0.087	0.087	0.297	0.682	(using error a)
block	1	0.022	0.022	0.089	0.766	
trt:block (error a)	1	0.293	0.293	1.17	0.2822	
trt:sp	5	14.715	2.943	11.733	**7.967e-09 *** **	
Residuals	94	23.579	0.251			

Table A4. Exp. 1 Percent germination: %germ ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	52637	10527	86.001	**< 2.2e-16 *** **	
trt	1	3899	3899	11.674	0.181	(using error a)
block	1	34	34	0.279	0.599	
trt:block (error a)	1	334	334	2.729	0.1019	
trt:sp	5	9427	1885	15.403	**4.818e-11 *** **	
Residuals	94	11507	122			

Table A5. Exp. 1 Harvest 1 height: log(height) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	9.577	1.916	44.370	**< 2.2e-16 *** **	
trt	1	0.288	0.288	2.764	0.345	(using error a)
block	1	0.077	0.077	1.774	0.184	
trt:block (error a)	1	0.104	0.104	2.412	0.12187	
trt:sp	4	1.236	0.309	7.155	**1.982e-05 *** **	
Residuals	217	9.368	0.043			

Table A6. Exp. 1 Harvest 1 dry mass: (mass^0.5) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	0.330	0.066	108.759	**< 2.2e-16 *** **	
trt	1	0.403	0.403	154.903	**0.049 ***	(using error a)
block	1	0.000	0.000	0.096	0.757	
trt:block (error a)	1	0.003	0.003	4.285	0.040 *	
trt:sp	4	0.022	0.006	9.122	**7.89e-07 *** **	
Residuals	217	0.132	0.001			

Table A7. Exp. 1 Harvest 1 R:S mass: (R:S^0.5) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	2.245	0.449	46.077	**<2e-16 *** **	
trt	1	1.843	1.843	1180.912	**0.0185***	(using error a)
block	1	0.000	0.000	0.016	0.898	
trt:block (error a)	1	0.002	0.002	0.16	0.6895	
trt:sp	4	0.064	0.016	1.636	0.166	
Residuals	217	2.115	0.010			

Table A8. Exp 1. Harvest 1 root length: root length ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	454.460	90.890	32.391	**< 2.2e-16 *** **	
trt	1	338.480	338.480	131.518	0.055	(using error a)
block	1	0.090	0.090	0.031	0.860	
trt:block (error a)	1	2.570	2.570	1.272	0.2607	
trt:sp	4	139.770	34.940	12.452	**3.897e-09 *** **	
Residuals	217	608.920	2.810			

Table A9. Exp 1. Harvest 1 R:S length: R:S length ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	34.90	6.98	24.84	0.000 ***	
trt	1	13.71	13.71	15.30	0.159	(using error a)
block	1	0.05	0.05	0.17	0.678	
trt:blk (a)	1	0.90	0.90	3.19	0.075	
trt:sp	4	4.47	1.12	3.98	0.004 **	**
Residuals	21	7.00	60.96	0.28		

Table A10. Exp. 1 Harvest 3 height: log(height) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	31.160	6.232	105.048	**0.000 *** **	
trt	1	18.653	18.653	20162.300	**0.004** **	(using error a)
block	1	0.130	0.130	2.193	0.140	
trt:block (error a)	1	0.001	0.001	0.016	0.901	
trt:sp	5	10.305	2.061	34.741	**0.000 *** **	
Residuals	264	15.662	0.059			

Table A11. Exp. 1 Harvest 3 dry mass: (mass^0.5) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	4.033	0.807	57.135	**0.000 *** **	
trt	1	15.929	15.929	193.186	**0.046***	(using error a)
block	1	0.048	0.048	3.364	0.168	
trt:block (error a)	1	0.083	0.083	5.841	0.016 *	
trt:sp	5	2.808	0.562	39.781	**0.000 *** **	
Residuals	264	3.727	0.014			

Table A12. Exp. 1 Harvest 3 R:S mass: (R:S^0.5) ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	1.189	0.238	27.463	**0.000 *** **	
trt	1	4.430	4.430	192.914	**0.046***	(using error a)
block	1	0.015	0.015	1.708	0.192	
trt:block (error a)	1	0.023	0.023	2.651	0.1047	
trt:sp	5	1.261	0.252	29.106	**0.000 *** **	
Residuals	264	2.287	0.009			

Table A13. Exp. 1 Harvest 3 root length: length ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	2.7E+03	5.5E+02	20.106	**0.000 *** **	
trt	1	1.5E+04	1.5E+04	2590.618	**0.013***	(using error a)
block	1	4.2E-02	4.2E-02	0.002	0.969	
trt:block (error a)	1	5.8E+00	5.8E+00	0.213	0.6447	
trt:sp	5	2.9E+03	5.7E+02	20.981	**0.000 *** **	
Residuals	264	7.2E+03	2.7E+01			

Table A14. Exp. 1 Harvest 3 RMR: RMR ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	0.424	0.085	26.324	**0.000 *** **	
trt	1	1.673	1.673	219.133	**0.043***	(using error a)
block	1	0.005	0.005	1.638	0.202	
trt:block (error a)	1	0.008	0.008	2.371	0.1248	
trt:sp	5	0.439	0.088	27.270	**0.000 *** **	
Residuals	264	0.850	0.003			

Table A15. Exp. 1 Harvest 3 SMR: SMR ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	0.182	0.036	11.956	**0.000 *** **	
trt	1	0.921	0.921	240.000	**0.041***	(using error a)
block	1	0.002	0.002	0.506	0.478	
trt:block (error a)	1	0.018	0.018	5.885	0.016 *	
trt:sp	5	0.049	0.010	3.194	**0.008****	
Residuals	264	0.804	0.003			

Table A16. Exp. 1 Harvest 3 LMR: LMR ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	0.631	0.126	34.543	**0.000 *** **	
trt	1	0.111	0.111	51.546	0.088	(using error a)
block	1	0.013	0.013	3.425	0.065	
trt:block (error a)	1	0.002	0.002	0.591	0.44273	
trt:sp	5	0.563	0.113	30.813	**0.000 *** **	
Residuals	264	0.965	0.004			

Table A17. Exp. 1 Harvest 3 RGR: RGR ~ trt+sp+trt:sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	0.003	0.001	20.520	**0.000 *** **	
trt	1	0.007	0.007	239.277	**0.000 *** **	
sp:trt	5	0.001	0.000	6.159	**0.000 *** **	
Residuals	212	0.006	0.000			

Table A18. Exp. 1 Harvest 3 SLA: SLA ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	3.E+04	6.E+03	26.125	**0.000 *** **	
trt	1	4.E+04	4.E+04	12122.890	**0.006 *** **	(using error a)
block	1	4.E+01	4.E+01	0.184	0.669	
trt:block (error a)	1	3.E+00	3.E+00	0.014	0.905	
trt:sp	5	1.E+03	3.E+02	1.106	0.362	
Residuals	104	2.E+04	2.E+02			

Table A19. Exp. 1 Harvest 3 FARM: FARM ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	2.E+06	3.E+05	4.009	**0.002** **	
trt	1	3.E+06	3.E+06	206.837	**0.044* **	(using error a)
block	1	7.E+04	7.E+04	0.887	0.347	
trt:block (error a)	1	1.E+04	1.E+04	0.160	0.690	
trt:sp	5	1.E+06	2.E+05	2.745	**0.019* **	
Residuals	264	2.E+07	8.E+04			

Table A20. Exp. 1 Harvest 3 R:S length: R:S length ~ trt:block+sp+trt+block+sp:trt

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	5	97.60	19.52	29.63	0.000 ***	
trt	1	110.74	110.74	0.04	0.041 *	(using error a)
block	1	0.26	0.26	0.40	0.529	
trt:block (error a)	1	0.47	0.47	0.72	0.399	
trt:sp	5	71.10	14.22	21.59	0.000 ***	
Residuals	264	173.91	0.66			

Table A21. Exp. 1 Harvest 3 RLR of height: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	17.806	3.561	28.807	< 2.2e-16 ***
Residuals	124	15.329	0.124		

Table A22. Exp. 1 Harvest 3 RLR of 1º root length: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	17.401	3.480	15.738	5.573e-12 ***
Residuals	124	27.420	0.221		

Table A23. Exp. 1 Harvest 3 RLR of dry mass: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	81.149	16.230	23.591	< 2.2e-16 ***
Residuals	124	85.306	0.688		

Table A24. Exp. 1 Harvest 3 RLR of R:S mass: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	14.462	2.892	17.422	4.881e-13 ***
Residuals	124	20.586	0.166		

Table A25. Exp. 1 Harvest 3 RLR of LMR: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	4.914	0.983	22.068	9.136e-16 ***
Residuals	124	5.522	0.045		

Table A26. Exp. 1 Harvest 3 RLR of SMR: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	1.683	0.337	5.729	8.621e-05 ***
Residuals	124	7.283	0.059		

Table A27. Exp. 1 Harvest 3 RLR of RMR: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	6.452	1.290	12.781	5.047e-10 ***
Residuals	124	12.518	0.101		

Table A28. Exp. 1 Harvest 3 RLR of FARM: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	29.489	5.898	16.409	1.988e-12 ***
Residuals	125	44.928	0.359		

Table A29. Exp. 1 Harvest 3 RLR of SLA: RLR ~ sp

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	5	0.756	0.151	3.455	0.009 **
Residuals	51	2.231	0.044		

Table A30. Exp. 2 Harvest 1 height: log(Height) ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	0.432	0.432	9.386	**0.003**	**	
light	1	1.598	1.598	165.252	**0.049**	*	(using error a)
block	1	0.282	0.282	6.125	**0.014**	*	
light:block (error a)	1	0.010	0.010	0.210	0.647		
light:sp	1	0.329	0.329	7.138	**0.008**	**	
Residuals	152	6.995	0.046				

Table A31. Exp. 2 Harvest 1 1º root length: length ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	174.98	174.98	60.180	**0.000**	***	(using error a)
light	1	140.20	140.20	1803.390	**0.015**	***	
block	1	2.36	2.36	0.811	0.369		
light:block (err a)	1	0.08	0.08	0.027	0.870		
light:sp	1	6.58	6.58	2.262	0.135		
Residuals	152	441.96	2.91				

Table A32. Exp. 2 Harvest 1 dry mass: log(mass) ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	8.478	8.478	60.297	**0.000**	***	
light	1	69.815	69.815	2027.050	**0.014**	***	(using error a)
block	1	0.231	0.231	1.642	0.202		
light:block (err a)	1	0.034	0.034	0.245	0.621		
light:sp	1	3.117	3.117	22.165	**0.000**	***	
Residuals	152	21.372	0.141				

Table A33. Exp. 2 Harvest 1 RMR: RMR ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	0.481	0.481	187.128	**0.000**	***	
light	1	0.362	0.362	101.210	0.063		(using error a)
block	1	0.003	0.003	1.101	0.296		
light:block (err a)	1	0.004	0.004	1.390	0.240		
light:sp	1	0.016	0.016	6.368	**0.013**	*	
Residuals	152	0.391	0.003				

Table A34. Exp. 2 Harvest 1 SMR: SMR ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	0.015	0.015	6.576	**0.011**	*	
light	1	0.129	0.129	544.950	**0.027**	***	(using error a)
block	1	0.002	0.002	0.728	0.395		
light:block (err a)	1	0.000	0.000	0.101	0.751		
light:sp	1	0.023	0.023	9.902	**0.002**	**	
Residuals	152	0.356	0.002				

Table A35. Exp. 2 Harvest 1 LMR: LMR ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	0.669	0.669	196.955	**0.000**	***	
light	1	0.059	0.059	29.786	0.115		(using error a)
block	1	0.009	0.009	2.630	0.107		
light:block (error a)	1	0.002	0.002	0.581	0.447		
light:sp	1	0.001	0.001	0.174	0.677		
Residuals	152	0.516	0.003				

Table A36. Exp. 1 Harvest 1 R:S mass: R:Sm ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	1.014	1.014	170.181	**0.000**	***	
light	1	0.748	0.748	128.587	0.056		(using error a)
block	1	0.006	0.006	0.940	0.334		
light:block (error a)	1	0.006	0.006	0.977	0.325		
light:sp	1	0.007	0.007	1.143	0.287		
Residuals	152	0.905	0.006				

Table A37. Exp. 2 Harvest 1 SSL: sqrt(SSL) ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	3106.8	3106.8	237.6	**0.000**	***	
light	1	5108.6	5108.6	969.5	**0.001**	**	(using error a)
block	2	273.1	136.5	10.4	**0.000**	***	
light:block (error a)	2	10.5	5.3	0.4	0.669		
light:sp	1	187.7	187.7	14.4	**0.000**	***	
Residuals	152	1922.1	13.1				

Table A38. Exp. 2 Harvest 1 R:S length: log(R:Sl) ~ H1 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
sp	1	8.173	8.173	87.396	**0.000**	***	
light	1	0.598	0.598	39.706	0.100		(using error a)
block	1	0.527	0.527	5.633	**0.019**	*	
light:block (error a)	1	0.015	0.015	0.161	0.689		
light:sp	1	0.059	0.059	0.630	0.429		
Residuals	152	14.214	0.094				

Table A39. Exp. 2 Harvest 2 height: log(Height) ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.397	0.199	3.560	**0.031**	*	
light	1	10.378	10.378	1427.512	**0.001**	***	(using error a)
water	1	0.001	0.001	0.022	0.890		(using error b)
comp	1	0.127	0.127	2.273	0.134		
sp	1	19.513	19.513	349.913	**0.000**	***	
block:light (error a)	2	0.015	0.007	0.130	0.878		
error b	4	0.152	0.038				
light:water	1	0.013	0.013	0.335	0.594		(using error b)
comp:sp	1	0.021	0.021	0.382	0.537		
light:comp	1	0.007	0.007	0.118	0.732		
light:sp	1	4.150	4.150	74.409	**0.000**	***	
water:comp	1	0.010	0.010	0.171	0.680		
water:sp	1	0.014	0.014	0.248	0.619		
water:comp:sp	1	0.003	0.003	0.048	0.827		
light:water:comp	1	0.003	0.003	0.054	0.816		
light:water:sp	1	0.025	0.025	0.450	0.504		
light:water:comp:sp	2	0.024	0.012	0.212	0.809		
Residuals	131	7.305	0.056				

Table A40. Exp. 2 Harvest 2 primary root length: root length ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	172.6	86.3	3.502	**0.033**	*	
light	1	11886.1	11886.1	281.536	**0.004**	**	(using error a)
water	1	0.6	0.6	0.012	0.918		(using error b)
comp	1	48.9	48.9	1.982	0.162		
sp	1	372.6	372.6	15.117	**0.000**	***	
block:light (error a)	2	84.4	42.2	1.713	0.184		
error b	4	213.9	53.5				
light:water	1	0.7	0.7	0.012	0.917		(using error b)
comp:sp	1	60.2	60.2	2.443	0.120		
light:comp	1	4.5	4.5	0.183	0.670		
light:sp	1	0.6	0.6	0.024	0.877		
water:comp	1	14.1	14.1	0.571	0.451		
water:sp	1	10.6	10.6	0.431	0.513		
water:comp:sp	1	5.5	5.5	0.224	0.637		
light:water:comp	1	87.9	87.9	3.568	0.061		
light:water:sp	1	92.9	92.9	3.770	0.054		
light:water:comp:sp	2	111.7	55.8	2.265	0.108		
Residuals	131	3228.9	24.6				

Table A41. Exp. 2 Harvest 2 plant dry mass: log(dry mass) ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	1.292	0.646	3.404	**0.036**	*	
light	1	169.091	169.091	1794.232	**0.001**	***	(using error a)
water	1	0.098	0.098	0.502	0.518		(using error b)
comp	1	3.255	3.255	17.155	**0.000**	***	
sp	1	6.762	6.762	35.640	**0.000**	***	
block:light (error a)	2	0.188	0.094	0.497	0.610		
error b	4	0.783	0.196				
light:water	1	0.030	0.030	0.156	0.713		(using error b)
comp:sp	1	0.023	0.023	0.119	0.731		
light:comp	1	0.330	0.330	1.738	0.190		
light:sp	1	6.133	6.133	32.325	**0.000**	***	
water:comp	1	0.026	0.026	0.139	0.710		
water:sp	1	0.050	0.050	0.262	0.610		
water:comp:sp	1	0.184	0.184	0.971	0.326		
light:water:comp	1	0.147	0.147	0.774	0.381		
light:water:sp	1	0.096	0.096	0.506	0.478		
light:water:comp:sp	2	0.554	0.277	1.461	0.236		
Residuals	127	24.096	0.190				

Table A42. Exp. 2 Harvest 2 SLA: SLA ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	512.5	256.2	1.255	0.293		
light	1	17381.2	17381.2	167.670	**0.006**	**	(using error a)
water	1	2.1	2.1	0.005	0.948		(using error b)
comp	1	622.1	622.1	3.048	0.086		
sp	1	81.6	81.6	0.400	0.530		
block:light (error a)	2	207.3	103.7	0.508	0.605		
error b	4	1701.8	427.7				
light:water	1	0.7	0.7	0.002	0.970		(using error b)
comp:sp	1	158.4	158.4	0.776	0.382		
light:comp	1	76.0	76.0	0.373	0.544		
light:sp	1	184.4	184.4	0.904	0.346		
water:comp	1	34.4	34.4	0.169	0.683		
water:sp	1	191.1	191.1	0.936	0.337		
water:comp:sp	1	52.6	52.6	0.258	0.614		
light:water:comp	1	69.7	69.7	0.342	0.561		
light:water:sp	1	190.0	190.0	0.931	0.339		
light:water:comp:sp	2	481.4	240.7	1.179	0.315		
Residuals	55	11227.3	204.1				

Table A43. Exp. 2 Harvest 2 RMR: RMR ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.010	0.005	2.059	0.132		
light	1	0.122	0.122	123.206	**0.008**	***	(using error a)
water	1	0.007	0.007	21.833	**0.010**	**	(using error b)
comp	1	0.027	0.027	11.416	**0.001**	***	
sp	1	1.052	1.052	439.079	**0.000**	***	
block:light (error a)	2	0.002	0.001	0.412	0.663		
error b	4	0.001	0.000				
light:water	1	0.000	0.000	1.062	0.361		(using error b)
comp:sp	1	0.001	0.001	0.336	0.563		
light:comp	1	0.001	0.001	0.568	0.452		
light:sp	1	0.031	0.031	12.887	**0.000**	***	
water:comp	1	0.000	0.000	0.055	0.814		
water:sp	1	0.000	0.000	0.015	0.904		
water:comp:sp	1	0.000	0.000	0.013	0.908		
light:water:comp	1	0.001	0.001	0.487	0.487		
light:water:sp	1	0.001	0.001	0.474	0.493		
light:water:comp:sp	2	0.001	0.001	0.301	0.740		
Residuals	127	0.304	0.002				

Table A44. Exp. 2 Harvest 2 SMR: SMR ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.020	0.010	5.440	**0.005**	**	
light	1	0.108	0.108	231.395	**0.004**	**	(using error a)
water	1	0.001	0.001	4.665	0.097		(using error b)
comp	1	0.000	0.000	0.068	0.794		
sp	1	0.002	0.002	1.288	0.259		
block:light (error a)	2	0.001	0.000	0.250	0.779		
error b	4	0.001	0.000				
light:water	1	0.002	0.002	17.253	**0.014**	*	(using error b)
comp:sp	1	0.000	0.000	0.155	0.694		
light:comp	1	0.004	0.004	1.906	0.170		
light:sp	1	0.008	0.008	4.129	**0.044**	*	
water:comp	1	0.000	0.000	0.016	0.901		
water:sp	1	0.001	0.001	0.291	0.591		
water:comp:sp	1	0.004	0.004	1.949	0.165		
light:water:comp	1	0.000	0.000	0.014	0.906		
light:water:sp	1	0.000	0.000	0.088	0.768		
light:water:comp:sp	2	0.004	0.002	1.173	0.313		
Residuals	127	0.238	0.002				

Table A45. Exp. 2 Harvest 2 LMR: LMR ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.004	0.002	0.586	0.558		
light	1	0.000	0.000	0.771	0.472		(using error a)
water	1	0.012	0.012	42.498	**0.003**	**	(using error b)
comp	1	0.024	0.024	7.705	**0.006**	**	
sp	1	0.954	0.954	309.548	**0.000**	***	
block:light (error a)	2	0.001	0.000	0.164	0.849		
error b	4	0.001	0.000				
light:water	1	0.004	0.004	15.006	**0.018**	*	(using error b)
comp:sp	1	0.000	0.000	0.042	0.838		
light:comp	1	0.001	0.001	0.169	0.682		
light:sp	1	0.008	0.008	2.504	0.116		
water:comp	1	0.000	0.000	0.093	0.761		
water:sp	1	0.000	0.000	0.098	0.755		
water:comp:sp	1	0.003	0.003	0.972	0.326		
light:water:comp	1	0.001	0.001	0.274	0.602		
light:water:sp	1	0.002	0.002	0.702	0.404		
light:water:comp:sp	2	0.002	0.001	0.245	0.783		
Residuals	127	0.391	0.003				

Table A46. Exp. 2 Harvest 2 FARM: FARM ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	13446	6723	1.747	0.178		
light	1	237529	237529	74.794	**0.013**	*	(using error a)
water	1	1732	1732	0.900	0.396		(using error b)
comp	1	63724	63724	16.560	**0.000**	***	
sp	1	935125	935125	243.009	**0.000**	***	
block:light (error a)	2	6352	3176	0.825	0.440		
error b	4	7698	1925				
light:water	1	954	954	0.496	0.520		(using error b)
comp:sp	1	11430	11430	2.970	0.087		
light:comp	1	1463	1463	0.380	0.539		
light:sp	1	27582	27582	7.168	**0.008**	**	
water:comp	1	1026	1026	0.267	0.607		
water:sp	1	467	467	0.122	0.728		
water:comp:sp	1	76	76	0.020	0.889		
light:water:comp	1	6569	6569	1.707	0.194		
light:water:sp	1	4316	4316	1.122	0.292		
light:water:comp:sp	2	7261	3630	0.943	0.392		
Residuals	127	488709	3848				

Table A47. Exp. 2 Harvest 2 R:S mass: R:S mass ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.052	0.026	1.975	0.143		
light	1	0.744	0.744	83.265	**0.012**	*	(using error a)
water	1	0.037	0.037	38.024	**0.004**	**	(using error b)
comp	1	0.116	0.116	8.830	**0.004**	**	
sp	1	4.978	4.978	380.148	**0.000**	***	
block:light (error a)	2	0.018	0.009	0.682	0.507		
error b	4	0.004	0.001				
light:water	1	0.002	0.002	2.155	0.216		(using error b)
comp:sp	1	0.000	0.000	0.011	0.915		
light:comp	1	0.008	0.008	0.593	0.443		
light:sp	1	0.331	0.331	25.288	**0.000**	***	
water:comp	1	0.001	0.001	0.110	0.741		
water:sp	1	0.001	0.001	0.087	0.769		
water:comp:sp	1	0.001	0.001	0.060	0.807		
light:water:comp	1	0.004	0.004	0.337	0.563		
light:water:sp	1	0.004	0.004	0.282	0.596		
light:water:comp:sp	2	0.006	0.003	0.211	0.810		
Residuals	127	1.663	0.013				

Table A48. Exp. 2 Harvest 2 R:S length: sqrt(R:S length) ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	1.123	0.562	7.508	**0.001**	***	
light	1	11.915	11.915	626.290	**0.002**	***	(using error a)
water	1	0.005	0.005	0.062	0.815		(using error b)
comp	1	0.071	0.071	0.946	0.333		
sp	1	31.318	31.318	418.788	**0.000**	***	
block:light (error a)	2	0.038	0.019	0.254	0.776		
error b	4	0.319	0.080				
light:water	1	0.040	0.040	0.500	0.518		(using error b)
comp:sp	1	0.111	0.111	1.480	0.226		
light:comp	1	0.016	0.016	0.212	0.646		
light:sp	1	4.394	4.394	58.762	**0.000**	***	
water:comp	1	0.001	0.001	0.016	0.901		
water:sp	1	0.021	0.021	0.278	0.599		
water:comp:sp	1	0.000	0.000	0.005	0.941		
light:water:comp	1	0.294	0.294	3.937	**0.049**	*	
light:water:sp	1	0.200	0.200	2.670	0.105		
light:water:comp:sp	2	0.395	0.198	2.641	0.075		
Residuals	129	9.647	0.075				

Table A49. Exp. 2 Harvest 2 SRL: log(SRL) ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.000	0.000	0.007	0.993		
light	1	3.357	3.357	192.994	**0.005**	***	(using error a)
water	1	0.366	0.366	101.750	**0.001**	***	(using error b)
comp	1	0.097	0.097	3.322	0.071		
sp	1	8.379	8.379	288.539	**0.000**	***	
block:light (error a)	2	0.035	0.017	0.599	0.551		
error b	4	0.014	0.004				
light:water	1	0.010	0.010	2.643	0.179		(using error b)
comp:sp	1	0.031	0.031	1.066	0.304		
light:comp	1	0.070	0.070	2.405	0.124		
light:sp	1	0.876	0.876	30.158	**0.000**	***	
water:comp	1	0.266	0.266	9.142	**0.003**	**	
water:sp	1	0.026	0.026	0.910	0.342		
water:comp:sp	1	0.002	0.002	0.069	0.793		
light:water:comp	1	0.001	0.001	0.036	0.851		
light:water:sp	1	0.038	0.038	1.322	0.253		
light:water:comp:sp	2	0.016	0.008	0.276	0.759		
Residuals	120	3.485	0.029				

Table A50. Exp. 2 Harvest 2 SSL: sqrt(SSL) ~ H2 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	29.6	14.8	3.226	**0.043**	*	
light	1	4484.2	4484.2	1061.071	**0.001**	***	(using error a)
water	1	6.5	6.5	1.000	0.374		(using error b)
comp	1	123.8	123.8	27.011	**0.000**	***	
sp	1	250.5	250.5	54.647	**0.000**	***	
block:light (error a)	2	8.5	4.2	0.922	0.400		
error b	4	26.2	6.6				
light:water	1	8.8	8.8	1.341	0.311		(using error b)
comp:sp	1	6.9	6.9	1.501	0.223		
light:comp	1	0.8	0.8	0.165	0.685		
light:sp	1	112.4	112.4	24.525	**0.000**	***	
water:comp	1	0.1	0.1	0.013	0.910		
water:sp	1	0.8	0.8	0.175	0.676		
water:comp:sp	1	3.2	3.2	0.697	0.405		
light:water:comp	1	6.1	6.1	1.327	0.252		
light:water:sp	1	0.7	0.7	0.146	0.703		
light:water:comp:sp	2	32.5	16.3	3.545	**0.032**	*	
Residuals	127	582.2	4.6				

Table A51. Exp. 2 Harvest 2 RLR of height: RLR ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	7.613	7.613	71.008	**0.000**	***
comp	1	0.037	0.037	0.343	0.560	
water	1	0.039	0.039	0.359	0.551	
sp:comp	1	0.005	0.005	0.049	0.825	
sp:water	1	0.102	0.102	0.949	0.333	
comp:water	1	0.000	0.000	0.002	0.965	
sp:comp:water	1	0.005	0.005	0.050	0.824	
Residuals	67	7.183	0.107			

Table A52. Exp. 2 Harvest 2 RLR of dry mass: RLR ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	9.596	9.596	26.049	**0.000**	***
comp	1	0.409	0.409	1.109	0.296	
water	1	0.081	0.081	0.220	0.641	
sp:comp	1	1.377	1.377	3.738	0.058	
sp:water	1	0.054	0.054	0.147	0.703	
comp:water	1	0.135	0.135	0.367	0.547	
sp:comp:water	1	0.003	0.003	0.008	0.929	
Residuals	63	23.208	0.368			

Table A53. Exp. 2 Harvest 2 RLR of R:S mass: RLR ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.735	0.735	5.649	**0.021**	*
comp	1	0.091	0.091	0.702	0.405	
water	1	0.006	0.006	0.048	0.827	
sp:comp	1	0.014	0.014	0.110	0.742	
sp:water	1	0.043	0.043	0.327	0.570	
comp:water	1	0.055	0.055	0.423	0.518	
sp:comp:water	1	0.050	0.050	0.386	0.537	
Residuals	63	8.196	0.130			

Table A54. Exp. 2 Harvest 2 RLR of SRL: RLR ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	1.671	1.671	30.854	**0.000**	***
comp	1	0.056	0.056	1.042	0.312	
water	1	0.019	0.019	0.356	0.553	
sp:comp	1	0.001	0.001	0.026	0.874	
sp:water	1	0.080	0.080	1.474	0.230	
comp:water	1	0.010	0.010	0.181	0.672	
sp:comp:water	1	0.072	0.072	1.332	0.253	
Residuals	58	3.141	0.054			

Table A55. Exp. 2 Harvest 2 RWR of height: RWR ~ RWR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.083	0.083	0.758	0.387
comp	1	0.008	0.008	0.073	0.788
light	1	0.019	0.019	0.177	0.676
sp:comp	1	0.041	0.041	0.375	0.543
sp:light	1	0.032	0.032	0.296	0.588
comp:light	1	0.007	0.007	0.066	0.797
sp:comp:light	1	0.052	0.052	0.472	0.495
Residuals	67	7.315	0.109		

Table A56. Exp. 2 Harvest 2 RWR of dry mass: RWR ~ RWR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.245	0.245	0.787	0.378
comp	1	0.014	0.014	0.044	0.835
light	1	0.153	0.153	0.492	0.486
sp:comp	1	0.059	0.059	0.190	0.665
sp:light	1	0.077	0.077	0.246	0.622
comp:light	1	0.374	0.374	1.201	0.277
sp:comp:light	1	0.050	0.050	0.160	0.690
Residuals	63	19.588	0.311		

Table A57. Exp. 2 Harvest 2 RWR of R:S mass: RWR ~ RWR mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.000	0.000	0.001	0.976	
comp	1	0.021	0.021	0.148	0.702	
light	1	0.002	0.002	0.016	0.900	
sp:comp	1	0.001	0.001	0.006	0.937	
sp:light	1	0.024	0.024	0.168	0.683	
comp:light	1	0.037	0.037	0.257	0.614	
sp:comp:light	1	0.024	0.024	0.168	0.684	
Residuals	63	9.030	0.143			

Table A58. Exp. 2 Harvest 2 RWR of SRL: RWR ~ RWR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.027	0.027	0.505	0.480	
comp	1	0.529	0.529	9.742	**0.003**	**
light	1	0.065	0.065	1.196	0.279	
sp:comp	1	0.000	0.000	0.003	0.958	
sp:light	1	0.036	0.036	0.662	0.419	
comp:light	1	0.014	0.014	0.255	0.615	
sp:comp:light	1	0.098	0.098	1.810	0.184	
Residuals	58	3.149	0.054			

Table A59. Exp. 2 Harvest 2 RCR of height: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.027	0.027	0.240	0.626
light	1	0.062	0.062	0.553	0.460
water	1	0.012	0.012	0.110	0.742
sp:light	1	0.010	0.010	0.089	0.767
sp:water	1	0.007	0.007	0.067	0.797
light:water	1	0.006	0.006	0.050	0.824
sp:light:water	1	0.013	0.013	0.115	0.736
Residuals	67	7.495	0.112		

Table A60. Exp. 2 Harvest 2 RCR of dry mass: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.018	0.018	0.052	0.821	
light	1	0.535	0.535	1.530	0.221	
water	1	0.068	0.068	0.195	0.660	
sp:light	1	1.606	1.606	4.594	**0.036**	*
sp:water	1	0.070	0.070	0.199	0.657	
light:water	1	0.071	0.071	0.202	0.654	
sp:light:water	1	0.003	0.003	0.007	0.933	
Residuals	63	22.030	0.350			

Table A61. Exp. 2 Harvest 2 RCR of R:S mass: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.136	0.136	1.074	0.304
light	1	0.032	0.032	0.252	0.617
water	1	0.061	0.061	0.485	0.489
sp:light	1	0.015	0.015	0.122	0.728
sp:water	1	0.002	0.002	0.018	0.894
light:water	1	0.004	0.004	0.033	0.856
sp:light:water	1	0.048	0.048	0.384	0.538
Residuals	63	7.957	0.126		

Table A62. Exp. 2 Harvest 2 RCR of SRL: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.080	0.080	1.422	0.238
light	1	0.159	0.159	2.839	0.097
water	1	0.459	0.459	8.183	**0.006** **
sp:light	1	0.004	0.004	0.062	0.804
sp:water	1	0.017	0.017	0.299	0.587
light:water	1	0.001	0.001	0.017	0.895
sp:light:water	1	0.007	0.007	0.121	0.729
Residuals	57	3.197	0.056		

Table A63. Exp. 2 Harvest 2 height--Light treatment: log(Height) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.151	0.076	1.115	0.334	
water	1	0.000	0.000	0.000	0.995	(using error a)
comp	1	0.029	0.029	0.430	0.514	
sp	1	20.900	20.900	308.632	**0.000** ***	
block:water (error a)	2	0.022	0.011	0.161	0.852	
comp:sp	1	0.008	0.008	0.122	0.728	
water:comp	1	0.010	0.010	0.153	0.697	
water:sp	1	0.035	0.035	0.518	0.474	
water:comp:sp	1	0.004	0.004	0.065	0.799	
Residuals	67	4.537	0.068			

Table A64. Exp. 2 Harvest 2 height--Shade treatment: log(Height) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.225	0.113	2.604	0.082	
water	1	0.002	0.002	0.018	0.906	(using error a)
comp	1	0.109	0.109	2.519	0.117	
sp	1	2.715	2.715	62.769	**0.000**	***
block:water (error a)	2	0.185	0.092	2.136	0.126	
comp:sp	1	0.023	0.023	0.533	0.468	
water:comp	1	0.001	0.001	0.013	0.909	
water:sp	1	0.002	0.002	0.035	0.853	
water:comp:sp	1	0.020	0.020	0.454	0.503	
Residuals	64	2.768	0.043			

Table A65. Exp. 2 Harvest 2 1º root length--Light treatment: length ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	291.1	145.6	3.465	**0.037**	*
water	1	0.1	0.1	0.001	0.976	(using error a)
comp	1	43.2	43.2	1.028	0.314	
sp	1	202.9	202.9	4.829	**0.031**	*
block:water (error a)	2	217.3	108.7	2.586	0.083	
comp:sp	1	138.6	138.6	3.300	0.074	
water:comp	1	85.7	85.7	2.040	0.158	
water:sp	1	90.7	90.7	2.159	0.146	
water:comp:sp	1	24.6	24.6	0.585	0.447	
Residuals	67	2815.0	42.0			

Table A66. Exp. 2 Harvest 2 1º root length--Shade treatment: length ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	18.0	9.0	1.395	0.255	
water	1	0.5	0.5	0.426	0.581	(using error a)
comp	1	12.2	12.2	1.893	0.174	
sp	1	161.8	161.8	25.022	**0.000**	***
block:water (error a)	2	2.4	1.2	0.189	0.829	
comp:sp	1	3.6	3.6	0.559	0.457	
water:comp	1	16.9	16.9	2.619	0.111	
water:sp	1	15.3	15.3	2.358	0.130	
water:comp:sp	1	2.0	2.0	0.310	0.580	
Residuals	64	413.9	6.5			

Table A67. Exp. 2 Harvest 2 dry mass--Light treatment: log(mass) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	1.120	0.560	2.062	0.135	
water	1	0.001	0.001	0.004	0.956	(using error a)
comp	1	2.944	2.944	10.839	**0.002**	**
sp	1	12.649	12.649	46.575	**0.000**	***
block:water (error a)	2	0.297	0.149	0.547	0.581	
comp:sp	1	0.130	0.130	0.479	0.491	
water:comp	1	0.140	0.140	0.516	0.475	
water:sp	1	0.128	0.128	0.471	0.495	
water:comp:sp	1	0.133	0.133	0.489	0.487	
Residuals	67	18.196	0.272			

Table A68. Exp. 2 Harvest 2 dry mass--Shade treatment: log(mass) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.533	0.266	2.709	0.075	
water	1	0.201	0.201	0.582	0.525	(using error a)
comp	1	0.618	0.618	6.281	**0.015**	*
sp	1	0.001	0.001	0.009	0.924	
block:water (error a)	2	0.691	0.345	3.511	**0.036**	*
comp:sp	1	0.516	0.516	5.242	**0.026**	*
water:comp	1	0.023	0.023	0.237	0.628	
water:sp	1	0.000	0.000	0.000	0.997	
water:comp:sp	1	0.040	0.040	0.402	0.528	
Residuals	60	5.900	0.098			

Table A69. Exp. 2 Harvest 2 SLA--Light treatment: SLA ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	157.99	78.99	0.991	0.384	
water	1	0.73	0.73	0.031	0.877	(using error a)
comp	1	658.45	658.45	8.263	**0.008**	**
sp	1	12.02	12.02	0.151	0.701	
block:water (error a)	2	47.43	23.71	0.298	0.745	
comp:sp	1	250.23	250.23	3.140	0.087	
water:comp	1	2.31	2.31	0.029	0.866	
water:sp	1	0.73	0.73	0.009	0.924	
water:comp:sp	1	407.22	407.22	5.110	**0.032**	*
Residuals	28	2231.24	79.69			

Table A70. Exp. 2 Harvest 2 SLA--Shade treatment: SLA ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	526.9	263.4	0.791	0.464	
water	1	0.8	0.8	0.001	0.978	(using error a)
comp	1	125.9	125.9	0.378	0.544	
sp	1	263.1	263.1	0.790	0.382	
block:water (error a)	2	1610.8	805.4	2.417	0.108	
comp:sp	1	18.8	18.8	0.057	0.814	
water:comp	1	108.8	108.8	0.327	0.572	
water:sp	1	336.3	336.3	1.009	0.324	
water:comp:sp	1	81.7	81.7	0.245	0.625	
Residuals	27	8996.1	333.2			

Table A71. Exp. 2 Harvest 2 RMR--Light treatment: RMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.009	0.005	1.845	0.166		
water	1	0.006	0.006	33.792	**0.028**	*	(using error a)
comp	1	0.017	0.017	6.766	**0.011**	*	
sp	1	0.747	0.747	301.914	**0.000**	***	
block:water (error a)	2	0.000	0.000	0.072	0.930		
comp:sp	1	0.000	0.000	0.060	0.807		
water:comp	1	0.001	0.001	0.409	0.525		
water:sp	1	0.000	0.000	0.152	0.698		
water:comp:sp	1	0.000	0.000	0.180	0.673		
Residuals	67	0.166	0.002				

Table A72. Exp. 2 Harvest 2 RMR--Shade treatment: RMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.002	0.001	0.469	0.628		
water	1	0.002	0.002	3.521	0.201		(using error a)
comp	1	0.011	0.011	4.568	**0.037**	*	
sp	1	0.338	0.338	146.488	**0.000**	***	
block:water (error a)	2	0.001	0.001	0.242	0.786		
comp:sp	1	0.000	0.000	0.167	0.684		
water:comp	1	0.000	0.000	0.131	0.718		
water:sp	1	0.001	0.001	0.321	0.573		
water:comp:sp	1	0.001	0.001	0.444	0.508		
Residuals	60	0.139	0.002				

Table A73. Exp. 2 Harvest 2 SMR--Light treatment: SMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.012	0.006	4.478	**0.015**	*	
water	1	0.002	0.002	12.543	0.071		(using error a)
comp	1	0.003	0.003	1.874	0.176		
sp	1	0.010	0.010	7.220	**0.009**	**	
block:water (error a)	2	0.000	0.000	0.142	0.868		
comp:sp	1	0.000	0.000	0.269	0.605		
water:comp	1	0.000	0.000	0.000	0.986		
water:sp	1	0.001	0.001	0.541	0.465		
water:comp:sp	1	0.000	0.000	0.022	0.883		
Residuals	67	0.089	0.001				

Table A74. Exp. 2 Harvest 2 SMR--Shade treatment: SMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.010	0.005	2.003	0.144		
water	1	0.000	0.000	6.944	0.119		(using error a)
comp	1	0.001	0.001	0.419	0.520		
sp	1	0.001	0.001	0.352	0.555		
block:water (error a)	2	0.000	0.000	0.018	0.982		
comp:sp	1	0.002	0.002	0.704	0.405		
water:comp	1	0.000	0.000	0.035	0.853		
water:sp	1	0.000	0.000	0.000	0.987		
water:comp:sp	1	0.006	0.006	2.461	0.122		
Residuals	60	0.148	0.002				

Table A75. Exp. 2 Harvest 2 LMR--Light treatment: LMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.000	0.000	0.042	0.959		
water	1	0.016	0.016	250.686	**0.004**	**	(using error a)
comp	1	0.006	0.006	2.076	0.154		
sp	1	0.587	0.587	193.498	**0.000**	***	
block:water (error a)	2	0.000	0.000	0.021	0.979		
comp:sp	1	0.001	0.001	0.320	0.574		
water:comp	1	0.001	0.001	0.320	0.573		
water:sp	1	0.002	0.002	0.706	0.404		
water:comp:sp	1	0.001	0.001	0.231	0.632		
Residuals	67	0.203	0.003				

Table A76. Exp. 2 Harvest 2 LMR--Shade treatment: LMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.005	0.003	0.806	0.452	
water	1	0.001	0.001	1.167	0.393	(using error a)
comp	1	0.018	0.018	5.800	**0.019**	*
sp	1	0.373	0.373	119.099	**0.000**	***
block:water (error a)	2	0.001	0.001	0.198	0.821	
comp:sp	1	0.000	0.000	0.155	0.695	
water:comp	1	0.000	0.000	0.021	0.885	
water:sp	1	0.001	0.001	0.222	0.639	
water:comp:sp	1	0.002	0.002	0.672	0.416	
Residuals	60	0.188	0.003			

Table A77. Exp. 2 Harvest 2 FARM--Light treatment: FARM ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	10495	5247	1.607	0.208	
water	1	3109	3109	3.770	0.192	(using error a)
comp	1	37096	37096	11.362	**0.001**	**
sp	1	344609	344609	105.548	**0.000**	***
block:water (error a)	2	1649	825	0.253	0.778	
comp:sp	1	10233	10233	3.134	0.081	
water:comp	1	1032	1032	0.316	0.576	
water:sp	1	1042	1042	0.319	0.574	
water:comp:sp	1	3513	3513	1.076	0.303	
Residuals	67	218751	3265			

Table A78. Exp. 2 Harvest 2 FARM--Shade treatment: FARM ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	13558	6779	1.507	0.230	
water	1	4	4	0.001	0.974	(using error a)
comp	1	26120	26120	5.805	**0.019**	*
sp	1	614040	614040	136.475	**0.000**	***
block:water (error a)	2	5468	2734	0.608	0.548	
comp:sp	1	4120	4120	0.916	0.342	
water:comp	1	6541	6541	1.454	0.233	
water:sp	1	3880	3880	0.862	0.357	
water:comp:sp	1	3106	3106	0.690	0.409	
Residuals	60	269957	4499			

Table A79. Exp. 2 Harvest 2 R:S mass--Light treatment: R:S mass ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.051	0.026	1.577	0.214		
water	1	0.031	0.031	603.084	**0.002**	**	(using error a)
comp	1	0.075	0.075	4.573	**0.036**	*	
sp	1	4.048	4.048	248.221	**0.000**	***	
block:water (error a)	2	0.000	0.000	0.003	0.997		
comp:sp	1	0.003	0.003	0.205	0.653		
water:comp	1	0.006	0.006	0.336	0.564		
water:sp	1	0.000	0.000	0.020	0.887		
water:comp:sp	1	0.000	0.000	0.027	0.870		
Residuals	67	1.093	0.016				

Table A80. Exp. 2 Harvest 2 R:S mass--Shade treatment: R:S mass ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.009	0.005	0.490	0.615		
water	1	0.010	0.010	3.607	0.198		(using error a)
comp	1	0.041	0.041	4.324	**0.042**	*	
sp	1	1.275	1.275	134.084	**0.000**	***	
block:water (error a)	2	0.005	0.003	0.280	0.757		
comp:sp	1	0.000	0.000	0.020	0.887		
water:comp	1	0.001	0.001	0.063	0.803		
water:sp	1	0.004	0.004	0.392	0.534		
water:comp:sp	1	0.004	0.004	0.409	0.525		
Residuals	60	0.570	0.010				

Table A81. Exp. 2 Harvest 2 R:S length--Light treatment: sqrt(R:S length) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.840	0.420	5.259	**0.008**	**	
water	1	0.003	0.003	0.020	0.902		(using error a)
comp	1	0.071	0.071	0.889	0.349		
sp	1	29.910	29.910	374.613	**0.000**	***	
block:water (error a)	2	0.304	0.152	1.904	0.157		
comp:sp	1	0.373	0.373	4.666	**0.034**	*	
water:comp	1	0.125	0.125	1.560	0.216		
water:sp	1	0.049	0.049	0.619	0.434		
water:comp:sp	1	0.094	0.094	1.176	0.282		
Residuals	67	5.349	0.080				

Table A82. Exp. 2 Harvest 2 R:S length--Shade treatment: sqrt(R:S length) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.360	0.180	2.593	0.083		
water	1	0.026	0.026	1.766	0.315		(using error a)
comp	1	0.017	0.017	0.242	0.625		
sp	1	5.719	5.719	82.502	**0.000**	***	
block:water (error a)	2	0.029	0.015	0.212	0.810		
comp:sp	1	0.010	0.010	0.145	0.704		
water:comp	1	0.167	0.167	2.409	0.126		
water:sp	1	0.144	0.144	2.083	0.154		
water:comp:sp	1	0.081	0.081	1.172	0.283		
Residuals	62	4.298	0.069				

Table A83. Exp. 2 Harvest 2 SRL--Light treatment: log(SRL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.021	0.011	0.356	0.702		
water	1	0.168	0.168	30.076	**0.032**	*	(using error a)
comp	1	0.246	0.246	8.197	**0.006**	**	
sp	1	2.030	2.030	67.756	**0.000**	***	
block:water (error a)	2	0.011	0.006	0.186	0.831		
comp:sp	1	0.021	0.021	0.698	0.407		
water:comp	1	0.119	0.119	3.987	0.050		
water:sp	1	0.000	0.000	0.009	0.925		
water:comp:sp	1	0.016	0.016	0.531	0.469		
Residuals	62	1.858	0.030				

Table A84. Exp. 2 Harvest 2 SRL--Shade treatment: log(SRL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.035	0.018	0.631	0.536		
water	1	0.198	0.198	91.621	**0.011**	*	(using error a)
comp	1	0.004	0.004	0.142	0.708		
sp	1	7.103	7.103	253.200	**0.000**	***	
block:water (error a)	2	0.004	0.002	0.077	0.926		
comp:sp	1	0.040	0.040	1.434	0.236		
water:comp	1	0.149	0.149	5.305	**0.025**	*	
water:sp	1	0.061	0.061	2.175	0.146		
water:comp:sp	1	0.002	0.002	0.085	0.771		
Residuals	58	1.627	0.028				

Table A85. Exp. 2 Harvest 2 SSL--Light treatment: sqrt(SSL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	23.854	11.927	2.629	0.080	
water	1	0.267	0.267	0.183	0.710	(using error a)
comp	1	49.013	49.013	10.802	**0.002**	**
sp	1	18.496	18.496	4.076	**0.047**	*
block:water (error a)	2	2.915	1.457	0.321	0.726	
comp:sp	1	3.656	3.656	0.806	0.373	
water:comp	1	2.122	2.122	0.468	0.496	
water:sp	1	1.268	1.268	0.280	0.599	
water:comp:sp	1	2.105	2.105	0.464	0.498	
Residuals	67	304.004	4.537			

Table A86. Exp. 2 Harvest 2 SSL--Shade treatment: sqrt(SSL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	19.380	9.690	2.090	0.133	
water	1	19.010	19.010	1.381	0.361	(using error a)
comp	1	71.630	71.630	15.448	**0.000**	***
sp	1	338.680	338.680	73.043	**0.000**	***
block:water (error a)	2	27.520	13.760	2.968	0.059	
comp:sp	1	38.230	38.230	8.244	**0.006**	**
water:comp	1	3.420	3.420	0.737	0.394	
water:sp	1	0.250	0.250	0.055	0.816	
water:comp:sp	1	0.430	0.430	0.093	0.761	
Residuals	60	278.200	4.640			

Table A87. Exp. 2 Harvest 3 height: log(Height) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.107	0.054	0.585	0.559		
light	1	16.295	16.295	172.099	**0.006**	**	(using error a)
water	1	0.000	0.000	0.002	0.967		(using error b)
comp	1	0.833	0.833	9.095	**0.003**	**	
sp	1	13.483	13.483	147.159	**0.000**	***	
block:light (error a)	2	0.189	0.095	1.033	0.359		
error b	4	0.597	0.149				
light:water	1	0.027	0.027	0.181	0.692		(using error b)
comp:sp	1	0.358	0.358	3.911	0.050		
light:comp	1	0.024	0.024	0.257	0.613		
light:sp	1	0.000	0.000	0.001	0.971		
water:comp	1	0.215	0.215	2.343	0.129		
water:sp	1	0.005	0.005	0.052	0.819		
water:comp:sp	1	0.229	0.229	2.500	0.117		
light:water:comp	1	0.001	0.001	0.009	0.925		
light:water:sp	1	0.103	0.103	1.122	0.292		
light:water:comp:sp	2	0.159	0.079	0.866	0.424		
Residuals	112	10.262	0.092				

Table A88. Exp. 2 Harvest 3 root tips/length: tips/length ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.134	0.067	0.682	0.508		
light	1	0.001	0.001	0.022	0.895		(using error a)
water	1	0.001	0.001	0.012	0.919		(using error b)
comp	1	0.224	0.224	2.284	0.134		
sp	1	9.703	9.703	99.037	**0.000**	***	
block:light (error a)	2	0.075	0.038	0.383	0.683		
error b	4	0.166	0.042				
light:water	1	0.058	0.058	1.400	0.302		(using error b)
comp:sp	1	0.006	0.006	0.065	0.799		
light:comp	1	0.760	0.760	7.758	**0.006**	**	
light:sp	1	0.269	0.269	2.743	0.101		
water:comp	1	0.010	0.010	0.103	0.749		
water:sp	1	0.021	0.021	0.212	0.646		
water:comp:sp	1	0.001	0.001	0.006	0.937		
light:water:comp	1	0.126	0.126	1.287	0.259		
light:water:sp	1	0.105	0.105	1.073	0.302		
light:water:comp:sp	2	0.214	0.107	1.092	0.339		
Residuals	112	10.973	0.098				

Table A89. Exp. 2 Harvest 3 plant dry mass: log(dry mass) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.484	0.242	0.701	0.498		
light	1	225.8	225.8	7192	**0.000**	***	(using error a)
water	1	0.051	0.051	0.123	0.744		(using error b)
comp	1	8.755	8.755	25.381	**0.000**	***	
sp	1	15.036	15.036	43.589	**0.000**	***	
block:light (error a)	2	0.063	0.031	0.091	0.913		
error b	4	1.645	0.411				
light:water	1	0.192	0.192	0.468	0.531		(using error b)
comp:sp	1	2.606	2.606	7.553	**0.007**	**	
light:comp	1	2.096	2.096	6.077	**0.015**	*	
light:sp	1	2.873	2.873	8.330	**0.005**	**	
water:comp	1	0.472	0.472	1.368	0.245		
water:sp	1	0.034	0.034	0.098	0.755		
water:comp:sp	1	0.249	0.249	0.723	0.397		
light:water:comp	1	0.157	0.157	0.455	0.501		
light:water:sp	1	0.286	0.286	0.830	0.364		
light:water:comp:sp	2	1.071	0.535	1.552	0.216		
Residuals	112	38.635	0.345				

Table A90. Exp. 2 Harvest 3 SLA: SLA ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	837	419	1.07	0.350		
light	1	65622	65622	151.17	**0.007**	**	(using error a)
water	1	735	735	2.01	0.251		(using error b)
comp	1	1818	1818	4.65	**0.036**	*	
sp	1	9451	9451	24.18	**0.000**	***	
block:light (error a)	2	868	434	1.11	0.337		
error b	4	1096	274				
light:water	1	1089	1089	2.98	0.183		(using error b)
comp:sp	1	123	123	0.31	0.578		
light:comp	1	995	995	2.55	0.116		
light:sp	1	1948	1948	4.98	**0.030**	*	
water:comp	1	1014	1014	2.59	0.113		
water:sp	1	160	160	0.41	0.525		
water:comp:sp	1	2159	2159	5.52	**0.022**	*	
light:water:comp	1	1437	1437	3.68	0.060		
light:water:sp	1	18	18	0.05	0.832		
light:water:comp:sp	2	672	336	0.86	0.429		
Residuals	54	21106	391				

Table A91. Exp. 2 Harvest 3 RMR: RMR ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.012	0.006	3.545	**0.032**	*	
light	1	0.029	0.029	167.249	**0.006**	**	(using error a)
water	1	0.006	0.006	2.519	0.188		(using error b)
comp	1	0.000	0.000	0.000	0.993		
sp	1	0.194	0.194	118.015	**0.000**	***	
block:light (error a)	2	0.000	0.000	0.107	0.899		
error b	4	0.009	0.002				
light:water	1	0.001	0.001	0.465	0.533		(using error b)
comp:sp	1	0.002	0.002	1.350	0.248		
light:comp	1	0.000	0.000	0.052	0.819		
light:sp	1	0.013	0.013	8.051	**0.005**	**	
water:comp	1	0.001	0.001	0.356	0.552		
water:sp	1	0.001	0.001	0.643	0.424		
water:comp:sp	1	0.003	0.003	1.878	0.173		
light:water:comp	1	0.000	0.000	0.267	0.607		
light:water:sp	1	0.006	0.006	3.889	0.051		
light:water:comp:sp	2	0.009	0.004	2.735	0.069		
Residuals	112	0.184	0.002				

Table A92. Exp. 2 Harvest 3 SMR: SMR ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.005	0.002	2.222	0.113	
light	1	0.013	0.013	12.881	0.070	
water	1	0.003	0.003	7.879	**0.048**	*
comp	1	0.000	0.000	0.026	0.872	
sp	1	0.016	0.016	15.102	**0.000**	***
block:light (error a)	2	0.002	0.001	0.946	0.391	
error b	4	0.001	0.000			
light:water	1	0.000	0.000	0.290	0.619	
comp:sp	1	0.000	0.000	0.394	0.532	
light:comp	1	0.001	0.001	1.108	0.295	
light:sp	1	0.014	0.014	12.957	**0.000**	***
water:comp	1	0.006	0.006	5.166	**0.025**	*
water:sp	1	0.000	0.000	0.151	0.698	
water:comp:sp	1	0.000	0.000	0.131	0.718	
light:water:comp	1	0.000	0.000	0.330	0.567	
light:water:sp	1	0.001	0.001	0.588	0.445	
light:water:comp:sp	2	0.000	0.000	0.200	0.819	
Residuals	112	0.121	0.001			

Table A93. Exp. 2 Harvest 3 LMR: LMR ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.006	0.003	1.235	0.295		
light	1	0.081	0.081	60.702	**0.016**	*	(using error a)
water	1	0.015	0.015	13.870	**0.020**	*	(using error b)
comp	1	0.000	0.000	0.009	0.927		
sp	1	0.097	0.097	43.202	**0.000**	***	
block:light (error a	2	0.003	0.001	0.596	0.553		
error b	4	0.004	0.001				
light:water	1	0.001	0.001	0.470	0.531		(using error b)
comp:sp	1	0.001	0.001	0.296	0.587		
light:comp	1	0.001	0.001	0.273	0.602		
light:sp	1	0.054	0.054	24.092	**0.000**	***	
water:comp	1	0.003	0.003	1.161	0.284		
water:sp	1	0.002	0.002	0.927	0.338		
water:comp:sp	1	0.005	0.005	2.049	0.155		
light:water:comp	1	0.002	0.002	0.722	0.397		
light:water:sp	1	0.003	0.003	1.308	0.255		
light:water:comp:sp	2	0.011	0.005	2.438	0.092		
Residuals	112	0.252	0.002				

Table A94. Exp. 2 Harvest 3 FARM: FARM ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	53408	26704	4.45	**0.014**	*	
light	1	1243496	1243496	125.79	**0.008**	**	(using error a)
water	1	38921	38921	2.60	0.182		(using error b)
comp	1	6754	6754	1.12	0.291		
sp	1	140882	140882	23.46	**0.000**	***	
block:light (error a)	2	19771	9885	1.65	0.197		
error b	4	59815	14954				
light:water	1	4800	4800	0.32	0.601		(using error b)
comp:sp	1	1111	1111	0.18	0.668		
light:comp	1	5101	5101	0.85	0.359		
light:sp	1	79508	79508	13.24	**0.000**	***	
water:comp	1	236	236	0.04	0.843		
water:sp	1	4374	4374	0.73	0.395		
water:comp:sp	1	66036	66036	11.00	**0.001**	**	
light:water:comp	1	2698	2698	0.45	0.504		
light:water:sp	1	3866	3866	0.64	0.424		
light:water:comp:sp	2	32449	16225	2.70	0.071		
Residuals	112	672552	6005				

Table A95. Exp. 2 Harvest 3 R:S mass: R:S mass ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.040	0.020	3.293	**0.041**	*	
light	1	0.106	0.106	141.8	**0.007**	**	(using error a)
water	1	0.021	0.021	2.476	0.191		(using error b)
comp	1	0.000	0.000	0.029	0.865		
sp	1	0.603	0.603	99.192	**0.000**	***	
block:light (error a)	2	0.002	0.001	0.123	0.884		
error b	4	0.035	0.009				
light:water	1	0.001	0.001	0.144	0.723		(using error b)
comp:sp	1	0.007	0.007	1.148	0.286		
light:comp	1	0.000	0.000	0.001	0.983		
light:sp	1	0.059	0.059	9.652	**0.002**	**	
water:comp	1	0.002	0.002	0.269	0.605		
water:sp	1	0.001	0.001	0.170	0.681		
water:comp:sp	1	0.008	0.008	1.378	0.243		
light:water:comp	1	0.002	0.002	0.281	0.597		
light:water:sp	1	0.021	0.021	3.479	0.065		
light:water:comp:sp	2	0.031	0.015	2.538	0.084		
Residuals	112	0.680	0.006				

Table A96. Exp. 2 Harvest 3 Root tips/root mass: log(tips/mass) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.267	0.134	1.003	0.370		
light	1	10.193	10.193	63.562	**0.015**	***	(using error a)
water	1	0.276	0.276	6.784	0.060		(using error b)
comp	1	1.314	1.314	9.880	**0.002**	**	
sp	1	13.036	13.036	97.990	**0.000**	***	
block:light (error a)	2	0.321	0.160	1.206	0.303		
error b	4	0.163	0.041				
light:water	1	0.003	0.003	0.077	0.795		(using error b)
comp:sp	1	0.561	0.561	4.214	**0.042**	*	
light:comp	1	0.581	0.581	4.365	**0.039**	*	
light:sp	1	1.030	1.030	7.743	**0.006**	**	
water:comp	1	0.004	0.004	0.029	0.866		
water:sp	1	0.002	0.002	0.014	0.905		
water:comp:sp	1	0.000	0.000	0.000	0.988		
light:water:comp	1	0.031	0.031	0.233	0.630		
light:water:sp	1	0.004	0.004	0.032	0.858		
light:water:comp:sp	2	0.116	0.058	0.436	0.648		
Residuals	112	14.900	0.133				

Table A97. Exp. 2 Harvest 3 SRL: log(SRL) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.167	0.084	1.421	0.246		
light	1	10.527	10.527	56.098	**0.017**	*	(using error a)
water	1	0.412	0.412	10.830	**0.030**	*	(using error b)
comp	1	0.579	0.579	9.833	**0.002**	**	
sp	1	1.904	1.904	32.354	**0.000**	***	
block:light (error a)	2	0.375	0.188	3.189	**0.045**	*	
error b	4	0.152	0.038				
light:water	1	0.042	0.042	1.091	0.355		(using error b)
comp:sp	1	0.565	0.565	9.604	**0.002**	**	
light:comp	1	0.048	0.048	0.815	0.369		
light:sp	1	0.435	0.435	7.395	**0.008**	**	
water:comp	1	0.002	0.002	0.038	0.845		
water:sp	1	0.007	0.007	0.113	0.738		
water:comp:sp	1	0.003	0.003	0.058	0.810		
light:water:comp	1	0.008	0.008	0.128	0.721		
light:water:sp	1	0.009	0.009	0.156	0.694		
light:water:comp:sp	2	0.031	0.016	0.263	0.769		
Residuals	112	6.591	0.059				

Table A98. Exp. 2 Harvest 3 SSL: sqrt(SSL) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	21.3	10.6	2.22	0.113		
light	1	4399.6	4399.6	3514	**0.000**	***	(using error a)
water	1	1.7	1.7	0.21	0.673		(using error b)
comp	1	75.0	75.0	15.67	**0.000**	***	
sp	1	1.5	1.5	0.32	0.572		
block:light (error a)	2	2.5	1.3	0.26	0.770		
error b	4	33.1	8.3				
light:water	1	0.1	0.1	0.01	0.923		(using error b)
comp:sp	1	22.3	22.3	4.66	**0.033**	*	
light:comp	1	5.1	5.1	1.07	0.304		
light:sp	1	19.9	19.9	4.17	**0.044**	*	
water:comp	1	19.0	19.0	3.97	**0.049**	*	
water:sp	1	6.2	6.2	1.30	0.256		
water:comp:sp	1	5.0	5.0	1.05	0.307		
light:water:comp	1	17.7	17.7	3.69	0.057		
light:water:sp	1	8.1	8.1	1.69	0.196		
light:water:comp:sp	2	20.7	10.3	2.16	0.120		
Residuals	112	536.2	4.8				

Table A99. Exp. 2 Harvest 3 RGR: RGR ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
light	1	16510	16510	176.87	**0.000**	***	
water	1	58	58	0.62	0.434		(using error a)
comp	1	2974	2974	31.85	**0.000**	***	(using error b)
sp	1	10579	10579	113.33	**0.000**	***	
light:water	1	17	17	0.19	0.667		
light:comp	1	584	584	6.25	**0.014**	*	
light:sp	1	5	5	0.05	0.818		
water:comp	1	128	128	1.37	0.243		(using error b)
comp:sp	1	531	531	5.69	**0.019**	*	
light:water:comp	1	158	158	1.69	0.196		
light:water:sp	2	204	102	1.09	0.339		
light:comp:sp	1	14	14	0.15	0.697		
water:comp:sp	1	238	238	2.55	0.113		
light:water:comp:sp	1	287	287	3.07	0.082		
Residuals	120	11202	93				

Table A100. Exp. 2 Harvest 3 stem diameter: log(diameter) ~ H3 model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.059	0.029	0.32	0.724		
light	1	55.855	55.855	874.13	**0.001**	**	(using error a)
water	1	0.094	0.094	1.03	0.368		(using error b)
comp	1	1.491	1.491	16.41	**0.000**	***	
sp	1	2.771	2.771	30.49	**0.000**	***	
block:light (error a)	2	0.128	0.064	0.70	0.497		
error b	4	0.366	0.092				
light:water	1	0.083	0.083	0.90	0.396		(using error b)
comp:sp	1	0.023	0.023	0.26	0.612		
light:comp	1	0.084	0.084	0.92	0.340		
light:sp	1	0.201	0.201	2.21	0.140		
water:comp	1	0.094	0.094	1.03	0.312		
water:sp	1	0.001	0.001	0.01	0.911		
water:comp:sp	1	0.094	0.094	1.04	0.311		
light:water:comp	1	0.001	0.001	0.01	0.903		
light:water:sp	1	0.083	0.083	0.91	0.341		
light:water:comp:sp	2	0.395	0.198	2.17	0.118		
Residuals	112	10.268	0.091				

Table A101. Exp. 2 Harvest 3 RLR of height: RLR ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.107	0.107	0.981	0.325	
comp	1	0.384	0.384	3.533	**0.064**	***
water	1	0.212	0.212	1.947	0.167	
sp:comp	1	0.371	0.371	3.414	0.069	
sp:water	1	0.322	0.322	2.965	0.090	
comp:water	1	0.004	0.004	0.036	0.849	
sp:comp:water	1	0.021	0.021	0.196	0.659	
Residuals	68	7.391	0.109			

Table A102. Exp. 2 Harvest 3 RLR of dry mass: RLR ~ RLR mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	6.271	6.271	14.197	**0.000**	***
comp	1	4.447	4.447	10.068	**0.002**	**
water	1	0.213	0.213	0.481	0.490	
sp:comp	1	0.145	0.145	0.327	0.569	
sp:water	1	0.361	0.361	0.817	0.369	
comp:water	1	0.189	0.189	0.429	0.515	
sp:comp:water	1	1.900	1.900	4.302	**0.042**	*
Residuals	68	30.036	0.442			

Table A103. Exp. 2 Harvest 3 RLR of R:S mass: RLR ~ RLR mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.487	0.487	9.506	**0.003**	**
comp	1	0.047	0.047	0.922	0.340	
water	1	0.166	0.166	3.238	0.076	
sp:comp	1	0.709	0.709	13.856	**0.000**	***
sp:water	1	0.497	0.497	9.719	**0.003**	**
comp:water	1	0.000	0.000	0.003	0.956	
sp:comp:water	1	0.020	0.020	0.382	0.539	
Residuals	68	3.480	0.051			

Table A104. Exp. 2 H3 RLR of root tips/length: tips ~ RLR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.260	0.260	5.945	**0.017**	*
comp	1	0.630	0.630	14.406	**0.000**	***
water	1	0.050	0.050	1.151	0.287	
sp:comp	1	0.085	0.085	1.939	0.168	
sp:water	1	0.040	0.040	0.910	0.343	
comp:water	1	0.157	0.157	3.597	0.062	
sp:comp:water	1	0.000	0.000	0.007	0.935	
Residuals	68	2.974	0.044			

Table A105. Exp. 2 Harvest 3 RWR of height: RWR ~ RWR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.010	0.010	0.090	0.765	
comp	1	0.484	0.484	4.541	**0.037**	*
light	1	0.068	0.068	0.636	0.428	
sp:comp	1	0.611	0.611	5.739	**0.019**	*
sp:light	1	0.202	0.202	1.893	0.174	
comp:light	1	0.003	0.003	0.030	0.864	
sp:comp:light	1	0.089	0.089	0.836	0.364	
Residuals	66	7.031	0.107			

Table A106. Exp. 2 Harvest 3 RWR of dry mass: RWR ~ RWR mo

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.033	0.033	0.077	0.782	
comp	1	0.883	0.883	2.095	0.153	
light	1	0.152	0.152	0.361	0.550	
sp:comp	1	0.678	0.678	1.609	0.209	
sp:light	1	0.384	0.384	0.910	0.344	
comp:light	1	0.345	0.345	0.818	0.369	
sp:comp:light	1	2.140	2.140	5.078	**0.028**	*
Residuals	66	27.813	0.421			

Table A107. Exp. 2 H3 RWR of R:S mass: RWR ~ RWR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.187	0.187	2.898	0.093	
comp	1	0.066	0.066	1.022	0.316	
light	1	0.162	0.162	2.500	0.119	
sp:comp	1	0.231	0.231	3.573	0.063	
sp:light	1	0.433	0.433	6.697	**0.012**	*
comp:light	1	0.000	0.000	0.000	0.996	
sp:comp:light	1	0.021	0.021	0.330	0.568	
Residuals	66	4.267	0.065			

Table A108. Exp. 2 H3 RWR of root tips/length: tips ~ RWR mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)
sp	1	0.0255	0.0255	0.4779	0.492
comp	1	0.0112	0.0112	0.2105	0.648
light	1	0.0672	0.0672	1.2614	0.266
sp:comp	1	0.0003	0.0003	0.0055	0.941
sp:light	1	0.022	0.022	0.4128	0.523
comp:light	1	0.1236	0.1236	2.3202	0.133
sp:comp:light	1	0.0029	0.0029	0.0551	0.815
Residuals	66	3.5159	0.0533		

Table A109. Exp. 2 Harvest 3 RCR of height: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.918	0.918	8.249	**0.006**	**
light	1	0.053	0.053	0.475	0.494	
water	1	0.336	0.336	3.021	0.088	
sp:light	1	0.091	0.091	0.814	0.371	
sp:water	1	0.569	0.569	5.115	**0.028**	*
light:water	1	0.000	0.000	0.000	0.998	
sp:light:water	1	0.068	0.068	0.611	0.438	
Residuals	56	6.234	0.111			

Table A110. Exp. 2 Harv. 3 RCR of dry mass: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	6.252	6.252	16.664	**0.000**	***
light	1	3.826	3.826	10.200	**0.002**	**
water	1	0.834	0.834	2.222	0.142	
sp:light	1	0.109	0.109	0.291	0.592	
sp:water	1	0.658	0.658	1.754	0.191	
light:water	1	0.590	0.590	1.572	0.215	
sp:light:water	1	1.633	1.633	4.352	**0.042**	*
Residuals	56	21.009	0.375			

Table A111. Exp. 2 Harv. 3 RCR of R:S mass: RCR ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.110	0.110	2.038	0.159	
light	1	0.007	0.007	0.131	0.719	
water	1	0.089	0.089	1.660	0.203	
sp:light	1	0.532	0.532	9.879	**0.003**	**
sp:water	1	0.218	0.218	4.049	**0.049**	*
light:water	1	0.001	0.001	0.012	0.913	
sp:light:water	1	0.016	0.016	0.302	0.585	
Residuals	56	3.013	0.054			

Table A112. Exp. 2 H3 RCR of root tips/length: tips ~ RCR model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
sp	1	0.000	0.000	0.005	0.945	
light	1	0.537	0.537	13.128	0.001	***
water	1	0.008	0.008	0.205	0.652	
sp:light	1	0.068	0.068	1.659	0.203	
sp:water	1	0.001	0.001	0.026	0.873	
light:water	1	0.093	0.093	2.286	0.136	
sp:light:water	1	0.002	0.002	0.055	0.816	
Residuals	56	2.289	0.041			

Table A113. Exp. 2 Harvest 3 height--Light treatment: log(Height) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.038	0.019	0.172	0.842	
water	1	0.002	0.002	0.151	0.735	(using error a)
comp	1	0.491	0.491	4.507	**0.038**	*
sp	1	7.760	7.760	71.203	**0.000**	***
block:water (error a)	2	0.032	0.016	0.145	0.866	
comp:sp	1	0.346	0.346	3.176	0.079	
water:comp	1	0.176	0.176	1.611	0.209	
water:sp	1	0.065	0.065	0.596	0.443	
water:comp:sp	1	0.301	0.301	2.757	0.102	
Residuals	64	6.975	0.109			

Table A114. Exp. 2 Harvest 3 height--Shade treatment: log(Height) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.718	0.359	4.949	**0.011**	*
water	1	0.013	0.013	0.057	0.834	(using error a)
comp	1	0.333	0.333	4.589	**0.037**	*
sp	1	5.211	5.211	71.844	**0.000**	***
block:water (error a)	2	0.448	0.224	3.091	0.054	
comp:sp	1	0.031	0.031	0.428	0.516	
water:comp	1	0.138	0.138	1.897	0.175	
water:sp	1	0.008	0.008	0.104	0.748	
water:comp:sp	1	0.033	0.033	0.457	0.502	
Residuals	48	3.554	0.073			

Table A115. Exp. 2 Harvest 3 root tips/root length--Light treatment: tips ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.0	0.013	0.122	0.885	
water	1	0.0	0.000	0.002	0.965	(using error a)
comp	1	1.1	1.052	10.032	**0.002**	**
sp	1	4.1	4.125	39.343	**0.000**	***
block:water (error a)	2	0.1	0.1	0.505	0.606	
comp:sp	1	0.1	0.123	1.173	0.283	
water:comp	1	0.1	0.107	1.020	0.316	
water:sp	1	0.1	0.068	0.649	0.424	
water:comp:sp	1	0.0	0.003	0.025	0.875	
Residuals	64	6.7	0.105			

Table A116. Exp. 2 Harvest 3 root tips/root length--Shade treatment: tips ~ L/S mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.2	0.1	0.878	0.422	
water	1	0.0	0.0	0.014	0.916	(using error a)
comp	1	0.2	0.2	2.308	0.135	
sp	1	5.6	5.6	62.963	**0.000**	***
block:water (error a)	2	0.1	0.1	0.757	0.475	
comp:sp	1	0.1	0.1	1.304	0.259	
water:comp	1	0.0	0.0	0.223	0.639	
water:sp	1	0.0	0.0	0.263	0.611	
water:comp:sp	1	0.0	0.0	0.194	0.662	
Residuals	48	4.3	0.1			

Table A117. Exp. 2 Harvest 3 dry mass--Light treatment: log(mass) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.140	0.070	0.151	0.860	
water	1	0.055	0.055	2.221	0.275	(using error a)
comp	1	9.891	9.891	21.369	**0.000**	***
sp	1	16.783	16.783	36.260	**0.000**	***
block:water (error a)	2	0.050	0.025	0.054	0.948	
comp:sp	1	1.853	1.853	4.003	**0.050**	*
water:comp	1	0.109	0.109	0.235	0.629	
water:sp	1	0.028	0.028	0.060	0.807	
water:comp:sp	1	1.129	1.129	2.438	0.123	
Residuals	64	29.622	0.463			

Table A118. Exp. 2 Harvest 3 dry mass--Shade treatment: log(mass) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.335	0.168	0.899	0.414	
water	1	0.011	0.011	0.018	0.905	(using error a)
comp	1	0.783	0.783	4.195	**0.046**	*
sp	1	1.563	1.563	8.376	**0.006**	**
block:water (error a)	2	1.190	0.595	3.189	**0.050**	*
comp:sp	1	0.632	0.632	3.386	0.072	
water:comp	1	0.575	0.575	3.079	0.086	
water:sp	1	0.309	0.309	1.655	0.204	
water:comp:sp	1	0.111	0.111	0.596	0.444	
Residuals	48	8.959	0.187			

Table A119. Exp. 2 Harvest 3 SLA--Light treatment: SLA ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	301.5	150.7	0.772	0.471	
water	1	1897.4	1897.4	38421	**0.003** *	(using error a)
comp	1	2695.4	2695.4	13.801	**0.001** ***	
sp	1	1584.3	1584.3	8.112	**0.008** **	
block:water (error a)	1	0.05	0.05	0.000	0.987	
comp:sp	1	24.1	24.1	0.123	0.728	
water:comp	1	11.9	11.9	0.061	0.807	
water:sp	1	31.4	31.4	0.161	0.691	
water:comp:sp	1	324.9	324.9	1.664	0.207	
Residuals	29	5663.9	195.3			

Table A120. Exp. 2 Harvest 3 SLA--Shade treatment: SLA ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	2713	1356	2.196	0.132	
water	1	52	52	0.251	0.666	(using error a)
comp	1	128	128	0.208	0.653	
sp	1	10899	10899	17.646	**0.000** ***	
block:water (error a)	2	415	208	0.336	0.718	
comp:sp	1	185	185	0.300	0.589	
water:comp	1	2484	2484	4.021	0.056	
water:sp	1	243	243	0.394	0.536	
water:comp:sp	1	2291	2291	3.710	0.066	
Residuals	25	15442	618			

Table A121. Exp. 2 Harvest 3 RMR--Light treatment: RMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.002	0.001	0.508	0.604	
water	1	0.003	0.003	3.915	0.186	(using error a)
comp	1	0.001	0.001	0.294	0.590	
sp	1	0.169	0.169	91.448	**0.000** ***	
block:water (error a)	2	0.002	0.001	0.413	0.663	
comp:sp	1	0.009	0.009	5.009	**0.029** *	
water:comp	1	0.000	0.000	0.093	0.762	
water:sp	1	0.001	0.001	0.272	0.604	
water:comp:sp	1	0.003	0.003	1.875	0.176	
Residuals	64	0.119	0.002			

Table A122. Exp. 2 Harvest 3 RMR--Shade treatment: RMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.011	0.006	4.105	**0.023**	*
water	1	0.002	0.002	0.669	0.499	(using error a)
comp	1	0.001	0.001	0.449	0.506	
sp	1	0.036	0.036	26.797	**0.000**	***
block:water (error a)	2	0.007	0.003	2.508	0.092	
comp:sp	1	0.003	0.003	2.175	0.147	
water:comp	1	0.000	0.000	0.240	0.626	
water:sp	1	0.005	0.005	3.716	0.060	
water:comp:sp	1	0.000	0.000	0.138	0.712	
Residuals	48	0.065	0.001			

Table A123. Exp. 2 Harvest 3 SMR--Light treatment: SMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.000	0.000	0.112	0.894	
water	1	0.002	0.002	2.435	0.259	(using error a)
comp	1	0.001	0.001	0.834	0.365	
sp	1	0.000	0.000	0.223	0.638	
block:water (error a)	2	0.001	0.001	0.476	0.624	
comp:sp	1	0.000	0.000	0.226	0.636	
water:comp	1	0.005	0.005	3.582	0.063	
water:sp	1	0.001	0.001	0.652	0.422	
water:comp:sp	1	0.001	0.001	0.395	0.532	
Residuals	64	0.083	0.001			

Table A124. Exp. 2 Harvest 3 SMR--Shade treatment: SMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.008	0.004	5.221	**0.009**	**
water	1	0.001	0.001	4.329	0.173	(using error a)
comp	1	0.001	0.001	0.830	0.367	
sp	1	0.027	0.027	34.724	**0.000**	***
block:water (error a)	2	0.001	0.000	0.323	0.725	
comp:sp	1	0.000	0.000	0.175	0.678	
water:comp	1	0.001	0.001	1.800	0.186	
water:sp	1	0.000	0.000	0.121	0.729	
water:comp:sp	1	0.000	0.000	0.080	0.778	
Residuals	48	0.038	0.001			

Table A125. Exp. 2 Harvest 3 LMR--Light treatment: LMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.001	0.000	0.165	0.849		
water	1	0.009	0.009	963.356	**0.001**	**	(using error a)
comp	1	0.000	0.000	0.027	0.869		
sp	1	0.155	0.155	54.382	**0.000**	***	
block:water (error a)	2	0.000	0.000	0.003	0.997		
comp:sp	1	0.006	0.006	2.157	0.147		
water:comp	1	0.003	0.003	1.093	0.300		
water:sp	1	0.000	0.000	0.019	0.891		
water:comp:sp	1	0.007	0.007	2.375	0.128		
Residuals	64	0.183	0.003				

Table A126. Exp. 2 Harvest 3 LMR--Shade treatment: LMR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.004	0.002	1.335	0.273	
water	1	0.007	0.007	3.163	0.217	(using error a)
comp	1	0.000	0.000	0.001	0.982	
sp	1	0.001	0.001	0.440	0.510	
block:water (error a)	2	0.004	0.002	1.432	0.249	
comp:sp	1	0.004	0.004	3.020	0.089	
water:comp	1	0.000	0.000	0.266	0.608	
water:sp	1	0.004	0.004	2.592	0.114	
water:comp:sp	1	0.000	0.000	0.023	0.881	
Residuals	48	0.069	0.001			

Table A127. Exp. 2 Harvest 3 FARM--Light treatment: FARM ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	4325	2163	0.545	0.583		
water	1	43946	43946	120.44	**0.008**	**	(using error a)
comp	1	9170	9170	2.311	0.133		
sp	1	209258	209258	52.727	**0.000**	***	
block:water (error a)	2	730	365	0.092	0.912		
comp:sp	1	8377	8377	2.111	0.151		
water:comp	1	2800	2800	0.706	0.404		
water:sp	1	250	250	0.063	0.802		
water:comp:sp	1	34360	34360	8.658	**0.005**	**	
Residuals	64	253998	3969				

Table A128. Exp. 2 Harvest 3 FARM--Shade treatment: FARM ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	63758	31879	3.656	**0.033**	*	
water	1	2514	2514	0.090	0.793		(using error a)
comp	1	111	111	0.013	0.911		
sp	1	187	187	0.022	0.884		
block:water	2	55891	27945	3.205	**0.049**	*	
comp:sp	1	32304	32304	3.705	0.060		
water:comp	1	7105	7105	0.815	0.371		
water:sp	1	3190	3190	0.366	0.548		
water:comp:sp	1	22156	22156	2.541	0.118		
Residuals	48	418554	8720				

Table A129. Exp. 2 Harvest 3 R:S mass--Light treatment: R:S mass ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.009	0.005	0.620	0.541		
water	1	0.015	0.015	3.321	0.209		(using error a)
comp	1	0.000	0.000	0.043	0.836		
sp	1	0.569	0.569	75.809	**0.000**	***	
block:water (error a)	2	0.009	0.005	0.610	0.547		
comp:sp	1	0.031	0.031	4.127	**0.046**	*	
water:comp	1	0.000	0.000	0.039	0.843		
water:sp	1	0.004	0.004	0.535	0.467		
water:comp:sp	1	0.009	0.009	1.178	0.282		
Residuals	64	0.481	0.008				

Table A130. Exp. 2 Harvest 3 R:S mass--Shade treatment: R:S mass ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.031	0.015	3.668	**0.033**	*	
water	1	0.006	0.006	0.541	0.539		(using error a)
comp	1	0.001	0.001	0.354	0.555		
sp	1	0.094	0.094	22.599	**0.000**	***	
block:water (error a)	2	0.022	0.011	2.661	0.080		
comp:sp	1	0.011	0.011	2.633	0.111		
water:comp	1	0.001	0.001	0.291	0.592		
water:sp	1	0.012	0.012	2.943	0.093		
water:comp:sp	1	0.001	0.001	0.161	0.690		
Residuals	48	0.200	0.004				

Table A131. Exp. 2 Harvest 3 rt tips/rt mass--Light treatment: log(tips) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.079	0.040	0.221	0.803	
water	1	0.057	0.057	0.694	0.492	(using error a)
comp	1	2.334	2.334	13.001	**0.001**	***
sp	1	4.162	4.162	23.186	**0.000**	***
block:water (error a)	2	0.163	0.082	0.454	0.637	
comp:sp	1	0.600	0.600	3.341	0.072	
water:comp	1	0.029	0.029	0.164	0.687	
water:sp	1	0.003	0.003	0.015	0.904	
water:comp:sp	1	0.000	0.000	0.000	0.993	
Residuals	64	11.487	0.180			

Table A132. Exp. 2 Harvest 3 rt tips/rt mass--Shade treatment: log(tips) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.731	0.365	5.139	**0.010**	**
water	1	0.336	0.336	21.698	**0.043**	* (using error a)
comp	1	0.000	0.000	0.000	0.993	
sp	1	9.021	9.021	126.898	**0.000**	***
block:water (error a)	2	0.031	0.016	0.218	0.805	
comp:sp	1	0.041	0.041	0.577	0.451	
water:comp	1	0.003	0.003	0.035	0.852	
water:sp	1	0.000	0.000	0.000	0.985	
water:comp:sp	1	0.000	0.000	0.000	0.990	
Residuals	48	3.412	0.071			

Table A133. Exp. 2 Harvest 3 SRL--Light treatment: log(SRL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.157	0.079	1.001	0.373	
water	1	0.103	0.103	4.388	0.171	(using error a)
comp	1	0.656	0.656	8.358	**0.005**	**
sp	1	0.334	0.334	4.253	**0.043**	*
block:water (error a)	2	0.047	0.024	0.299	0.742	
comp:sp	1	0.441	0.441	5.613	**0.021**	*
water:comp	1	0.009	0.009	0.115	0.736	
water:sp	1	0.012	0.012	0.156	0.694	
water:comp:sp	1	0.003	0.003	0.032	0.859	
Residuals	64	5.022	0.079			

Table A134. Exp. 2 Harvest 3 SRL--Shade treatment: log(SRL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.424	0.212	6.484	**0.003**	**	
water	1	0.428	0.428	13.107	**0.001**	***	(using error a)
comp	1	0.053	0.053	1.631	0.208		
sp	1	1.729	1.729	52.898	**0.000**	***	
block:water	2	0.123	0.061	1.878	0.164		
comp:sp	1	0.132	0.132	4.045	**0.050**	*	
water:comp	1	0.002	0.002	0.062	0.805		
water:sp	1	0.002	0.002	0.063	0.804		
water:comp:sp	1	0.005	0.005	0.168	0.684		
Residuals	48	1.569	0.033				

Table A135. Exp. 2 Harvest 3 SSL--Light treatment: sqrt(SSL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.247	0.124	0.045	0.956		
water	1	0.687	0.687	0.837	0.457		(using error a)
comp	1	68.120	68.120	24.990	**0.000**	***	
sp	1	15.620	15.620	5.730	**0.020**	*	
block:water (error a)	2	1.642	0.821	0.301	0.741		
comp:sp	1	2.768	2.768	1.016	0.317		
water:comp	1	0.409	0.409	0.150	0.700		
water:sp	1	0.185	0.185	0.068	0.795		
water:comp:sp	1	1.440	1.440	0.528	0.470		
Residuals	64	174.460	2.726				

Table A136. Exp. 2 Harvest 3 SSL--Shade treatment: sqrt(SSL) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	9.720	4.860	0.645	0.529		
water	1	0.920	0.920	0.071	0.815		(using error a)
comp	1	12.520	12.520	1.661	0.204		
sp	1	7.040	7.040	0.935	0.339		
block:water (error a)	2	25.690	12.840	1.705	0.193		
comp:sp	1	27.160	27.160	3.604	0.064		
water:comp	1	35.120	35.120	4.661	**0.036**	*	
water:sp	1	15.590	15.590	2.068	0.157		
water:comp:sp	1	18.030	18.030	2.393	0.128		
Residuals	48	361.690	7.540				

Table A137. Exp. 2 Harvest 3 RGR--Light treatment: RGR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
water	1	12	12	0.099	0.755		
comp	1	2796	2796	22.786	**0.000**	***	(using error a)
sp	1	6443	6443	52.510	**0.000**	***	
comp:sp	1	349	349	2.848	0.096		
water:comp	1	0.70	0.70	0.006	0.941		
water:sp	1	137	137	1.120	0.294		
water:comp:sp	1	515	515	4.197	**0.044**	*	
Residuals	68	8343	123				

Table A138. Exp. 2 Harvest 3 RGR--Shade treatment: RGR ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
water	1	57	57	1.031	0.315		
comp	1	506	506	9.212	**0.004**	**	(using error a)
sp	1	4403	4403	80.098	**0.000**	***	
comp:sp	1	213	213	3.866	0.055		
water:comp	1	263	263	4.774	**0.033**	*	
water:sp	1	72	72	1.309	0.258		
water:comp:sp	1	10	10	0.172	0.680		
Residuals	52	2859	55				

Table A139. Exp. 2 Harvest 3 stem diameter--Light treatment: log(diam) ~ L/S model

	Df	Sum Sq	Mean Sq	F value	Pr(>F)		
block	2	0.004	0.002	0.020	0.980		
water	1	0.124	0.124	6.866	0.120		(using error a)
comp	1	1.117	1.117	10.934	**0.002**	**	
sp	1	2.444	2.444	23.936	**0.000**	***	
block:water (error a)	2	0.036	0.018	0.177	0.838		
comp:sp	1	0.219	0.219	2.141	0.148		
water:comp	1	0.086	0.086	0.844	0.362		
water:sp	1	0.021	0.021	0.205	0.652		
water:comp:sp	1	0.193	0.193	1.893	0.174		
Residuals	64	6.536	0.102				

Table A140. Exp. 2 Harvest 3 stem diameter--Shade treatment: log(diam) ~ L/S mode

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
block	2	0.306	0.153	2.005	0.146	
water	1	0.006	0.006	0.043	0.855	(using error a)
comp	1	0.433	0.433	5.684	**0.021**	*
sp	1	0.544	0.544	7.140	**0.010**	*
block:water (error a)	2	0.288	0.144	1.892	0.162	
comp:sp	1	0.094	0.094	1.233	0.272	
water:comp	1	0.050	0.050	0.652	0.423	
water:sp	1	0.046	0.046	0.600	0.442	
water:comp:sp	1	0.000	0.000	0.005	0.945	
Residuals	48	3.732	0.076			

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Jason Schatz was born in Dubuque, IA, where he graduated from Wahlert High School in 2000. He graduated from Iowa State University in 2004 with a B.S. in Environmental Science and minors in Botany and Philosophy.

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