Early Field Performance and Allometry of Three Inland Northwest Conifer Species, Influence of Root Growth Potential and Site Characteristics

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by

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Authorization to Submit Thesis

This thesis of Jacob August Reely, submitted for the degree of Master of Science with a Major in Natural Resources and titled "**Early Field Performance and Allometry of Three Inland Northwest Conifer Species, Influence of Root Growth Potential and Site Characteristics,"** has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*) containerized seedlings were evaluated for aeroponic root growth potential (RGP) and planted on sites with variable soil environments. The sites differed in aspect and soil moisture environment; north-aspect (wet), north-aspect (dry) and south-aspect. Height and diameter growth, as well as survival, were evaluated over the first two seasons after planting. During the first growing season seedlings were destructively sampled to create specific allometric models and evaluate how seedling biomass accumulation and partitioning patterns were influenced by RGP and soil conditions, and how this relates to the growth and survival of planted seedlings. Douglas-fir and western larch seedlings have significantly lower growth and survival on a south-aspect site, than on north-aspect sites but seem more influenced by site aspect differences than site soil moisture differences. All species accumulated greater biomass on sites without soil moisture limitations. Grand fir seedlings did not exhibit differences in two-year field performance across sites, but did exhibit different patterns of biomass allocation on the south-aspect site favoring shoot growth on the south-aspect site. The increased presence of competing vegetation resulted decreased growth and survival of planted seedlings after two growing seasons. Douglas-fir seedlings two-year survival increased with RGP on the wet north-aspect but decreased with RGP on the dry north-aspect site; grand fir seedlings with high RGP had greater survival on either north-aspect site. However, grand fir seedlings with high RGP the south-aspect site and western larch seedlings on the dry north-aspect site had lower survival than other seedlings. All species responded variably to within site differences in soil moisture and temperature, but there was not consistent response, and it seems that differences in growth and survival are more related to between site differences. RGP was a successful predictor of survival for the more stress-tolerant species on north-aspects, but Douglas-fir displayed a negative relationship between survival and RGP on the dry north-aspect site. Results will help managers better understand how RGP results relate to field performance and provide a mechanistic understanding of periodic changes in seedling morphology and how they relate to early growth and survival on common planting sites in the region.

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Dedication

To my family.

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Prologue

The Inland Northwest (INW) is geographically delineated by the Interior Columbia River Basin (Hessburg and Agee 2003). From southeastern British Columbia, the region extends south and includes much of Washington and Oregon east of the Cascades, Idaho north of the Snake River, and western Montana. Summers in the INW are characterized by prolonged periods with little or no precipitation (Cooper et al. 1991). Winter and spring climate is inland maritime, with prolonged periods of light precipitation and snow accumulation at higher elevations and generally overcast skies and high humidity (Cooper et al. 1991). East of the Rocky Mountains, winter temperatures are much colder than on the west side; the relatively mild winters experienced by Northern Idaho partially explain the high productivity of forests in this region (Franklin and Waring 1980).

Due to the presence of highly productive forests and species richness of the region, industrial forestry has historically been a staple of the economy of the INW. This is still true today, in 2016 forest products in Idaho were a $2.67 billion-dollar industry that employed 12,479 people (Cook et al. 2017). Timber harvesting in Idaho totaled 1.16 million board feet in 2016 with timber harvesting on private lands providing 64 percent of Idaho's timber harvest volume, compared to 13.4 percent of timber harvest volume coming from federal lands (Cook et al. 2017). This is surprising considering that of Idaho's 16.5 million acres of timberlands only 17 percent of the acreage is under private ownership, compared to the 72 percent of timberland acreage under United States Forest Service ownership (Miles 2016). In a state like Idaho, where most timber is harvested on a relatively small area of privately owned timberlands, forest management in the region is becoming more intensive with forest managers relying on even-aged silviculture and utilizing clearcut harvesting and artificial forest regeneration methods rather than historical harvesting regimes. This is reflected in seedling production in Idaho where more than 5 million conifer seedlings were produced and nearly 11,000 acres were planted with conifer seedlings (Hernández et al. 2017).

One obstacle faced by forest managers in the region is plantation failure. In the INW successful forest regeneration depends, in part, on the availability of high quality planting stock (Lavender 1990). Seedling quality is a term that is used by forest managers to characterize the ability of a planted seedling to grow and survive on a given planting site, or a seedling's field performance (Duryea 1985). Field performance of seedlings depends, largely on matching morphological and physiological qualities of seedlings that have been linked to field performance (Ritchie 1984; Rose et al. 1990; Wakeley 1954). Physiological metrics of seedling quality like root growth potential (RGP) have been found to be associated with the field performance of INW species (L'Hirondelle et al. 2007; Ritchie 1985) and morphological characteristics like height, root collar diameter (RCD), height to diameter ratio (H:D) and root to shoot ratio (R:S) have all been successfully used as useful metrics of seedling quality (Thompson 1985).

To complicate matters, in the INW successful reforestation is largely dictated by environmental characteristics of the planting site. Topography, temperature, moisture, and vegetative communities all influence the field performance of seedlings in the region (Stathers et al. 1990). Moisture stress is often the primary cause of plantation failures in areas, like the INW, with growing season drought (Arnott 1975; Hobbs 1992), and moisture stress can significantly decrease the growth of conifer seedlings (Zahner 1968). This is why in the INW volcanic ash present in the upper soil profile originating from the eruption of Mount Mazama in southeast Oregon during the Holocene era, and the increased water holding capacity of these ash cap soils contribute to the highly productive forests of the region (McDaniel and Wilson 2007). Temperature also influences conifer seedling growth (Barney 1951; Lyr and Garbe 1995) and high temperature has been shown to be a significant cause of seedling mortality in the region (Haig 1936; Haig et al. 1941; Shearer 1967). Topography and vegetative communities further influence the available moisture and surface temperatures of a given planting site (De Vries 1963; Eash et al. 2015; Spittlehouse and Childs 1990), and in the INW site productivity is often characterized by vegetative community and dictated by aspect and elevation (Cooper et al. 1991).

It has been shown that in this region reforestation success can be maximized through the selection of appropriate planting stock, and pairing seedlings with the appropriate morphological and physiological characteristics to a given planting site (Hobbs 1992). Studies have shown that both morphological (Koon and O'Dell 1977) and physiological (Kozlowski 1971) characteristics of seedlings can be manipulated by utilizing various nursery cultural techniques, such as planting density, container size, lift date, and storage. Since planting and production of conifer seedlings in the region is prevalent and likely to remain a staple of the forest industry in the INW, yet current seedling mortality rates are relatively high, forest managers in the INW could benefit from a thorough understanding of those seedling attributes that can be measured and manipulated before a seedling is planted, and how these morphological and physiological attributes of seedlings of the various species native to the INW that are commonly used in reforestation projects contribute the growth and survival of these seedlings and the highly variable planting sites common throughout the region.

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Chapter 1: Two-Year Field Performance of Three Inland Northwest Conifer Species; Influence of Root Growth Potential, Morphology, and Site Characteristics

Abstract

Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*) containerized seedlings were evaluated for aeroponic root growth potential (RGP) and planted on sites with variable soil environments. The sites differed in aspect and soil moisture environment. Height and diameter growth and survival were evaluated across two growing seasons. Soil moisture and temperature were measured continually at 15 cm and 50 cm below the soil surface; seedling ground cover was measured in the second growing season. Regardless of species, RGP did not influence seedling field performance. Grand fir seedlings with greater initial size did not grow as large as smaller seedlings; regardless of species, seedlings that grew taller in the first growing season were more likely to survive the second growing season. Douglas-fir seedling survival increased with soil moisture, but there was no influence of soil moisture on western larch and grand fir seedling field performance; this was attributed to a mild drought year. There were negative effects of high soil temperatures on seedling field performance of each species. As the cover of competing vegetation increased, Douglas-fir and western larch seedlings responded by favoring height growth at the cost of diameter growth and grand fir seedlings reduced height growth at no cost of diameter growth. Increased slash cover resulted in a positive influence on the growth of Douglas-fir and grand fir seedlings, likely due to microsite alteration. Results should help forest managers with planting stock selection and site preparation decision-making.

Introduction

Often, forest regeneration suffers or fails as a result of uninformed management decisions regarding appropriate planting stock selection due to: (1) a lack of knowledge of the ecological characteristics of different species and how those characteristics affect the performance of various species in managed systems (Jahn 1982); (2) lack of knowledge of the growth and yield of different species, grown in different compositions and densities on sites of variable quality (Assmann 1970); (3) difficulties regarding appropriate planting stock selection while considering management goals, ecological factors, and silvicultural options (Klinka and Feller 1984); and (4) uncertainty about how present management decisions will be influenced by future economics. Klinka and Feller (1984) emphasized that appropriate planting stock selection in southwestern British Columbia depends on ecological factors and management goals. Inherent ecological characteristics of species (growth habit, stress-tolerance, etc.) influence the growth and survival of different species on different sites; certain site conditions will allow one species to grow and survive better than another species planted on a given site, but not on every site.

Management decisions regarding desired future stand structure and composition are dictated both by management objectives. The selection of appropriate tree species and species combinations should: (1) maximize the potential productivity of the site; (2) establish reliably and be tolerant of potential future stresses, (3) be silviculturally feasible (Klinka and Feller 1984). In southwestern Oregon and northern California, guidelines for the selection of appropriate stock type emphasize matching morphological characteristics (size) and physiological condition of seedlings that will maximize success on a given site (Hobbs 1992).

Many have tried to define what quality means in the context of a seedling, confounded by the fact that seedling quality is not a static concept, as a seedling of high quality on a given site, when planted elsewhere, could be of a lower quality. Remarking on the importance of site specific success of a seedling when considering seedling quality, Duryea (1985) described high quality seedlings as “those that meet defined levels of survival and growth on a particular planting site.” This echoes the common theme that any definition of seedling quality must be evaluated on field performance, or the growth and survival of the seedling once outplanted.

Wakeley (1954) was a pioneer in identifying that seedling quality assessments should be based on both morphological and physiological characteristics of the seedling. Therefore, assessments of seedling quality should include a seedling’s response to a given environment, performance attributes (i.e. root growth potential, cold hardiness); as well as, the measurement of specific attributes of the seedling (i.e. morphology, dormancy, nutrition), also known as material attributes (Ritchie 1984). Both performance and material attributes provide information on how a seedling might perform in the field. This is the basis of the Target Seedling Concept, used by nurseries to grow seedlings with specific, or target, morphological and physiological characteristics that have been quantitatively linked to high field performance (Rose et al. 1990), or defined by the forest managers to meet specific reforestation needs.

Root growth potential (RGP) is commonly used as a measure of seedling quality, as it is a physiological measurement of a seedling's ability to grow roots in a favorable environment. RGP testing is performed in an environment conducive to root growth and does not account for the range of environmental conditions a seedling is exposed to when outplanted. However, a seedling that is able to quickly grow new roots when planted in a new environment will overcome the stress of transplanting more quickly than a seedling with reduced root growth, as it is more quickly "coupled" with the new environment (Grossnickle 2005). Conceptually, this makes sense and in practice RGP has served as an indicator of seedling vigor (Ritchie and Dunlap 1980), field performance has been positively linked to RGP in NW conifers (Ritchie 1985), especially western larch (*Larix occidentalis*) and inland Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), (L'Hirondelle et al. 2007).

It is worth noting that there is variability in RGP as a predictive measure of seedling quality because RGP is not positively correlated with survival for every species, for those species where RGP does have a positive correlation with survival, the relationship is often weak (Ritchie 1984). The interaction of physiological characteristics which regulate root growth are inherent to a seedling, controlled by environmental factors, and can be influenced by nursery culture (Kozlowski 1971). For these reasons, some have made the argument that sole use of RGP as an analog for field performance is logically flawed (Simpson and Ritchie 1997).

Site quality is highly correlated with physical properties of the soil, like moisture and temperature (Zahner 1968); it has been found that soil moisture is more strongly tied to tree growth responses than the nutrient availability of the soil for certain tree species (Stoeckler 1960). In drought-prone areas, characteristic of the Inland Northwest, moisture stress is the most common cause of forest plantation failure (Arnott 1975; Hobbs 1992). Moisture stress can reduce conifer seedling growth by more than 50% and initiate dormancy in certain species, including Douglas-fir (Zahner 1968). Moisture stress directly influences plant growth by altering the turgor pressure of plant cells and through the inhibition of enzyme activity (Teskey and Hinckley 1986). Soil temperature influences the shoot growth (Lyr and Garbe 1995) and root growth (Barney 1951) of conifer seedlings, generally growth increases with soil temperature to a certain point when it becomes inhibitive. The soil temperature also influences the internal water status of conifer seedlings (Kaufmann 1977).

The presence of vegetation on a reforestation site influences reforestation success, directly, by introducing competition for resources via alterations to the soil water budget from increased transpiration at the critical time of seedling establishment (Spittlehouse and Childs 1990). Indirectly, the presence, density, and distribution of competing vegetation also influences the soil surface temperature by altering the albedo of the soil surface (De Vries 1963).

It should be noted that occasionally, even with appropriate planting stock selection, and site and environmental conditions favorable to successful establishment, conifer plantations still occasionally fail (Stewart and Beebe 1974). While there have been many studies that examine how RGP relates to field performance of planted seedlings and how site characteristics influence the seedling growth and survival, there is very little research examining how the expression of RGP is influenced by site characteristics. The specific objectives of this study are to: (1) investigate the impact of RGP on seedling growth and survival over two growing seasons; (2) investigate the impact of soil moisture on seedling growth and survival over two growing seasons; (3) investigate the impact of soil temperature on seedling growth and survival over two growing seasons; (4) investigate the impact of competing vegetation and slash cover on seedling growth and survival over two growing seasons.

Methods

Planting Stock

Various Douglas-fir, grand fir, and western larch seedlots were tested for RGP in aeroponic chambers at the University of Idaho Center for Forest Nursery and Seedling Research Lab in winter 2015/spring 2016. Seedlots were grown at various nurseries across northwestern U.S. and western Canada. All seedlings were grown in Beaver Plastics 8L

Styroblock containers ((Stuewe & Sons Inc., Tangent, OR). The planting stock was considered to be of high quality by the respective nursery of origin.

Seedlings were stored in a cooler with temperature fluctuating between -2.22°C and 0°C until the time of root growth potential (RGP) testing. Initial measurements of shoot height, root collar diameter (RCD) and root volume were taken after the soil was washed from the roots. Shoot height was measured with a ruler, RCD measured with calipers, and root volume with graduated cylinder and scale using Archimedes' Principle.

Root Growth Potential

RGP testing was conducted in aeroponic chambers using a pulsating garden sprinkler attached to a 1/6 h.p. utility submersible pump that sprayed the roots with water to stimulate growth over a 28-day period. The chamber air temperature and water temperature were kept constant at 20°C. The sprinkler was run for 1 minute, then turned off for 4 minutes for the duration of the testing. Lighting in the chamber was provided by LED lights as well as natural light from windows in the lab. Each LED light fixture was comprised of 8 modules, each module is approximately 4 cm by 123 cm with 87 bulbs each, emitting 85:10:5 red:blue:green (DR/W LED 120-110V, Philips). Lighting schedule was alternating 10 hours on and 14 hours off for the duration of the test. At the end of each test, the number of new root tips produced were counted.

Site Description

The study was installed on Potlatch Forest Holdings, Inc. land approximately 4.72 km east of Bovill in Latah Co., ID (elev. ~975 m) (Figure 1.1). The site was a western redcedar habitat type(Cooper et al. 1991). 2010 to 2016 data from a nearby ground-based NOAA weather station in Elk River, ID (elev. ~266 m) was used to determine that mean annual precipitation is 58.8 cm, mean annual snow accumulation is 88.6 cm, and mean annual maximum temperature is 36.5 °C, mean annual minimum temperature is -18.2 °C. Prior to harvest, the site was occupied by an even-aged stand with a species composition of 30% Douglas-fir, 15% grand fir, 15% western larch, and 15% other species. The stand was clearcut harvested in 2013, there had been no site preparation activities after the time of harvest.

Experimental Design

The experiment was designed to evaluate differences in the growth and survival of three tree species (western larch, Douglas-fir, and grand fir), and three sites with hypothesized differences in site conditions: (1) north aspect, (2) north aspect with supplemental watering, and (3) south aspect.

Seedlings were planted in a completely randomized block, split-plot design with three blocks. Seedlots were the split-plot factor while RGP rating was the whole-plot factor. Each species x RGP ratings combinations were replicated three times at each site. Species x RGP combinations were randomly assigned to one row within a block (3 blocks/site); blocks were based on slope position (upper, middle, lower slope).

For each row 30 seedlings of a single seedlot were planted along the contour of the slope, spaced 4 ft.; in the same row, another 30 seedlings of the paired seedlot were planted along the same contour and with the same spacing, creating a split-plot factor of seedlot-within-block. Beginning with the first seedling in a row, every other seedling was tagged for observations of growth and survival (16 seedlings/seedlot/row). Untagged seedlings were reserved for destructive measurements (Chapter 2).

Site Treatments

Prior to planting, the sites were treated with a broadcast application of glyphosate herbicide to control existing vegetation in April 2016. The treatment applied glyphosate at 2.8 kg active ingredient (a.i.) per hectare mixed with 2% (v/v) nonionic surfactant in water. The application was applied with a CO_2 powered backpack sprayer (Bellspray Inc. Model 4F) with a 2.74 m overhead extended boom equipped with a single KLC-9 flood tip nozzle. The sprayer was calibrated to apply 140.33 liters per hectare of mix to the sites. Standing woody vegetation was hand-cut and moved off-site. To prevent nearby grazing activities from interfering with the study each installation was enclosed with a 1.83-m high fence.

On July 12, 2016 a direct application of glyphosate was applied to the south-aspect site. Glyphosate at a 5% concentration was mixed with water and 2% nonionic surfactant in Birchmeier Iris® four-gallon backpack sprayers with an adjustable cone nozzle. The nozzle was adjusted to produce a medium-sized droplet size to minimize spray drift and damage to crop trees. Seedlings were protected from herbicide contact by placing buckets over the top of the seedling. The treatment was deemed necessary because the site became heavily occupied by bracken fern (*Pteridium aquilinum*). Some seedlings were incidentally damaged by herbicide; surveys of herbicide damage were made in August 2016 and any seedlings with visible herbicide damage were removed from the analysis.

On September 6, 2016, the north-aspect site with the supplemental watering treatment received 3,406 liters of supplemental water. Watering was performed by hand with a hose. Watering regime was such that on the site each block was roughly separated into thirds, creating 9 separate watering areas approximately 0.28 ha. in size. The individual watering chose a central location within each watering area and used the hose to evenly spray the area. After 15 minutes the individual moved to the next location. Each watering area was visited twice.

Data Collection

Observations of height measured from the ground line to the tip of the terminal leader, diameter measured at ground line, and survival were made in June 2016, October 2016. and August 2017.

Soil moisture and temperature were monitored within each block of the study site for the duration of the study using Em50 data loggers and 5TM soil moisture and temperature sensors (Decagon Devices, Pullman WA). Volumetric water content (VWC) (m^3/m^3) and temperature (°C) were measured at 5-10 min. intervals; sensors were placed at depths of 15 cm and 50 cm below the soil surface. To account for the variability of logging debris on the site from prior harvesting activity, sensors were placed under characteristic areas within each block where the soil surface was covered in coarse woody debris and areas that were free of coarse woody debris.

Daily average soil moisture and temperature was calculated for each soil sensor. Summer soil moisture and temperature was determined by the average daily soil moisture and soil temperature at each depth for the summer of 2016 (June 1, 2016 to September 30, 2016) and from the beginning of summer 2017 until the time of final measurements (August 14-16, 2017). For each depth, summer averages of soil VWC and temperature under coarse woody debris and those under bare ground were calculated and used in analysis (Table 1.1). Despite the supplemental watering treatment, this north-aspect site which received the treatment had the lowest soil moisture during the active growing season.

In August of 2017, estimates of competing vegetation and slash (coarse woody debris) were collected. A ½ m quadrat frame was centered over the planting spot of tagged seedlings and cover was estimated visually by the same individual to the nearest 10%. Vegetation cover estimates were made categorically (shrub, forb, fern, grass, thistle).

Statistical Analyses

Growth response variables are individual seedling changes in height (cm), diameter (mm) from the time of planting to the end of the second growing season. Individual seedling survival was determined at the end of the second growing season. Significance was assessed at the α=0.05 level. All analyses for this study were performed using R software (Version 3.3.2) .

Analysis of the additive effects of initial size, RGP, average summer soil moisture (m^3/ m^3) and temperature (°C), as well as competing vegetation by life form (% cover), and slash (% cover) on the total growth of seedlings was performed using species-specific, linear, mixed-effects regression models using the gaussian distribution (package nlme) (Pinheiro et al. 2014). Residuals approximated a normal distribution, and mean variance. Analysis was performed using R package "nlme" (Pinheiro et al. 2014) ; seedlot was the random effect. Diameter growth models utilized a logarithmic transformation of the response variable.

Analysis of the additive effects of seedling height at the end of the first growing season, RGP, average summer soil moisture (m^3/ m^3) and temperature (°C), as well as competing vegetation by life form (% cover), and slash (% cover) on the survival of seedlings at the end of the second growing season was performed using species-specific, logistic mixed-effects regression models using the binomial distribution, Analysis was performed using R package "lme4" (Bates 2010); seedlot was the random effect.

Due to high correlation between the soil temperature at the two depths below the soil surface (0.96), the soil temperature at a depth of 15 cm below the soil surface was solely used in analysis. Full models with a weighted variance structure using a power function of initial (June 2016) height or diameter were tested against full models with an unweighted variance structure. If the weighted variance structure significantly improved the fit of the model, then that model was used; otherwise the simpler model was used for analysis.

Additional analysis consisted of selecting the “best” model. Model selection was performed by removing insignificant predictor variables from the model individually, hierarchically removing the least significant variable, determined by p-value, and running the model again until only significant predictor variables remained. If the sign of a regression estimate of a given parameter returned from analysis was known to be biologically incorrect then that term was removed from the final model.

Results

Root Growth Potential

Regardless of species, RGP did not have a significant influence on the two-year field performance of planted stock (Tables 1.2-1.4).

Morphology

There was a significant, negative relationship between the two-year height and diameter growth of grand fir and initial height and diameter; western larch and Douglas-fir growth were not significantly influenced by initial morphology (Table 1.2-1.3). Regardless of species, there was a significant, positive relationship between the odds of seedlings surviving two years and the height of that seedling at the end of the first growing season (Table 1.4).

Soil Moisture

Grand fir seedlings exhibited a significant, positive relationship between soil moisture content at 15 cm below the soil surface and two-year height growth but otherwise there was no influence of soil moisture at either depth on the two-year growth of planted seedlings (Tables 1.2-1.3). Douglas-fir seedlings exhibited a significant positive relationship between the odds of two-year survival and soil moisture at a depth of 50 cm below the soil surface (Table 1.4).

Soil Temperature

Douglas-fir and western larch seedlings exhibited significant, negative relationships between height and diameter growth and soil temperature (Tables 1.2-1.3). Douglas-fir and western larch exhibited similar rates of growth loss with increasing temperature, but western larch was slightly more sensitive than Douglas-fir (Figure 1.2-1.3). Western larch and grand fir seedlings exhibited a significant, negative relationship between two-year survival and soil temperature (Table 1.4). Western larch seedling two-year survival was generally higher than grand fir, but as soil temperatures increased western larch seedling survival decreased more dramatically (Figure 1.4).

Ground Cover

Competing vegetation had a variable influence on two-year seedling height growth depending on the species (Table 1.2). Douglas-fir and western larch seedlings grew taller with increasing thistle cover and Douglas-fir seedlings grew taller with increasing shrub cover. Grand fir seedlings exhibited less height growth as forb cover increased. Douglas-fir and grand fir seedling height growth increased with slash cover.

Competing vegetation had a negative influence on two-year diameter growth of Douglas-fir and western larch seedlings (Table 1.3). Douglas-fir and western larch diameter growth was negatively related to both, shrub and forb cover. Western larch diameter growth also decreased as bracken-fern and grass cover increased. Douglas-fir seedling diameter growth increased with slash cover. Regardless of species, the odds of a seedling surviving two years were not significantly influenced by competing vegetation or slash cover (Table 1.4).

Discussion

Root Growth Potential

While many studies have found that RGP is an accurate predictor of field performance, there exist considerable studies where there has been minimal correlation, or an absence of correlation between field performance and RGP. During the heyday of RGP testing for seedling quality a review of the state of the science conducted by Binder et al. (1988) found that RGP testing has low accuracy, low precision, and low repeatability largely due to the large variability in testing conditions and procedures, and large variability in the RGP for a given seedlot depending on testing conditions. Del Campo et al. (2007) found that the ability of RGP to predict field performance of Aleppo pine was dependent on seedling lift date. Sutton (1987) failed to find any correlation between RGP and field performance until the third year after planting and attributed it to heterogeneity in the conditions between planting sites.

Brissette and Roberts (1984) found no correlation between RGP and field performance of loblolly pine, but it was attributed to the generally high survival that resulted from favorable growing conditions. This may be the reason that there was no detectable influence of RGP on two-year field performance in this study; across the duration of the experiment Latah Co., ID did not experience drought conditions. Throughout the summer of 2016, Palmer Drought Severity Index (PDSI) in Latah Co. ranged from -1.0 to -1.9 indicating abnormally dry conditions, and in 2017 from July to the time of final measurements, PDSI in Latah Co. ranged from 0 to -1.9; compare this to the summer of 2015 where PDSI in Latah Co. ranged from -2.0 to -4.9 indicating moderate to extreme drought (NDMC 2017). Likely, the relatively mild growing conditions that occurred during this experiment did not allow for the expression RGP as it relates to stress-tolerance.

Morphology

The results of this study indicate an odd relationship between growth, survival, and morphology. It is generally recognized that conifer seedlings with greater initial height tend to grow taller, this has been found for Norway spruce (Schmidt-Vogt 1981), red pine (Curtis 1955), and loblolly pine (McGilvray and Barnett 1982). This is attributed to the high correlation between seedling height and needle number, which is indicative of photosynthetic capacity (Armson and Sadreika 1974). Similarly, conifer seedlings with a large initial diameter have been found to grow larger over time (Anstey 1971; Blair and Cech 1974).

In this study, the initial height western larch and Douglas-fir seedlings were not influential on two-year height growth and grand fir seedling initial height growth was negatively related to two-year height growth. Research performed by Menzies et al. (1985) on radiata pine has shown that the predictive ability of initial height on height growth is reliable only for relatively short seedlings, under 30 cm, and seedlings with greater initial heights had little or decreased height growth, comparatively. This may explain the lack of a positive relationship between two-year height growth and the initial height in this study where the average initial height of western larch, Douglas-fir, and grand fir seedlings was, 37 cm, 34 cm, and 29 cm, respectively. Alternatively, in this study those trees with greater initial aboveground size may have had an suboptimal root to shoot ratio (R:S) and were susceptible to planting shock.

Grand fir is a species with strictly determinate growth habit, with a period of shoot elongation lasting from mid-May to the end of June, a short time period compared to the time of vegetative bud development which begins as shoot elongation ends and continues until vegetative buds become dormant in mid-November; these vegetative buds contain all the leaf primordia (potential growth) for the next growing season (Owens 1984). Grand fir seedlings with relatively large initial height and diameter grew significantly less across two growing seasons. This may be explained by the seedling growth in the nursery, grand fir seedlings that favored shoot elongation as germinants and ended up being larger leaving the nursery, but those smaller seedlings may have favored bud development as germinants. Therefore, these larger seedlings leaving the nursery likely had less potential growth, stored as leaf primordia in vegetative buds, at the time of planting. Those seedlings that were initially the tallest were not necessarily the tallest seedlings at the end of the two-years, but seedlings that grew faster survived better across the duration of this study.

Soil Moisture

There was general lack of influence of soil moisture at either depth on the field performance of planted seedlings, which is counter-intuitive as moisture stress is often attributed as the cause of plantation failure throughout the region. However, due to the mildness of the summer drought experienced during this study, it is likely that seedlings did not experience drought-stress intense enough prevent recovery or induce dormancy. Douglas-fir seedlings exhibited a positive relationship between survival and soil moisture at a depth of 50 cm below the soil surface, which is interesting as Douglas-fir is more tolerant of dry soil conditions than the other two study species, but it is also more tolerant of other environmental stresses like high temperatures (Minore 1979). This may have allowed Douglas-fir seedlings to respond positively to soil moisture deep in the soil profile, which is more indicative of the moisture holding capacity of the soil than the more variable soil moisture at shallower depths. Likely, western larch and grand fir seedlings were overwhelmed by other site conditions and were not able to realize benefits of increased soil moisture as it was a mild drought year.

Alternatively, there may be another reason that relatively high soil moisture on the sites did not result in increased field performance. In Idaho forests, root disease has been found on 35% of dead or dying trees, and accounting for 26%-35% of growth loss (James et al. 1984); the most common agents of root disease in the region are parasitic fungi of the genus *Armillaria* (James et al. 1984; Mallett and Maynard 1998). The incidence of *Armillaria* pathogenicity has been found to be as high as 65% in the western redcedar habitat type (McDonald et al. 1987). Further, it has been found that *Armillaria* in Interior British Columbia occurs with greater frequency where soil moisture is relatively high (Cruickshank et al. 1997) and the incidence of *Armillaria* infection increases on soils with poor permeability and soil moisture remains near the soil surface (Ono 1970). This may explain the lack of positive influence of soil moisture on the field performance of planted seedlings, as negative effects of soil moisture were removed from analysis and considered biologically infeasible.

Soil Temperature

Temperature effects plant growth and survival. Many enzymes which facilitate any biological process have optimal temperature ranges, annual growth cycle of many plants is, in part, regulated by temperature, and temperature extremes limit plant growth and distribution and can cause physical injury to seedlings (Lavender 1990). High temperatures negatively influence woody plants via growth inhibition, carbon starvation, and the denaturation of essential proteins, among other things (Levitt 1980b). The optimal temperature for plant respiration is generally higher than the optimal temperature for photosynthesis (Kramer and Kozlowski 1979). As a result, increasing temperature from moderate to extreme reduces net photosynthesis but increases respiration, hampering and the ability of conifers seedlings to accumulate carbohydrates (Decker 1944). Further, woody plant transpiration increases with temperature (Kramer and Kozlowski 1979) which can lead to dehydration. It has been found that in this region soil surfaces in clear-cuts can reach temperatures high enough to damage plant tissue for several hours a day during the growing season (Hungerford 1980) and that planted seedling mortality increases with soil temperature (Helgerson 1989).

Western larch seedlings field performance was not surprisingly negatively related to soil temperature. as it has been well documented that high surface temperatures and droughty conditions associated with a south-aspects in this region are not conducive to western larch regeneration (Schmidt et al. 1976). It has been shown that naturally regenerated western larch seedling mortality is six times higher, and occurs two weeks earlier on south and west aspects than north aspects (Shearer 1967). High temperatures have been found to be the primary cause of western larch seedling mortality, more injurious than drought-stress (Haig 1936; Shearer 1967).

It is interesting that there were negative effects of high soil temperatures on grand fir survival, but not Douglas-fir survival; and that there were negative effects of high soil temperatures on Douglas-fir growth, but not grand fir growth. Both species are generally considered to have similar tolerance to heat injury (Foiles 1959), being more tolerant than co-occurring conifers (Schubert and Adams 1971). However, it has been shown that Douglas-fir seedlings have higher heat tolerance than grand fir seedlings (Baker 1929); and when grown in full sun, grand fir seedling mortality due to insolation is 13% greater than Douglas-fir (Haig et al. 1941).

Grand fir seedlings did not exhibit inhibition of growth caused by high temperatures, but high temperatures significantly decreased the odds of grand fir seedling survival; and the opposite was seen in Douglas-fir seedlings. Heat tolerance in plants is due, in part, to the ability of plant proteins to resist permanent changes in chemical or physical structure, or the thermostability of plant proteins (Levitt 1980a). It has been shown that increased conifer heat tolerance can be achieved by brief exposure to sub-lethal high temperatures (Colombo et al. 1992; Koppenaal et al. 1991). Immediately, when exposed to high temperatures, conifer seedlings produce proteins, coined heat-shock proteins (HSPs) which are correlated to heat tolerance (Colombo et al. 1992). The role of HSPs in heat tolerance are largely unknown, but it is generally accepted that HSPs are involved in a plant's tolerance to high temperatures (Vierling 1991), and that different conifer species produce different HSPs of different mass (Gifford and Taleisnik 1994). Research has shown that Douglas-fir seedlings produce HSPs (Kaukinen et al. 1996), but it is unknown whether grand fir produces HSPs. Perhaps Douglas-fir seedling HSP production is more energetically expensive than grand fir resulting in depletion of stored carbohydrates and growth inhibition, but results in greater tolerance of high temperatures. It is interesting that grand fir seedlings did not show significant growth reductions in relation to increased soil temperatures, but survival was significantly decreased; this relationship has been documented for seedlings of other North American tree species (Fisichelli et al. 2014).

Ground Cover

Many studies have shown that the increased presence of competing vegetation negatively influences the field performance of planted conifer seedlings (MacDonald and Weetman 1993; Wagner 2000). This is due, in part to competition for resources (Berkowitz et al. 1995). Research has helped illustrate the positive effects of vegetation control on early stand growth by increasing available soil moisture (Flint and Childs 1987; Newton and Preest 1988; Watt et al. 2003), available soil nutrients (Smethurst and Nambiar 1995; Zutter et al. 1999), and complimentarily increasing both soil moisture availability and soil nutrient availability (Elliott and White 1987; Powers and Reynolds 1999). In short, the presence of competing vegetation reduces available resources, and planted seedlings exhibit decreased field performance as a result. In this study, planted seedlings generally responded to forb (non-thistle), grass, and fern competition with either decreased height or decreased diameter growth, or both; but there was no influence on survival.

Douglas-fir and western larch seedlings in this study responded to cumulative competing vegetation by growing taller and skinnier, and grand fir seedlings exhibited decreased height growth. This response has been observed of Douglas-fir seedlings and seedlings of other *Larix* species responding to light competition (Mason et al. 2004) as well as other conifer species (Wagner et al. 1999). Grand fir seedlings responded to light competition with decreased height growth only, this is likely explained by grand fir being the most shade-tolerant species in this study (Minore 1979) and can persist in shade.

Interestingly, as thistle cover increased, Douglas-fir and western larch seedlings grew taller with no accompanying decrease in diameter growth. Research conducted by Randall and Rejmánek (1993) found no negative influence of thistle competition on ponderosa pine seedlings until the second year. It may be that the heavy herbicide-use in the first year of our study set back thistle on the site enough that negative influence of thistle was not observed for the duration of this study. Further, a thistle is a spiny biennial forb which spends the first growing season and overwinters as a rosette. The spreading nature of the rosette reduces available growing space for potential competitors and the spines discourage herbivory (Schulze et al. 2005).

There is a trade-off between height growth and diameter growth, as height growth is important if a seedling is to compete with neighboring vegetation (King 1990; Mäkelä

1986). Height growth can come at the expense of diameter growth which provides mechanical support, as well as regulates the exchange of moisture and nutrients between the roots and the crown of the seedling (King 1990; Mäkelä 1986). It has been shown that, in the establishment phase, seedlings of other species favor height growth over diameter growth, and those seedlings with the greatest initial height growth maintain dominant crown positions after the establishment phase (Sumida et al. 1997). Douglas-fir and western larch respond to cumulative vegetation increases by growing taller and skinnier, while grand fir grows shorter there is no decrease in stability associated with the other species. As grand fir is the most shade-tolerant species in this study (Minore 1979) conservative height growth in the presence of competition may not be a hindrance, as grand fir does not require a dominant position in the crown as it can persist in the understory.

In this study slash tends to increase growth of relatively shade-tolerant species/determinate growth species. This may be that the presence of coarse woody debris may protect seedlings from direct sunlight, shading the basal portion of seedling stems provides effective prevention of heat damage (Helgerson 1989). Coarse woody debris also influences surface temperatures, in the heat of the day in July in Wyoming, surface temperatures are much lower in harvested areas where woody debris is present on the site than either cleared or burned areas likely due to differences in albedo between surface types and differences in thermal conductivity, and soil moisture losses are greater from exposed soil surfaces than those covered with harvesting residues (Hungerford 1980). Coarse woody debris contains 12 of 17 nutrients essential to plant life of higher orders (Harmon et al. 1986). Whether by altering the temperature, moisture, or nutrient availability of the soil, the presence of slash in the seedling microsite provides benefits to seedling growth.

Management Implications

The results of this study suggest, as other studies have (Brissette and Roberts 1984), that the benefits of RGP as a metric of seedling survival may be best suited to stressful planting sites. There may be no benefit to planting larger seedlings, in this region. They are more expensive to produce and have no positive benefit on initial growth. Seed stock selection should favor genotypes and nursery culture that provide increased growth upon outplanting, not necessarily those genotypes that grow best in favorable nursery environments.

The results of this study suggest that seedling field performance is more greatly influenced by high soil temperatures than low soil moisture. An analysis by the Intergovernmental Panel on Climate Change (2014) suggests that global temperatures will continue to increase; therefore current planting stock selection should favor those species and genotypes with greatest heat tolerance, which may be better adapted to future conditions. Western larch should be planted with care, as the results of this study support other studies which suggest that in the next 70 years the range that western larch can grow will be greatly reduced (Rehfeldt and Jaquish 2010). More research into HSPs could help guide management decisions regarding planting stock selection.

Vegetation control is important in producing sturdy seedlings, and if there are areas where chemical site preparation cannot be used for logistic or budget constraints, planting more shade-tolerant species is a viable option. Slash management site preparation activities should favor strategies that leave slash on site (e.g. scattering or mastication) over pile-and-burn strategies, if seedling growth is a priority; although this will likely increase planting costs.

Tables

Table 1.1 2016-2017 average summer soil temperature and soil moisture at two depths from the soil surface.

	Soil Temperature (°C)		Soil Moisture (m^3/m^3)	
Site	15 cm	50 cm	15 cm	50 cm
north-aspect	13.84 (13.61-13.98)	12.02 (11.85-12.15)	0.25 (0.20-0.31)	0.21 (0.18-0.28)
north-aspect with supplemental watering	14.68 (13.95-16.01)	12.92 (12.36-13.67)	0.19 (0.15-0.22)	0.18 (0.14-.024)
south-aspect	16.59 (15.99-17.32)	14.96 (14.54-15.52)	0.24 (0.19-0.33)	0.20 (0.16-0.22)

Table 1.2 Seedling two-year height growth parameter coefficients and standard errors for three Inland Northwest conifer species.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	81.003	7.801	52.178	4.355	4.264	0.475
Int. Ht.	-	-	-	-	-0.052	0.013
RGP	-	-	-	-	-	-
VWC (15 cm)	-	-	-	-	2.914	0.942
VWC (50 cm)	-	-	-	-	-	-
Temp.	-2.893	0.519	-2.156	0.280	-	-
Slash	-	-	0.151	0.027	0.010	0.004
Forb	-	-	-	-	-0.010	0.004
Thistle	0.273	0.104	0.176	0.049	-	-
Shrub	-	-	0.075	0.029	-	-
Fern	-	-	-	-	-	-
Grass	-	-	-	-	-	-

Table 1.3 Seedling two-year diameter growth parameter coefficients and standard errors for three Inland Northwest conifer species

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	2.819	0.181	2.408	0.186	1.865	0.172
Int. Diam.	-	-	-	-	-0.139	0.038
RGP	-	-	-	-	-	-
VWC (15 cm)	-	-	-	-	-	-
VWC (50 cm)	-	-	-	-	-	-
Temp.	-0.046	0.012	-0.040	0.012	-	-
Slash	-	-	0.003	0.001	-	-
Forb	-0.003	0.001	-0.003	0.001	-	-
Thistle	-	-	-	-	-	-
Shrub	-0.005	0.001	-0.003	0.001	-	-
Fern	-0.008	0.003	-	-	-	-
Grass	-0.003	0.002	-	-	-	-

*Parameter values and standard errors on log scale.

Table 1.4 Seedling two-year survival parameter coefficients and standard errors for three Inland Northwest conifer species

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	8.030	1.815	-	-	-	-
Yr. 1 Ht.	0.053	0.014	0.034	0.014	0.119	0.025
RGP	-	-	-	-	-	-
VWC (15 cm)	-	-	-	-	-	-
VWC (50 cm)	-	-	7.297	2.939	-	-
Temp.	-0.531	0.109	-	-	-0.125	0.052
Slash	-	-	-	-	-	-
Forb	-	-	-	-	-	-
Thistle	-	-	-	-	-	-
Shrub	-	-	-	-	-	-
Fern	-	-	-	-	-	-
Grass	-	-	-	-	-	-

Figures

Figure 1.1 Aerial photo of planting sites.

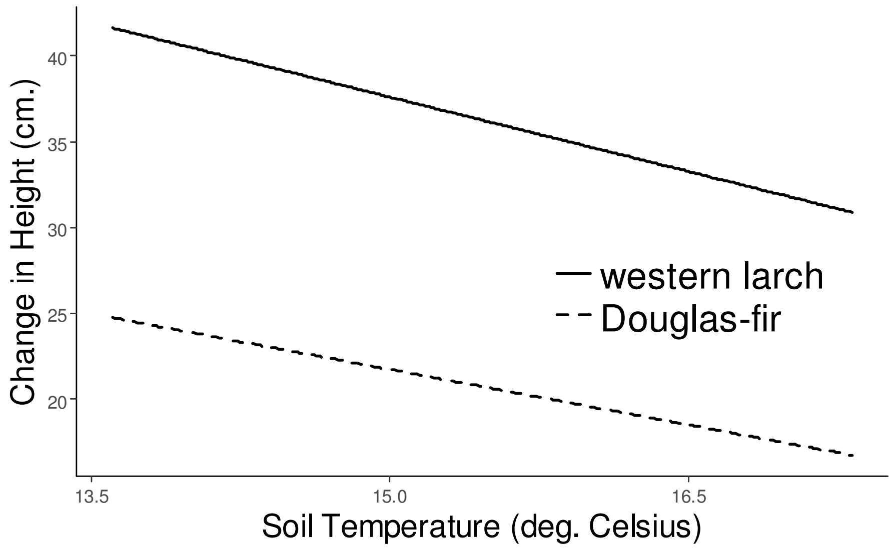

Figure 1.2 Observed relationship between soil temperature on two-year height growth of Douglas-fir and western larch seedlings.

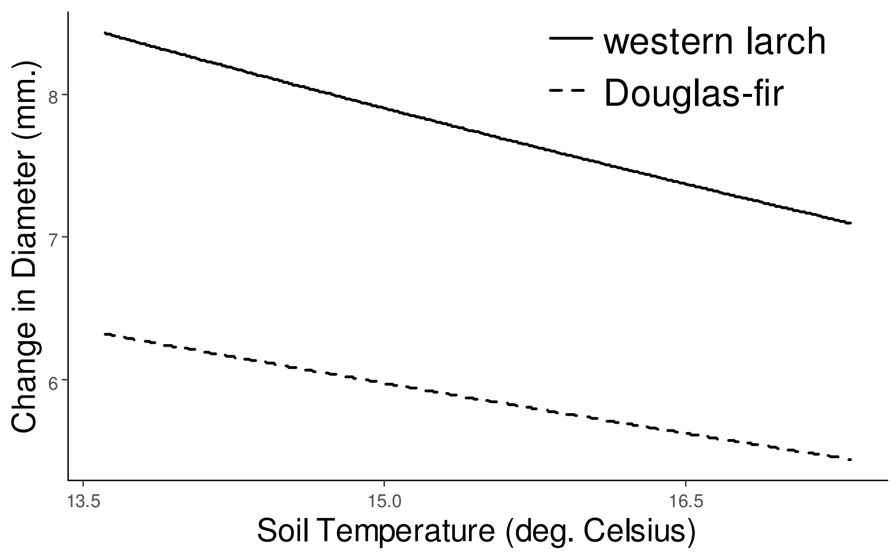

Figure 1.3 Observed relationship between soil temperature on two-year diameter growth of Douglas-fir and western larch seedlings.

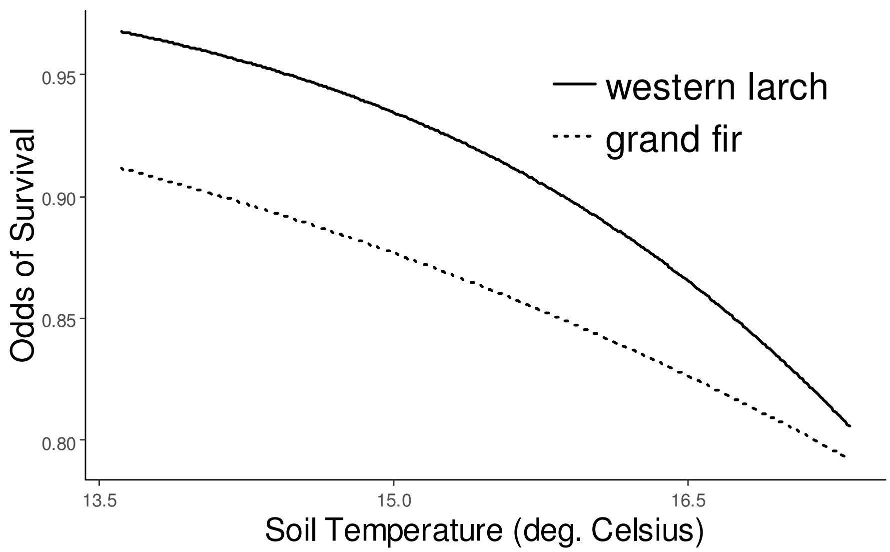

Figure 1.4 Influence of soil temperature on two-year survival of western larch and grand fir seedlings.

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Chapter 2: First-Year Temporal Biomass Allocation of Inland Northwest Conifer Seedlings in Response to Root Growth Potential and Site Characteristics

Abstract

Conifer plantations are susceptible to failure, especially in regions with annual growing-season droughts. Common reasons for plantation failure include unfavorable environmental conditions and poor seedling quality, but often the mechanisms of seedling success are not properly understood. This investigation aims to examine biomass allocation of seedlings of variable quality, determined by root growth potential (RGP), to different growing environments over the first growing season, and how these responses influenced survival over two growing seasons. Interior Douglas-fir (*Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco), grand fir (*Abies grandis*), and western larch (*Larix occidentalis*) were planted on three sites in northern Idaho, USA that differed in aspect and seasonal soil moisture. Biomass allocation and morphology differed among species in response to growing season changes in soil moisture and temperature. Regardless of species, seedlings favored height growth over diameter growth with increasing soil temperature. Douglas-fir favored root biomass production with increasing soil temperature, while western larch and grand fir favored shoot biomass production with increasing soil temperature. Douglas-fir and western larch total biomass production were lower when RGP was high. The odds of survival for Douglas-fir and grand fir seedlings at the end of the second growing season increased with final first-year root to shoot ratio (R:S). Results suggest that seedling morphology and biomass allocation patterns are influenced by environmental conditions and seedling quality. Results will help guide management decisions regarding species and stocktype selections, which are becoming increasingly important for future success of reforestation efforts.

Introduction

Plants acquire water and nutrients from the soil via the root system, and structural carbon is created in the shoot of the plant via photosynthesis. The Optimal Partitioning

Theory (OPT) states that a plant will allocate biomass to whichever organ acquires the most limiting resource because there is an evolutionary tradeoff between allocation of biomass to above- and belowground structures. Global patterns of biomass partitioning and intraspecific variation in biomass partitioning patterns of plants have been shown to be consistent with the OPT (Gedroc et al. 1996; McCarthy and Enquist 2007). According to the OPT if water or nutrients are limiting resources then plants will allocate more biomass to the root system. However, if light is the limiting resource then the allocation of biomass will favor shoot growth. Therefore, the relative allocation of biomass towards component structures (e.g. foliage, roots, stem) provide information as to how a plant is responding to the environment.

Allocation of plant resources and the amount of available resources are largely regulated by the environment (Bazzaz and Grace 1997). The allocation of limited resources drawn from the environment are allocated towards either vegetative growth (above or below-ground) or reproductive structures, which vary seasonally and with species, genetics, age, size, community structure, and the length of the growing season (Kozłowski 1992). The internal allocation of carbon and acquired elements towards the production of compounds (e.g. lignin, DNA, chlorophyll, amino acids) and non-structural carbon comprise up to 95% of a plant's total biomass (Bazzaz and Grace 1997). The energetic cost of production of these various compounds varies; the construction of lipids, soluble phenolics, proteins, and lignin are relatively expensive, while the construction of carbohydrates and organic acids are relatively cheap, in the context of the carbon budget of plants (Bazzaz and Grace 1997). These costs are influenced by the environment (Bazzaz and Grace 1997), and the relative concentrations of these compounds varies with available nutrients (Waring et al. 1985).

Conifer seedling root growth (Barney 1951; Kaufmann 1977), foliar mass accumulation (Boucher et al. 2001) and shoot extension (Lyr and Garbe 1995), increase with soil temperature until temperatures becomes extreme. Soil temperatures can induce changes to conifer seedling root morphology, where high soil temperatures result in long, thin roots with little branching (Wilcox and Ganmore-Neumann 1975) and low soil temperatures result in short, thick roots with more branching (Alvarez-Uria and Körner 2007; Lavender and Overton 1972). High soil temperatures also result in decreased root-to-shoot ratio (R:S) (Domisch et al. 2001). Moisture stress in conifers species can result in the production of smaller needles (Linder et al. 1987; Lotan and Zahner 1963; Miller 1965), and increased leaf abscission (Hennessey et al. 1992). Moisture limitations can also induce conifers to allocate relatively less carbon to woody tissues and coarse roots (Gower et al. 1992; Waring and Pitman 1985).

Trees grow allometrically, with dimensional relationships between tree structures like roots, foliage, and woody components. For example a tree's diameter has a disproportionate dimensional relationship to the height of the tree; this has been shown for nearly every North American tree species (McMahon 1973; Ter-Mikaelian and Korzukhin 1997), a concept used to develop forest growth and yield models (Assmann 1970). Species-specific allometric biomass equations have been developed for most North American tree species but most research is devoted to mature trees rather than seedlings, despite biomass partitioning patterns changing with tree age (Helmisaari et al. 2002; Satoo and Madgwick 1982). Additionally, relatively little research has been conducted examining belowground allometric relationships, even though belowground biomass in conifers accounts for nearly 20% of the total biomass (Kurz et al. 1996).

Seedling quality is generally described in terms of growth and survival on a particular planting site (Duryea 1985). Wakeley (1954) identified that any seedling quality assessment should be based on morphological and physiological characteristics of seedlings. Accurate assessment of seedling quality includes measures of morphological and physiological characteristics of seedlings, and the seedlings' response to a given planting environment (Ritchie 1984). This is a concept used by forest nurseries to grow seedlings with target morphological and physiological characteristics that are related to field performance (Rose et al. 1990).

Biomass partitioning relationships like R:S have been used to evaluate seedling quality (Thompson 1985). Numerous investigations have found that seedling survival often increases with initial R:S (Hermann 1964; Koon and O'Dell 1977; Lopushinsky and Beebe 1976; Tanaka et al. 1976). Nursery cultural practices can be used to manipulate R:S and thus morphological attributes of seedling quality. For example, bareroot nursery stock R:S can be manipulated by nursery techniques like undercutting and wrenching (Koon and O'Dell 1977; Rook 1971; Tanaka et al. 1976). Container nursery stock R:S can be manipulated through container size (Endean and Carlson 1975), container density (Timmis and Tanaka 1976), and growing media (Lackey and Alm 1982). Another morphological seedling attribute that has been shown to predict conifer seedling quality is the sturdiness quotient (height-to-diameter ratio [H:D]) (Menzies et al. 1985; Roller 1976). H:D indicates the stocky or spindly nature of a seedling's shoot growth, and seedlings with a high H:D are generally more susceptible to damage following planting (Roller 1976). H:D is calculated by dividing the total height of a seedling (cm) by the diameter of the seedling (mm) (Dickson et al. 1960; Thompson 1985), although many studies utilize a unitless H:D (Haase 2007). R:S and H:D are important parameters in indices of seedling quality which have been used to accurately predict conifer seedling quality (Dickson et al. 1960; Iyer and Wilde 1982; Ritchie 1984)

Physiological metrics of seedling quality include root growth potential (RGP), cold hardiness, and leaf gas exchange, among others. RGP evaluates a seedling's ability to grow roots in a favorable environment, such as a mist chamber or potted in a greenhouse. While RGP does not account for the range of environmental conditions a seedling is exposed to when planted, RGP testing provides results that help nurseries and landowners rapidly screen seedlots that may exhibit poor field performance. Additionally, seedlings that are able to quickly grow new roots when planted in a new environment will overcome the stress of transplanting more quickly than a seedling with reduced root growth, as it is more quickly "coupled" with the new environment (Grossnickle 2005). Conceptually, this makes sense and in practice RGP has served as an indicator of seedling vigor (L'Hirondelle et al. 2007; Ritchie and Dunlap 1980).

The influence of seedling allometry, RGP, and site characteristics on seedling survival have been explored, often by isolating a single factor. However, little research has been conducted to quantify the relative contribution of these factors on the field performance of planted conifer seedlings. Using western larch, interior Douglas-fir, and grand fir as study species, the specific objectives of this study were to: (1) develop species-specific seedling allometric models; (2) investigate the temporal effects of soil moisture, soil temperature, and RGP on morphology and biomass partitioning; and (3) investigate how the early seedling survival on different sites was influenced by biomass partitioning, environmental conditions, and RGP.

Methods

Planting Stock

Various Douglas-fir, grand fir, and western larch seedlots were tested for RGP in aeroponic mist chambers at the University of Idaho Center for Forest Nursery and Seedling Research Lab in winter 2015 and spring 2016. Seedlots were grown at various nurseries across northwestern U.S. and western Canada. All seedlings were grown in Beaver Plastics 8L Styroblock containers (Stuewe & Sons Inc., Tangent, OR).

Seedlings were stored in a freezer with temperature fluctuating between -2.22°C and 0°C until the time of root growth potential (RGP) testing. Initial measurements of shoot height, root collar diameter (RCD) and root volume were taken after the soil was washed from the roots. Shoot height was measured with a ruler, RCD measured with calipers, and root volume with graduated cylinder and scale using Archimedes' Principle.

Root Growth Potential

RGP testing was conducted in aeroponic chambers using a pulsating garden sprinkler attached to a 1/6 horsepower utility submersible pump that sprayed the roots with water to stimulate growth over a 28-day period. The air temperature and water temperature in the aeroponic chambers were kept constant at 20°C. The sprinkler was run 1 minute, and rested 4 minutes for the duration of the testing. Lighting over the chamber was provided by LED lights as well as natural light from windows in the lab. LED lighting was chosen as it has been shown to promote greater growth, gas exchange, and chlorophyll production of conifer seedlings (Apostol et al. 2015). Each LED light fixture was comprised of 8 modules, with dimensions of each module 4 cm by 123 cm and 87 bulbs, emitting 85:10:5 red:blue:green (DR/W LED 120-110V, Philips). Lighting schedule was alternated 10 hours on and 14 hours off for the duration of the test. At the end of each test, the number of new white root tips longer than 1 cm were counted.

Site Description

The study was installed on Potlatch Forest Holdings, Inc. land approximately 4.72 km east of Bovill, Idaho (elev. ~975 m). The site was a western redcedar habitat type (Cooper et al. 1991). 2010 to 2016 data from a nearby ground-based NOAA weather station in Elk River, ID (elev. ~266 m) was used to determine that mean annual precipitation was

58.8 cm, mean annual snow accumulation was 88.6 cm, while the mean annual maximum temperature was 36.5 °C, and mean annual minimum temperature was -18.2 °C (NOAA National Climatic Data Center 2018). Prior to harvest, the site was occupied by a naturally-regenerated even-aged second-growth stand composed of 30% Douglas-fir, 15% grand fir, 15% western larch, and 15% other species. The stand was clearcut harvested in 2013with no additional management until seedlings were planted.

Data from the Natural Resources Conservation Service (NRCS) Web Soil Survey (2016) were used to determine the soil series present on the study site. Present series consist of Brequito-Mushell Complex, Dworshak-Brequito Complex, and Hubub-Lostpete Complex. Soils are all characterized as well-drained soils of the order andisol or alfisol. Present soil series have upper horizons composed of volcanic ash over loess, alluvium, or colluvium Secondary soil horizon parent materials consist of granite or gneiss, except in the Hubub-Lostpete Complex in which secondary horizons are derived from quartzite and mica schist parent materials. Plant available water content of these soil series ranges from 28.79 to 35.37 cm (NRCS Web Soil Survey 2016).

Experimental Design

The experiment was designed to evaluate differences in the aboveground morphology, biomass partitioning, and survival of three conifer seedling species (western larch, Douglas-fir, and grand fir), and three sites with hypothesized differences in moisture and temperature regimes: (1) north aspect, (2) north aspect with supplemental watering, and (3) south aspect.

Seedlings of each species were planted in a completely randomized block, split-plot design with three blocks. Seedlots were the split-plot factor, while RGP rating was the whole-plot factor. Each species x RGP rating combination was replicated three times at each site. Species x RGP combinations were randomly assigned to one row within a block (3 blocks/site); blocks were based on slope position (upper, middle, lower slope).

For each row 30 seedlings of a single seedlot were planted along the contour of the slope, spaced 1.22 m x 1.22 m; in the same row, another 30 seedlings of the paired seedlot were planted along the same contour and with the same spacing, creating a split-plot factor of seedlot-within-block. Beginning with the first seedling in a row, every other seedling was tagged for observations of growth and survival (16 seedlings/seedlot/row). Untagged seedlings were reserved for destructive sampling.

Site Treatments

One week before planting, a broadcast application of glyphosate herbicide was applied to all three sites to control existing vegetation. The treatment applied glyphosate at a rate of 2.8 kg active ingredient (a.i.) per hectare mixed with 2% (v/v) nonionic surfactant in water. The application was applied with a CO_2 powered backpack sprayer (Bellspray Inc. Model 4F) with a 2.74 m overhead extended boom equipped with a single KLC-9 flood tip nozzle. The sprayer was calibrated to apply 140.33 hectare ha^{-1} of mix to the sites. Standing woody vegetation was hand-cut and moved off-site. To prevent nearby grazing activities from interfering with the study each installation was enclosed with a 1.83-m high fence.

On July 12, 2016 a direct application of glyphosate (5% concentration mixed with water and 2% nonionic surfactant) was applied to the south-aspect site using Birchmeier Iris® backpack sprayers with an adjustable cone nozzle. The nozzle was adjusted to produce a medium-sized droplet size to minimize spray drift and crop-tree damage. Seedlings were protected from herbicide contact by placing buckets over the top of the seedling during application. The treatment was deemed necessary because the site became heavily occupied by bracken fern (*Pteridium aquilinum*). Some seedlings were incidentally damaged by herbicide; surveys of herbicide damage were made in August 2016 and any seedlings with visible herbicide damage were removed from the analysis.

On September 6, 2016, the north-aspect site with the supplemental watering treatment received 3,406 l of supplemental water. Watering was performed by hand with a hose. Water was applied to the site by separating each of the three blocks into thirds, creating 9 separate watering areas, each approximately 0.28 ha. in size. The person watering chose a central location within each watering area and used the hose to evenly spray the area. After 15 minutes the individual moved to the next location. Each watering area was visited twice.

Data Collection and Analysis

Soil moisture and temperature were measured within each block across the experiment for two full growing seasons using Em50 data loggers and 5TM soil moisture and temperature sensors (Decagon Devices, Pullman WA). Volumetric water content

(VWC) (m^3/m^3) and temperature (°C) were measured at 5-minute intervals with sensors at depths of 15 cm and 50 cm below the soil surface. To account for the variability of logging debris on the site from prior harvesting activity, sensors were placed in areas within each block where the soil surface was covered in coarse woody debris and areas that were free of coarse woody debris.

Daily average soil moisture and temperature was calculated for each soil sensor. Average soil moisture and temperature were calculated from the time of planting (May 5, 2016) to the time of first growth measurement (June 6-22, 2016), time between first growth measurement and second growth measurement (August 2-23, 2016), and time between the second growth measurement and final growth measurement (October 4-30, 2016). Average soil temperature and moisture was calculated for August 2016 as it is the hottest month of the season; average soil temperature and moisture was also calculated dry months of the 2016 growing season (July 1-September 30) and the 2017 growing season (July 1-August 6). For each depth, soil moisture and temperature under coarse woody debris and under bare ground were averaged. Due to high Pearson's correlation between the soil moisture (ρ=0.51) and temperature (ρ=0.76) at 15 cm and 50 cm depths, only 50 cm measurements was used in analysis. Despite the supplemental watering treatment at one of the north-aspect sites, this site consistently had the lowest average soil moisture content across the growing season (Table 2.1).

Observations of height measured from the ground line to the tip of the terminal leader and diameter measured at ground line of field planted seedlings were made in June (June 6-22), August (Aug. 2–23), and October (Oct. 4–30) of 2016. Observations of individual seedling survival were collected in May (May 14-16) and August (Aug. 14-16) of 2017.

A single seedling of each seedlot reserved for destructive sampling was selected at random from each block at each site and excavated in June (15th-24th) and September (3rd-5th) 2016. Height and diameter of the sampled seedlings were collected prior to harvest followed by carefully excavating the seedling from a 0.13-m^3 hole (0.30 m radius, depth of 0.46 m). Soil was carefully removed from the seedling's root mass by hand, then the seedling was separated into aboveground and belowground components, placed in a drying oven, and dried to constant mass (65°C for 72 hrs.). The aboveground and below ground biomass were weighed; aboveground biomass was separated into woody and foliar components and weighed separately.

Statistical Analyses

Species-specific non-linear allometric models were fit to biomass measurements of destructively sampled seedlings using the power function. Due to the lack of bias, non-linear power models are preferable to other allometric models (Payandeh 1981). Allometric models were developed using the nlme package (Pinheiro et al. 2016) in R, using seedlot-within-site as random-effects. Component root, woody, and foliar biomass power parameters were estimated with SAS using PROC MODEL; model parameters were calculated using iterative seemingly unrelated regression analysis (ITSUR) forcing additivity of component parameters to the sum of the total biomass. ITSUR accounts for potential inconsistencies between the sum of predicted biomass components and the whole tree biomass (Bi et al. 2004). Parameters were estimated as functions of seedling height and diameter including an intercept. The best fitted model was selected by minimizing the Akaike Information Criterion (AIC) and root mean square error (RMSE).

Biomass models were used to predict component biomass and R:S of non-destructively sampled measured throughout the first growing season using measured height and diameter. Individual seedling changes in morphology and differences in component biomass partitioning across the first growing season were used as response variables in species-specific linear, mixed-effects, repeated measures regression models to examine the influence of RGP, soil temperature, and soil moisture. Seedlot was the random effect. Residuals approximated a normal distribution with a mean variance of zero. Analysis was performed using R package “nlme” (Pinheiro et al. 2014). Full models with a weighted variance structure using a power function of seedling diameter were tested against full models with an unweighted variance structure. If the weighted variance structure significantly improved the fit of the model, then that model was used; otherwise the simpler model was used for analysis.

The probability of an individual seedling surviving the first winter after planting was examined by testing the influence of RGP, initial R:S, and August 2016 soil moisture and soil temperature on survival in May 2017 using mixed-effects logistic regression models with the binomial distribution and seedlot as the random effect. Similar survival models using the probability of an individual seedling surviving to the end of the second growing season after planting were used to examine the influence of RGP, average 2016 and 2017 growing season soil temperature and soil moisture, and seedling R:S at the end of the first growing season. Significance was assessed at the $\alpha=0.05$ level. All analyses were performed using R software (Version 3.3.2) (Team 2017). Logistic regression was performed using R package “lme4” (Bates 2010).

Results

Allometric Models

Woody stem biomass, foliar biomass, and root biomass were all positively correlated with stem diameter for each species, while height was only correlated with western larch root and woody stem biomass (Table 2.3). Parameter estimates for a given biomass component differed substantially among species. For example, for a 3 mm diameter seedling, the models predicted foliage biomass of 1.1 g, 2.2 g, and 2.6 g for western larch, Douglas-fir, and grand fir, respectively. Including seedlot-within-site as a random effect improved the fit of all models and reduced model error except for the models of western larch foliar biomass and grand fir root biomass. In general, models were strongest for western larch explaining over 80% of the variance, while the poorest fitting models were Douglas-fir and grand fir foliar biomass.

Effects of Soil Temperature and Moisture, and Seedling Quality on Biomass

The influence of soil moisture on component (stem woody, foliar, and root) biomass accumulation showed trends that were generally consistent within species, but these trends were not consistent between species. Apart from western larch woody biomass, the main effect of soil moisture was not significantly correlated with biomass accumulation (Tables 2.4-2.6). However, the interaction of soil moisture and time was significantly correlated with biomass accumulation for all species, except for Douglas-fir foliage biomass. Douglas-fir and western larch generally displayed a negative correlation between biomass accumulation and the interaction of soil moisture and time, but this correlation was positive for grand fir (Figures 2.4 A-2.6 A).

There was a positive relationship between the main effect of soil temperature on each component biomass accumulation, regardless of species (Tables 2.4 – 2.6). The interaction of soil temperature and time was negatively related to grand fir woody biomass accumulation (Table 2.4), Douglas-fir foliar biomass accumulation (Table 2.5), and grand fir root biomass accumulation (Table 2.6). While significant, the effect of the interaction of soil temperature and time on Douglas-fir foliar biomass accumulation was slight (Figure 2.5 B).

The main effect of RGP was not significant for component biomass accumulation, regardless of species; however, the interaction of RGP and time had a significant, negative effect on each component biomass accumulation of Douglas-fir and western larch seedlings (Table 2.4-2.6) (Figures 2.1 C- 2.3 C).

Seedling sturdiness, measured by H:D, and R:S showed somewhat consistent trends within a species, but the species differed in their response. H:D and R:S of western larch were negatively correlated with soil temperature and time, while only H:D was positively correlated with soil moisture (Tables 2.7-2.8). This compares with Douglas-fir, where soil temperature was not correlated with H:D and only weakly correlated with R:S. Interestingly, Douglas-fir H:D showed a strong positive correlation with soil moisture. Grand fir H:D was not correlated to either the main effect of soil moisture or the interaction of soil moisture and time. However grand fir R:S exhibited a strong negative correlation with the main effect of soil moisture, and was also negatively correlated to temperature and the interaction of temperature and time. Figures 2.4 A and 2.5 A illustrate the species-specific H:D and R:S response to soil moisture across the first growing season; Figures 2.4 B and 2.5 B illustrate the same response to soil temperature.

There was a positive relationship between RGP and grand fir H:D, while the interaction of RGP and time had a negative effect on western larch H:D (Table 2.7). RGP alone had no effect on R:S of any species, while the interaction of RGP and time had a slight, but significant, positive effect on Douglas-fir R:S and a slight, but significant, negative effect on western larch R:S.

Overwinter and Second Year Survival

The odds of western larch and Douglas-fir seedlings surviving the first winter after planting was negatively related to soil temperature in August of the first season (Table 2.9). The odds of western larch seedlings further surviving to the end of the second growing season were negatively related to the average growing season soil temperature in the second year (Table 2.10). Soil moisture in August of the first growing season was not significantly related to overwinter survival of any species (Table 2.9). However the odds of a grand fir seedling surviving the second growing season was positively related to the average second growing season soil moisture content (Table 2.10).

Seedling morphology in the first year were somewhat related to overwinter and second season survival. The odds of Douglas-fir and grand fir seedlings surviving the first winter after planting was positively related to initial R:S (Table 2.9), with Douglas-fir more sensitive than grand fir (Figure 2.6). The odds of Douglas-fir and grand fir seedlings further surviving the 2017 growing season were positively related to seedling R:S at the end of the first growing season (Table 2.10). Compared to overwinter survival, grand fir seedlings with high R:S had greater odds of surviving the second growing season than Douglas-fir seedlings with high R:S (Figure 2.10).

RGP had no significant effect on the overwinter or second season survival of any species (Tables 2.9 - 2.10).

Discussion

Allometic Models

Allometric models using the power function adequately predicted seedling above- and belowground biomass for all three conifer species. The minimal difference in model fit between models that included site and seedlot as random effects and models without random effect indicate that foliage biomass of western larch seedlings were similar across the range of environments and seedlots throughout the first growing season. This may be explained in part by the deciduous foliar habit of western larch, where foliage is regenerated each year and is likely dependent on current conditions (Gower and Richards 1990). In contrast, the random effects of seedlot and site explained a large amount of the variation in foliage production of grand fir and Douglas-fir seedlings. Legacy nursery influences on foliage production are likely more evident with these evergreen species since the older foliage developed the previous year. In addition, bud length and number of needle primordia tend to vary by nursery growing regime (Khan et al. 1996), which can influence first year foliage biomass production in species with determinant growth habits.

Species Differences in Biomass Partitioning

Western larch and grand fir exhibited contrasting patterns of biomass partitioning throughout the first growing season, with R:S of western larch decreasing over time and grand fir increasing over time. Previous research demonstrates that species with indeterminate growth habit display different seasonal patterns of biomass partitioning than species with a determinate growth habit (Gower et al. 1995). Conifers with indeterminate shoot growth habit allocate carbon to new foliage and elsewhere within the plant throughout the growing season as long as conditions are suitable for growth (Gower et al. 1995). Comparatively, determinate species allocate most stored and newly assimilated carbon to shoot elongation early in the growing season coinciding with foliage flush (Gower et al. 1995). Assimilated carbon is then allocated towards stem and root development later in the season (Gower et al. 1995). Douglas-fir did not follow either pattern, even though the species is considered a determinant species, and instead R:S stayed constant throughout the first growing season. Douglas-fir seedlings can exhibit indeterminate growth during the first year after planting if bud set was delayed in the previous growing season (Graham and Hobbs 1994), which could be a cause of the observed response since foliage biomass also increased with time similar to western larch.

Soil Moisture Effects on Biomass Partitioning and Accumulation

Soil moisture had positive effects on H:D of Douglas-fir and western larch seedlings but no effect on grand fir. This is consistent with previous reports that height growth of western larch increases with progressively less moisture stress under high light conditions (Vance and Running 1985). Competing vegetation can also significantly deplete soil moisture (Roberts et al. 1995), corroborating the results found in Chapter 1 that competing vegetation negatively influenced height through two growing seasons. Greater H:D of Douglas-fir and western larch with adequate moisture is a strategy exhibited by seedlings in the establishment phase to outcompete neighboring vegetation for light resources (King 1990; Mäkelä 1986). Since water is not limiting, seedlings can continue to allocate growth towards height to gain a competitive advantage. Favorable moisture and the positive correlations with H:D could be a reason for the apparent indeterminant growth of western larch and Douglas-fir during the first year. In contrast, grand fir H:D did not respond to soil moisture, or the presence of competing vegetation (Chapter 1). This suggests the species has strong, yet conservative, control over aboveground growth under a wide range of growing conditions.

According to the OPT, R:S should decrease with increasing soil moisture, as favorable moisture requires less scaverngingof roots for limited moisture reserves and can instead allocate more resources to light capture (Gower et al. 1995; McCarthy and Enquist 2007). While this relationship was observed for Douglas-fir and grand fir seedlings, western larch exhibited the opposite relationship (positive effect of moisture × time interaction). Negative correlations between all biomass components and moisture were found for western larch, which contrasts results of Vance and Running (1985) who found a non-significant decrease in allocation to root biomass but also significantly lower allocation to shoot biomass for western larch seedlings with decreasing moisture. The reductions in seedling biomass with increasing moisture could be due to the species preference for moderate moisture conditions, and possibly a curvilinear peak in biomass, where biomass decreases with too high or too low moisture. This hypothesis is difficult to examine with the current study since plant moisture stress did not reach levels deemed stressful for western conifers. Regardless, the positive correlation between R:S and moisture suggests that as moisture was lower, allocation to shoot biomass decreased more rapidly than root biomass.

Even though early season soil moisture had a limited effect on early season biomass accumulation, the correlation became more pronounced as the season progressed. Douglas-fir and western larch aboveground biomass accumulation decreased with increasing soil moisture, which is counter-intuitive; however these species' affinity for height growth, while likely lending competitive advantage, can result in decreased aboveground biomass accumulation due to favoring height over diameter growth (Khan et al. 2000). Grand fir root biomass accumulation increased with soil moisture, which is inconsistent with OPT. Since grand fir exhibits a relatively short period of shoot growth (Owens 1984), it's likely that the species begins root growth earlier than the other study species and growth is greatest where soil moisture is high. This agrees with the results of this study and also may explain why grand fir is able to attain deeper rooting depths than the other species in this study (Nicoll et al. 2006).

Soil Temperature Effects on Biomass Partitioning and Accumulation

Soil temperature had a negative effect on seedling H:D across the growing season, with the greatest effect on western larch. Increasing temperature also had negative effects on both height and diameter growth, with a disproportionately greater effect on height growth (Chapter 1). This suggests that the decrease in H:D with temperature was more strongly influenced by sensitivity of height. Even though greater soil temperatures can accelerate biological processes, excessive temperatures can results from high amounts of solar radiation (Eash et al. 2015). Seedling stem damage occurs in the form of lesions when surface temperatures reach 52 °C (Helgerson 1989), which is common in clearcuts during summers in the northern Rockies (Hungerford 1990). Seedlings that are damaged or exposed to excessive temperatures would be expected to respond with reductions in growth. It is still unclear why temperature had a disproportionately more negative effect on height than diameter. Possibly, heat damage to the base of the seedling resulted in stem lesions which when healed result in a swelling at the base of the seedling where diameter measurements were taken.

R:S was slightly greater at higher temperatures for western larch with a more pronounced positive response for Douglas-fir. Douglas-fir root growth begin when soil temperatures exceed 5 °C, and increases rapidly between 10 °C and 20 °C (Lopushinsky and Max 1990). Average soil temperature ranged from an average growing season minimum of 11.1 °C to a maximum of 17.3 °C at a 15 cm depth, which is within the optimal range suggested by Lopushinsky and Max (1990). This may be why Douglas-fir and western larch root biomass increased with temperature. In contrast, grand fir exhibited a seasonal difference in root biomass response to temperature, where in June and August root biomass increased with temperature, while an opposite trend was observed in October. Grand fir also exhibited an opposite pattern to the other species of increasing root biomass with soil moisture in October, so it is possible that the decline with greater temperature was the result of greater root growth at microsites with greater moisture that would inherently have lower temperature.

Even though grand fir foliage biomass increased with greater temperatures regardless of month, woody biomass declined with temperature as well as root biomass. This resulted in a decline in R:S ratio for this species with temperature that was opposite of western larch and Douglas-fir. The minimal response of woody and root biomass to temperature compensated for the increases in foliage biomass to results in an overall decline in R:S. Much of this relationship could be attributed to the strong deterministic growth habit of the species, where height and lateral growth continued until terminal budset (Chapter 1), followed by greater allocation to aboveground woody biomass and root biomass allocation.

RGP Effects on Biomass Partitioning and Accumulation

Seedlots with higher RGP had lower above- and belowground biomass accumulation. While RGP has been linked to increased conifer seedling survival (L'Hirondelle et al. 2007; Ritchie 1985); it is generally accepted that RGP is indicative of a seedlings' ability to produce roots and effectively couple with a new planting environment (Grossnickle 2005). However, the mild drought conditions experienced in the first growing season, a site considered high productivity for tree growth, lack of observed drought-stress, and the energetic costs associated with root growth may explain the results. In times of drought, a well-developed root system will allow for greater absorptive area to acquire limited available soil moisture. However, root construction (production and maintenance) is energetically expensive, more so than shoot construction (Ryan et al. 1996).

Overwinter and Second Year Survival

Overwinter survival of Douglas-fir and grand fir seedlings was greater when the initial R:S was higher at the beginning of the first year. Seedlings that had higher R:S at the end of the first season also had greater survival during the second growing season. The ability of seedlings to grow more roots and withstand mid-season drought (Arnott 1975; Hobbs 1992) likely influenced these positive relationships. Seedlings with greater root biomass and a higher R:S typically uptake more water from the soil (Burdett 1990), which can help balance water loss through transpiration. Therefore, seedlings that favor root growth over shoot growth may invest more resources in surviving potentially stressful future environmental conditions and are better adapted to survive summer droughts.

Excessive heat can also damage seedlings and increase mortality (Haig 1936; Helgerson 1989; Shearer 1967). Western larch survival was negative correlated with increasing temperature, which confirms previous reports that high temperatures can be the primary cause of western larch seedling mortality in this region (Haig 1936; Shearer 1967) Even though Douglas-fir is considered more heath tolerant (Baker 1929; Haig et al. 1941), overwinter survival also decreased with greater first year soil temperature, possibly due to seedling sensitivities to environmental extremes during the first growing season. Comparatively, second year Douglas-fir survival was not related to soil temperature. It is possible that Douglas-fir acquired a heat-tolerance during the second season from exposure at the planting site. Research has shown that Douglas-fir seedlings produce heat stress proteins (HSP's) in response to sub-lethal high temperatures (Kaukinen et al. 1996). Perhaps the production of HSP's by Douglas-fir seedlings allow for an acquired tolerance to high temperatures in future growing seasons.

Tables

Table 2.1 Average daily soil moisture and temperature at each planting site at two depths beneath the soil surface.

		Soil Temperature (°C)		Soil Moisture (m^3/m^3)	
Site	Time	15 cm	50 cm	15 cm	50 cm
north-aspect	0	12.10 (11.81-12.47)	10.10 (10.02-10.21)	0.31 (0.27-0.35)	0.22 (0.17-0.31)
	1	13.69 (13.63-13.74)	11.72 (11.43-12.02)	0.31 (0.26-0.37)	0.23 (0.17-0.33)
	2	11.41 (11.10-11.57)	11.27 (11.24-11.32)	0.26 (0.22-0.34)	0.21 (0.15-0.30)
	3	13.21 (12.96-13.37)	12.01 (11.81-12.25)	0.27 (0.24-0.35)	0.21 (0.16-0.31)
	4	15.12 (14.93-15.21)	12.09 (12.01-12.25)	0.18 (0.12-0.21)	0.20 (0.16-0.22)
north-aspect (w/ watering)	0	12.89 (12.06-13.44)	10.34 (9.84-10.74)	0.29 (0.27-0.31)	0.20 (0.14-0.30)
	1	14.51 (13.59-15.97)	12.23 (11.79-12.62)	0.27 (0.22-0.30)	0.19 (0.13-0.28)
	2	13.01 (11.75-14.71)	12.52 (11.64-13.60)	0.20 (0.13-0.24)	0.17 (0.12-0.23)
	3	14.15 (13.37-15.96)	12.85 (12.26-13.63)	0.22 (0.15-0.26)	0.18 (0.12-0.24)
	4	15.74 (15.02-16.70)	13.17 (12.63-13.92)	0.12 (0.12-0.12)	0.18 (0.15-0.22)
south-aspect	0	12.95 (12.31-13.53)	11.74 (11.29-12.03)	0.32 (0.28-0.31)	0.24 (0.17-0.29)
	1	16.52 (15.94-17.33)	14.77 (14.66-15.14)	0.29 (0.24-0.37)	0.21 (0.16-0.24)
	2	13.44 (12.96-14.06)	13.56 (13.23-14.01)	0.28 (0.24-0.36)	0.22 (0.16-0.26)
	3	15.92 (15.53-16.62)	14.85 (14.63-15.27)	0.27 (0.22-0.36)	0.20 (0.16-0.23)
	4	17.86 (16.89-18.71)	15.22 (14.43-16.15)	0.14 (0.10-0.23)	0.19 (0.16-0.22)

* Time 0 indicates May to June 2016; Time 1 indicates June to August 2016; Time 2 indicates August to October 2016; Time 3 indicates 2016 growing season (July-Sept.); Time 4 indicates 2017 growing season (July-August). Range in parantheses.

Table 2.2 Average initial seedling size and R:S and average August 2016 pre-dawn water potential for each study species at each planting site.

Species	Site	Initial Height (cm)	Initial Diameter (mm)	Initial R:S (g/g)	August 2016 PMS (Mpa)
Douglas-fir	North-aspect	34.64	4.10	0.34	-0.39
	North-aspect (w/ watering)	31.86	4.29	0.35	-0.51
	South-aspect	35.97	4.25	0.35	-0.47
western larch	North-aspect	37.96	3.88	0.31	-0.41
	North-aspect (w/ watering)	36.68	4.05	0.31	-0.49
	South-aspect	37.69	4.19	0.30	-0.48
grand fir	North-aspect	28.89	4.23	0.39	-0.40
	North-aspect (w/ watering)	27.42	4.52	0.40	-0.51
	South-aspect	29.68	4.33	0.36	-0.53

Table 2.3 Power coefficients for predicting biomass components (BC) from diameter (*D*, mm) and height (*H*, cm) for individual species.

BC (g)	coefficients			R^2 fixed	R^2 random	RMSE fixed	RMSE random
	a	b	c				
WL_{RB}	0.007 (0.003)	1.293 (0.146)	0.900 (0.154)	0.84	0.88	0.502	0.432
WL_{FB}	0.114 (0.018)	1.841 (0.076)		0.81	0.81	0.822	0.822
WL_{WB}	0.004 (0.002)	1.443 (0.097)	1.155 (0.119)	0.92	0.94	0.876	0.785
DF_{RB}	0.272 (0.054)	1.328 (0.112)		0.60	0.65	0.608	0.585
DF_{FB}	0.932 (0.186)	0.797 (0.118)		0.32	0.58	1.007	0.795
DF_{WB}	0.159 (0.032)	1.816 (0.110)		0.73	0.75	0.817	0.788
GF_{RB}	0.215 (0.075)	1.655 (0.214)		0.49	0.49	0.762	0.762
GF_{FB}	0.818 (0.212)	1.049 (0.165)		0.36	0.53	0.931	0.799
GF_{WB}	0.168 (0.046)	1.847 (0.167)		0.65	0.70	0.630	0.580

* Model form is $y = a * D^{b} * H^{c}$ or $y = a * D^{b}$; Species are indicated with two-letter code; western larch (WL), Douglas-fir (DF), grand fir (GF). Biomass components are indicated in subscripts; root biomass (RB), foliar biomass (FB), woody biomass (WB). Standard errors in parentheses.

Table 2.4 First growing season H:D (cm/mm) parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	11.382	0.386	7.849	0.255	-	-
RGP	-	-	-	-	0.264	0.020
Temp.	-0.220	0.024	-	-	0.043	0.022
VWC	2.468	0.485	1.575	0.429	-	-
Time	-0.829	0.124	-0.488	0.222	-	-
RGP x Time	-0.014	0.006	-	-	-	-
Temp. x Time	-	-	-0.047	0.018	-0.041	0.003
VWC x Time	-	-	-	-	-	-

Table 2.5 First growing season R:S (g/g) parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	0.338	0.009	0.320	0.008	0.465	0.009
RGP	-	-	-	-	-	-
Temp	-0.003	0.001	0.003	0.000	-0.005	0.001
VWC	-	-	-	-	-0.073	0.009
Time	-0.037	0.007	-	-	0.082	0.007
RGP x Time	> -0.001	> -0.001	< 0.001	< 0.001	-	-
Temp x Time	0.002	0.001	-	-	-0.005	0.001
VWC x Time	0.024	0.006	-0.008	0.004	-	-

Table 2.6 First growing season woody biomass (g) parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	-	-	0.848	0.195	-	-
RGP	-	-	-	-	-	-
Temp.	0.121	0.014	0.099	0.016	0.220	0.008
VWC	1.003	0.437	-	-	-	-
Time	3.193	0.206	1.768	0.156	2.053	0.249
RGP x Time	-0.041	0.006	-0.024	0.006	-	-
Temp. x Time	-	-	-	-	-0.132	0.019
VWC x Time	-4.357	0.699	-1.660	0.322	0.863	0.355

Table 2.7 First growing season foliar biomass (g) parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	-	-	2.077	0.219	0.878	0.181
RGP	-	-	-	-	-	-
Temp.	0.105	0.008	0.073	0.014	0.265	0.015
VWC	-	-	-	-	-	-
Time	1.956	0.106	1.115	0.178	-	-
RGP x Time	-0.025	0.004	-0.012	0.004	-	-
Temp. x Time	-	-	-0.027	0.013	-	-
VWC x Time	-2.363	0.338	-	-	1.897	0.119

Table 2.8 First growing season root biomass (g) parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	-	-	0.867	0.121	0.887	0.280
RGP	-	-	-	-	-	-
Temp.	0.078	0.005	0.073	0.010	0.138	0.025
VWC	-	-	-	-	-	-
Time	1.265	0.081	0.963	0.093	1.659	0.280
RGP x Time	-0.017	0.003	-0.011	0.004	-	-
Temp. x Time	-	-	-	-	-0.100	0.023
VWC x Time	-1.363	0.259	-0.776	0.189	0.671	0.288

Table 2.9 Overwinter survival parameter estimates for western larch, Douglas-fir, and grand fir seedlings.

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	15.863	1.906	-	-	-	-
Temp.	-0.835	0.113	-0.307	0.130	-	-
VWC	-	-	-	-	-	-
RGP	-	-	-	-	-	-
Init. R:S	-	-	24.540	6.154	6.787	0.437

Table 2.10 Second growing season survival parameter estimates for western larch, Douglas-fir, and grand fir seedlings

	western larch		Douglas-fir		grand fir	
Parameter	Value	Std.Error	Value	Std.Error	Value	Std.Error
(Intercept)	6.9936	2.0206	-	-	-7.759	2.472
2016 VWC	-	-	-	-	-	-
2017 VWC	-	-	-	-	10.144	5.047
2016 Temp.	-	-	-	-	-	-
2017 Temp.	-0.2562	0.1229	-	-	-	-
RGP	-	-	-	-	-	-
R:S	-	-	7.9944	0.4379	19.682	5.455

Figures

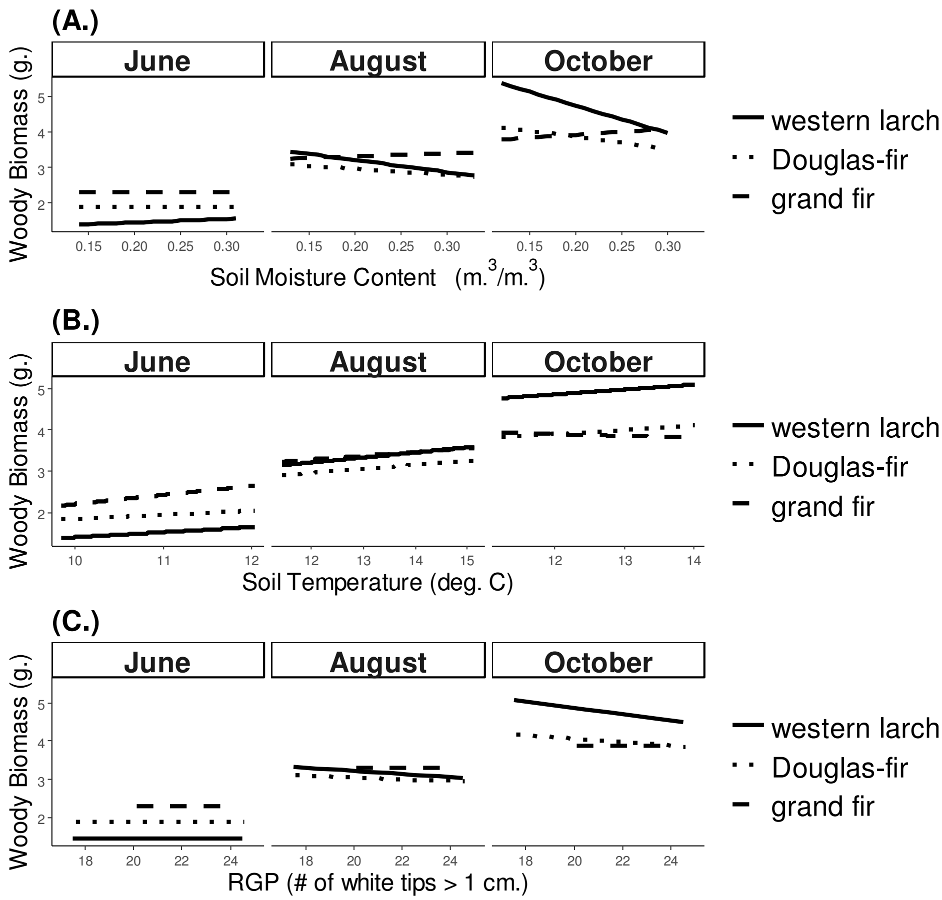

Figure 2.1 Influence of soil environment and RGP on woody biomass accumulation of western larch, Douglas-fir, and grand fir seedlings across the first growing season.

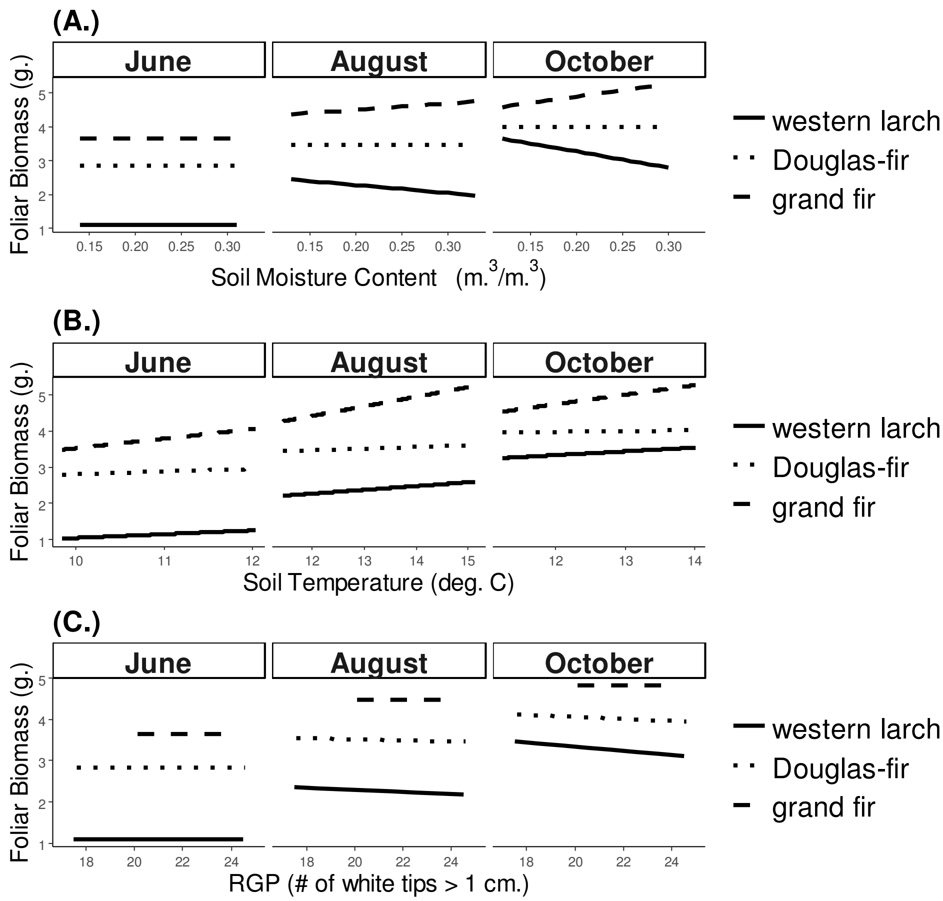

Figure 2.2 Influence of soil environment and RGP on foliar biomass accumulation of western larch, Douglas-fir, and grand fir seedlings across the first growing season.

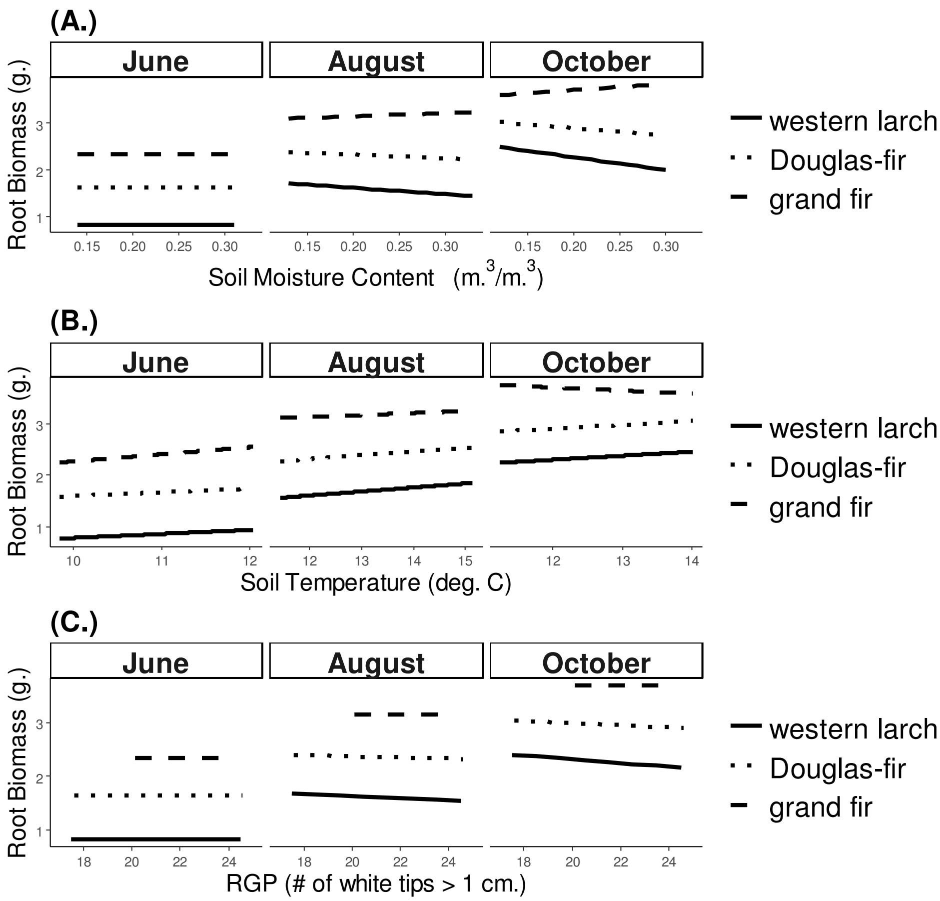

Figure 2.3 Influence of soil environment and RGP on root biomass accumulation of western larch, Douglas-fir, and grand fir seedlings across the first growing season.

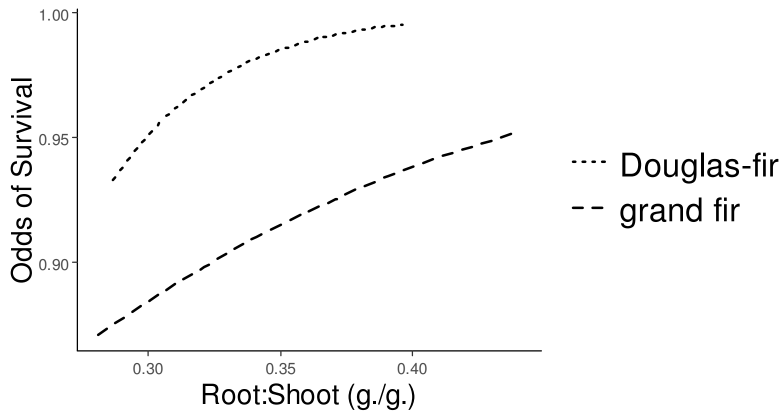

Figure 2.6 Influence of initial R:S of Douglas-fir and grand fir seedlings on the odds of surviving overwinter.

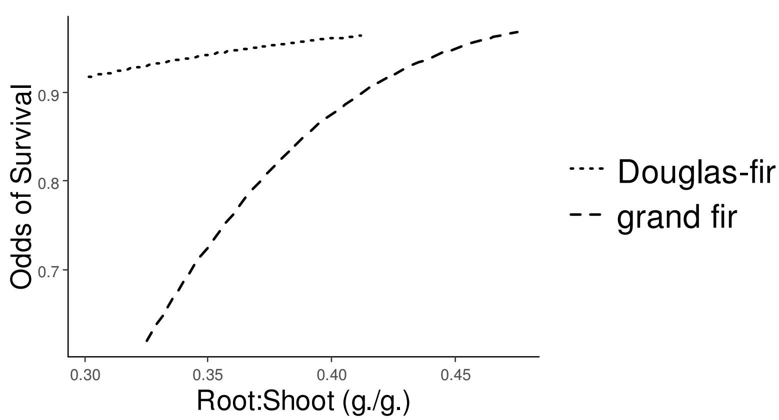

Figure 2.7 Influence of R:S of Douglas-fir and grand fir seedlings at the end of the first growing season on the odds of surviving the second growing season.

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Epilogue

Across the first two growing seasons there were significant effects of root growth potential (RGP) and soil environment on the field performance (growth and survival) and morphological development of planted western larch, Douglas-fir, and grand fir containerized seedlings planted on sites typical of the Inland Northwest (INW). Across the duration of this study aspects of the seedling planting environment was the primary driver of seedling field performance, and morphological aspects of seedlings rather than physiological aspects seem to be better predictors of seedling field performance. High soil temperature was the primary determining factor of seedling field performance, having significant negative effects on seedling field performance and seedling morphological development. The root-to-shoot ratio (R:S) of seedlings at the time of planting and at the end of the first growing season were indicative of increased odds of a seedling survival. Seedling physiological characteristics that are generally accepted to increase field performance like RGP and soil environmental characteristics known to have positive influence on seedling field performance had variable and irregular effects on seedling field performance which may be due to favorable growing conditions experienced during the study.

In this study soil temperature was the primary driver of seedling field performance and had significant influence on seedling morphological development across the first growing season. At the end of the second growing season western larch and Douglas-fir seedlings growing in areas with high soil temperatures exhibited significantly decreased height and diameter growth; Douglas-fir and grand fir planted in areas with high soil temperature also exhibited significantly decreased odds of survival at the end of the second growing season. Western larch and Douglas-fir seedlings' odds of surviving the first growing season were also negatively influenced by high soil temperatures. High soil temperatures significantly influenced seedling morphological aspects like R:S and height-to-diameter ratio (H:D). In a region like the INW where the growing season is characterized by high temperatures these results are compelling since global temperatures are expected to increase due to global warming.

Seedling morphology was the best plant characteristic that indicated seedling field performance, but seedling morphology and biomass accumulation was significantly influenced by soil temperature. Douglas-fir and grand fir seedlings with high initial R:S had greater odds of surviving the second growing season. Regardless of species, seedling biomass accumulation increased with soil temperature, but soil temperature had a negative influence on seedling H:D. There were variable effects of soil temperature on R:S; interestingly, soil temperature increased western larch and Douglas-fir seedlings' R:S increased with soil temperature, but the effect was negative for grand fir. Empirically, this was the most significant cause of each species' seedling two-year field performance, indicating a complex and species-specific relationship between the growth rate and biomass partitioning patterns of seedlings and their environmental stress-tolerance.

The observed relationships in this study between the effects of soil moisture and RGP on the early field performance and morphological development of seedlings were unexpected and sometimes counter-intuitive. There was little influence of soil moisture on the field performance of seedlings. This is likely due to the mild and unseasonal favorable growing season drought conditions experienced during the study. Likewise, there was no observed influence of RGP on the survival of planted seedlings, however there was a trend where seedlings of each study species with high RGP exhibited decreased above and belowground biomass accumulation. The relationship between relative growth rate and stress-tolerance have been previously explored (see Chapter 2); however, the relationship between RGP and relative growth rate are less understood. It may be that RGP is indicative of seedlots with greater stress-tolerance, specifically drought-tolerance, but these effects are only evident during periods of high stress.

The purpose of this study was to add to the collective knowledge-base of forest regeneration techniques in the INW, explore specific challenges to forest regeneration in the region, and develop a mechanistic understanding of these challenges. The results of this study indicate that environmental characteristics of a given planting site are significant drivers of plantation success or failure in the region; however, there is further evidence of the importance of nursery culture on seedling success and that morphological and physiological attributes of seedlings that can be measured prior to the planting of a seedling may be used to evaluate the quality of seedlings. Further research into mechanisms of heat-tolerance, such as heat-stress proteins (HSPs) and the relationship between RGP, growth rate, and stress-tolerance would be beneficial for forest regeneration programs in the INW and globally in other regions with harsh growing season environments.