Impact of Gap Size on Environmental Conditions, Survival, and Early Growth of 5 Pacific Northwest Species

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Abstract

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The formation of forest gaps and their resulting size and shape is highly variable across forest types and can produce a wide range of patterns in seedling establishment. The impact of gap size on microclimate and seedling growth and survival after planting, specifically in mixed-species stands is poorly studied. This study examines the influence of gap size on the light environment, soil moisture distribution, and understory vegetation dynamics and in turn, how these environmental characteristics effect seedling survival, health, and growth of 5 Pacific Northwest native tree species with varying shade and drought tolerances. More than 5000 seedlings were planted in groups of 5 individuals, both monoculture and mixed-species pentads, across 16 clear-cut plots of 4 sizes (0.05, 0.1, 0.25, and 0.5 ha). Larger gaps were found to have higher light and lower vegetation cover, while gap size had no influence on soil moisture. Initial mortality of conifer species was largely determined by high soil moisture in dense, clay soils, specifically in the most downslope row of gaps. Douglas-fir (26.8%) and western hemlock

(27.9%) mortality was significantly higher than western redcedar (5.0%), red alder (6.9%), and grand fir (8.1%) mortality. Chlorophyll fluorescence tracked over summer drought months suggested that as soils became drier, seedling health improved for all species. Environmental predictors of growth differed by species but were consistently influenced by abiotic factors soil moisture and light as well as biotic factors vegetation and ungulate browse. Increasing soil moisture and light led to positive growth for all species except western hemlock which was not significantly impacted. Increased height of surrounding understory vegetation led to reductions in basal area increment in western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Douglas-fir (*Pseudotsuga menziesii*), and grand fir (*Abies grandis*). Western hemlock and western redcedar saw increased growth as vegetation cover increased until full coverage where growth then decreased. Red alder (*Alnus rubra*), western redcedar, and western hemlock were significantly impacted by ungulate browse which occurred in half of western redcedar and red alder seedlings. Western redcedar saw an increase in basal area increment in response to browse while red alder and western hemlock saw reductions in height. No influence of surrounding seedling competition was found two years post planting. Overall, gap size impacts both abiotic and biotic environmental characteristics and these differing microclimates resulted in varying seedling growth and survival among species. Further research in this long-term experimental site is necessary to determine when mixed-species plantings begin interacting and how these interactions are influenced by gap size and shifts in microclimate.

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Introduction

Forest gaps, or gaps in the canopy, occur around the world in response to small-scale disturbances (McCarthy et al. 2011; Runkle et al. 1987). These disturbances include wind events, single-tree mortality, and small-scale insect or disease outbreaks (Kennedy, 2012). Gap formation influences stand development by increasing snag and woody debris inputs and facilitating establishment or release of understory seedlings and are often tied to accelerating complex, mature forest habitat (Franklin et al. 2002). Gap formation is also at the foundation of lower-intensity silviculture systems which aim to harvest timber while maintaining continuous forest cover, with gaps renewing regeneration (Schutz et al. 2016). Heavy thinning treatments in Douglas-fir stands (e.g., 75 trees/ha) are necessary for increased seedling regeneration and growth as they increase light availability (Maas-Hebner et al. 2005; Chan et al. 2006; Cole and Newton 2009; Lam et al. 2011). Though forest gaps have been studied extensively, their variability of size, shape, frequency, and location generally limit broad generalizations among forest types (Yamamoto et al. 2005).

Light is often a predominant factor in the success of regeneration in forest gaps. As the size of gaps increases, the light levels and gradient between shaded and sunlit areas increases, though the duration of light is generally transitory (Canham et al. 1990; Runkle et al. 1987). In tall Douglas-fir-hemlock forests, however, light penetration through single-tree gaps was not significantly different than light regimes in the understory of closed canopy forests due to the tall trees producing a high ratio of surrounding forest height to the diameter of the gap (Canham et al. 1990). The size of gaps plays a key role in the distribution of light to the gap floor, which diminishes through time as crowns expand. In fact, these forests require gaps >1.0 times the canopy height to allow light to the gap (Gray et al. 2002; Sprugel et al. 2009).

The expansion of gaps is often necessary to maintain high light conditions that favor shade-intolerant species (Vepakomma et al. 2012). After the initial formation of a gap, the boundaries of the gap begin to shift over time. Often smaller, weaker trees around the gap edge die and increase the size of the gap. Mortality of edge individuals has been found to be higher in larger gaps with the majority caused by wind damage (Carter et al. 2017). The expansion of gaps can lead to mixed age stands similar to an irregular shelterwood system and create more random patterns of light availability and soil moisture within the gap. This increase in gap size can also increase the amount of light available to seedlings that were formerly on the edge and lead to differential growth patterns. Areseneault (2011) found that a decade after gap formation, regeneration of both shade-tolerant and shade-intolerant species increased due to increasing light availability from canopy edge mortality over time.

The response of seedlings to forest gaps is highly variable and likely influenced by forest type and gap size and shape. The differences in the microclimate within gaps of varying shapes and sizes influence the regeneration of both seedlings and understory vegetation. Vegetation is predominantly more abundant in gaps and positions within gaps with the highest diffuse light (Diaci et al. 2008; Weber et al. 2014). A previous study in a *Quercus-Pinus* forest in Alabama found a positive relationship between the size of the gap and species diversity within it (Weber et al. 2014). In the southern Appalachians, however, the basal area of woody vegetation was highest in small gaps but in large gaps, there was the greatest increase in vegetation between sampling dates (Runkle et al. 1987). The impacts of vegetation cover associated with gaps are particularly important in the success of seedling regeneration. Increasing light availability is not only useful for tree species, but for the understory vegetation which often grows much more vigorously and can quickly outcompete seedlings (Maguire et al. 2009; Roberts et al. 2005; Wagner et al. 1989).

Though many studies have found that seedling density is higher within gaps than in the understory of surrounding canopy (Streit et al. 2009; Wright et al. 1998; Runkle et al. 1987), contrasting findings from *Picea abies* forests in the Swiss Alps suggest that regeneration is lower in larger gaps than under canopy (Arevalo et al. 2007). Arguments for increased density of seedlings in gaps generally follow the notion that the varying light environments within a gap can produce viable conditions for both shade-intolerant and shade-tolerant species (Adamic et al. 2017; Gray et al. 1996; Poznanovic et al. 2014). In the Dinaric forests of Slovenia, gaps lead to the preservation of mid-tolerant and shade-tolerant species and increased species richness (Adamic et al. 2017), while a study on the impact of gap position in interior cedar-hemlock forests found little evidence of gap partitioning (Wright et al. 1998). These contrasting findings indicate that the variability in gaps or forest types may lead to different ecological responses from the species present. Furthermore, the autecological responses of many important tree species to light and water availability are often not well understood or variable across soils (Drever and Lertzman 2001, Carter and Klinka 1992).

It has been suggested that mixed-species stands may be more resilient to natural disturbances due to an increase in structural heterogeneity and diversity in species' response to specific disturbances (Thompson et al. 2009). The new push for mixed-species stands stems from a desire to return forests to pre-harvest conditions including increased diversity, animal habitat, and resilience to disturbance, but even in Europe where research on mixed species silviculture systems has received considerable attention in the recent decades, there remains unanswered questions (Coll et al. 2017). In the Pacific Northwest where 13% of the United States softwood is harvested, the majority of production forests are planted as monocultures of Douglas-fir (*Pseudotsuga menziesii*) or western hemlock (*Tsuga heterophylla*), and the success and economic importance of plantation forestry in the region has likely slowed exploration in mixed species systems (WA Department of Commerce 2017; Talbert and Marshall 2005). The impacts of shifting monoculture production stands to mixed-species is still unclear as there have been few long-term studies on their productivity, most of which have focused on mixed species plantings incorporating nitrogen fixing species (e.g., *Alnus rubra* with western redcedar, Courtin and Harper 2018), or more commonly with Douglas-fir (Binkley 1983)).

Gap partitioning of canopy light in mixed-species stands, specifically for timber value, also shows promise. A study conducted by Amoroso et. al. (2006) on Douglas-fir and western hemlock found that the productivity of a mixed stand versus a monoculture stand was dependent on the initial stocking density where at highest densities, mixed-species stands had a comparable volume per hectare to the monocultures and at the lowest densities, monocultures had a much higher volume. Long-term studies on mixed-species stands and their initiation in forest gaps may increase the likelihood of landowners shifting from monoculture to mixed-species stands if both production and forest health are benefitted.

Douglas-fir – hemlock forests have been studied extensively for their role in timber production and the success of seedling regeneration and survival is vital to the continuation of this industry. The species involved in this study represent a range of shade and moisture tolerances and are likely to respond differently to the microclimates within gaps of varying sizes (Minore et al. 1979). For example, western redcedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) have been shown to reach maximal height and radial growth at low light levels, while Douglas-fir (*Pseudotsuga menziesii*) performed considerably higher at moderate to high light (Carter et al. 2003; Drever et al. 2001; Khan et al. 2000). In studies looking at combined impacts of light and soil moisture, red alder (*Alnus rubra*) allocates growth to aboveground biomass in full light and limited water in contrast to Douglas-fir which allocates growth to roots (Chan et al. 2003).

Though abiotic factors such as light and soil moisture are often utilized as predictors for the success of a species, the impact of vegetation and ungulate activity can vary across forest gaps and significantly alter the outcome of plantings (Wagner et al. 1991; Maas-Hebner et al. 2005; Maguire et al. 2009). In the Oregon Coast Range, models of Douglas-fir sapling performance designated competing vegetation and animal damage as significant predictors of survival (Wagner et al. 1991). Another study found that Douglas-fir foliar nitrogen was higher in plots where vegetation had been controlled compared to those that had not, indicating that surrounding vegetation impacts the growth of seedlings (Roberts et al. 2005).

Though each species represented in this study has been extensively studied in regards to one or two factors, little is known about the combination of both abiotic and biotic factors under the influence of forest gaps. With an increase in the desire to develop stands that replicate natural disturbances on the landscape, it is vital to understand the success of these dominant species in wide ranging microclimates and how knowledge of their specific needs may allow for more efficient planting in both natural and artificial forest gaps.

In this study, we focus on the impacts of forest gaps, including gap size, light, soil moisture, vegetation, and ungulate activity, on the survival and growth of seedlings of 5 tree species with varying tolerances, *Pseudotsuga menziesii, Tsuga heterophylla, Alnus rubra, Abies grandis*, and *Thuja plicata*, in a Douglas-fir – hemlock forest. These species are arranged in mixed species groups across 16 plots of 4 different gap sizes at the University of Washington

Center for Sustainable Forestry at Pack Forest stand Oliver's Folly. The gaps were arranged along 4 rows in recently harvested clear cut plots as a long-term study with plans to expand these gaps within the next 10 years as the basis for an expanding gap experiment. We address the following questions: (1) Does gap size impact light, soil moisture distribution, and understory vegetation dynamics? (2) Does gap size influence seedling survival and growth? (3) How does microclimate differentially impact species? We hypothesize that gap size will influence the microclimate within the gaps and that these environmental gradients will have differential impacts on seedling growth dependent on species. Each species will likely not have the same set of predictors for each growth and survival measure.

Methods

Field Methods

Study area

This experiment was conducted at the University of Washington Center for Sustainable Forestry at Pack Forest (46˚50’N; 122˚16’W), located approximately 80km south of Seattle (Washington, USA) (Figure 1). The study site is located in Oliver’s Folly (46˚50’33.00” N; 122˚16’53.84” W), a 95-year-old stand comprised of mostly naturally regenerated Douglas-fir (*Pseudotsuga menziesii*), western redcedar (*Thuja plicata*), western hemlock (*Tsuga heterophylla*), Port Orford cedar (*Chamaecyparis lawsoniana*), red alder (*Alnus rubra*), and black cottonwood (*Populus trichocarpa*) (Figure 2). Common understory species of the stand include salal (*Gaultheria shallon*), trailing blackberry (*Rubus laciniatus*), sword fern (*Polystichum munitum*), and red huckleberry (*Vaccinium parvifolium*). The elevation of the site ranges from 360-410m. Port Orford cedar was planted on site as early as 1930, although not well documented, and has since naturalized. The region is known for relatively cool temperatures and high rainfall, with an average temperature of 3.4˚C in January and 17.2˚C in August. Mean annual precipitation is 1470mm which predominantly falls in the winter (NOAA).

The study site has deep (> 80” to restriction), somewhat poorly drained silty clay loam of the Scamman soil series formed from mixed materials from glacial sources on terraces and adjacent foothills. The soils are typically wet November-March with 28 to 40cm (11 to 16 inches) to a perched water table, and are dry during 45-60 consecutive days in the summer months (Web Soil Survey, 2021). The study site is located on a north facing slope (Avg: 8.9%, Range: -33.9% – +3.1%), with poorer drainages on flatter areas.

Gap Creation and Planting

In total, 3.6 ha (8.92 acre), 16% of the of the 22.67 ha (56 acre) stand, was clear-cut harvested into 16 circular plots randomly assigned to 16 points arranged along 4 timber extraction skid roads. The 16 experimental plots were divided into 4 groups of different sizes: 0.05, 0.1, 0.25, and 0.5 ha (0.12, 0.25, 0.62, and 1.24 acres) (Figure 2). The diameter of each gap size is as follows: 0.05 ha = 25m, 0.1 ha = 35.5m, 0.25 ha = 56.5m, 0.5 ha = 80m. Harvest operations removed timber and the majority of slash; residual slash was piled on the edges of the plots. No vegetation control measures were taken at the time of harvesting or prior to planting. Harvest operation took place in September 2018 and the planting spacing was measured, flagged, and planted February-April 2019.

Seedlings of Douglas-fir, western redcedar, western hemlock, red alder, and grand fir were planted into groups of 5 seedling (hereafter referred to as pentads), with a central seedling of one species surrounded by four seedlings of another species or the same species. Each surrounding seedling was planted 1m from the center seedling while center seedlings of each pentad were 6m apart (Figure 3). All 25 possible combinations of the five species planted are equally represented across the study in a randomized design. The total number of seedlings planted was 5265, or 1053 of each species. For this study, measurements were taken on the center seedling of each pentad. Red alder, western redcedar, and grand fir were planted as 2-0's (2 years growing in a bed), western hemlocks were planted as plug+1's (one year in greenhouse plug and then transplanted to a bed for a year), while Douglas-fir were one year-old plugs. In March 2020, dead seedlings were replanted to allow long-term interactions of developing trees to be studied. The number of center seedlings replanted in this study were red alder – 4, western redcedar – 4, western hemlock – 24, Douglas-fir – 10, grand fir – 4.

Environmental Measures

Soil moisture was measured beneath the center seedling of each pentad using a Hydrosense II Soil Moisture Sensor in August 2019. Light was measured by taking a hemispherical image above each center seedling with a Nikon D90 camera with a circular fisheye lens and then analyzing the percentage of canopy openness using Gap Light Analyzer software (GLA, 2020). These images were taken in December 2020 when deciduous trees no longer had leaves. Presence or absence of browse was recorded for each center seedling in January 2019 and December 2020 and coded as 0 (no browse) and 1 (browsed). Ungulate browse damage was common, indicated by missing terminal buds and cut branches for conifer species and bud removal and snapped tops for red alder.

Seedling and Vegetation Measures

The pentad arrangement of seedlings is designed to assess competition among seedling species, and we focus additional measures on the center seedlings in the pentads to explore early competitive interactions. The survival and health of the center seedling of the pentad was visually assessed on a scale of 0 to 4, with 0 being dead and 4 being full health in August 2019 and September – November 2020. A score of 3 indicated mostly healthy leaves/needles with few chlorotic sections, a score of 2 indicated half healthy and half chlorotic leaves/needles, and a score of 1 indicated mostly chlorotic leaves/needles with few green and healthy. The surrounding species' survival rating of each seedling in the cardinal directions (N, S, E, and W) was measured in July 2019 and September – November 2020. Center seedling root collar diameter (to nearest 0.1mm) and height (to nearest cm) were measured for each surviving seedling in August 2019 and September – November 2020.

The dominant understory vegetation species, the species covering most ground cover, within each pentad was recorded in December 2020. Dominant vegetation was recorded by species then later analyzed by order to determine whether competitive interactions between vegetation and seedlings differs by vegetation order. Additionally, vegetation was measured as binary, above (1) or below (0) the height of the center seedling, to assess the possible impacts of understory species blocking light to the pentad. This measure is relative to the height of the center seedling. Percent coverage of vegetation within the pentad was also measured in increments as a proxy for vegetation competition (0%, 25%, 50%, 75%, and 100%).

Chlorophyll fluorescence, a measure of photosystem II efficiency, was measured 3 times between July and September 2020 on a subset of the seedlings (plots AA, AB, AC, AD, AE, and the top third of plot DA), representing a contrast between the driest and wettest environments (n= 222 seedlings). This metric was chosen to track potential influences of summer drought on seedling physiology. Dark-adapting clips were attached to each center seedling and allowed to sit for 30 minutes before an Opti-Sciences OS30p+ fluorometer was used to measure fluorescence. Fluorescence is measured as the variable fluorescence (*Fv*) divided by the maximum fluorescence (*Fm*), producing the *Fv/Fm* value utilized to compare seedlings (Maxwell, 2000).

Statistical Analyses

Survival

Survival of the center seedlings was calculated from September 2020 seedling health metrics by converting the 0 to 4 scale to a binary scale with 0 coding dead and 1-4 coded as (1) living seedlings. Seedlings that had been marked dead in September 2020 as well as seedlings that had been replanted in March 2020 (necessary for longer term experimental goals) were utilized to test the impacts of environmental conditions on survival. Replanted seedlings were marked as dead because they did not survive the initial year after planting and may not have experienced the same environmental pressures as seedlings that had survived since initial planting. Generalized linear models with binomial distributions for binary survival (0 and 1) and logit link functions were used to determine which environmental variables were significantly predicting survival for each species individually.

Chlorophyll fluorescence

An analysis of variance (ANOVA) was applied to the chlorophyll fluorescence data to test differences among species and the months in which the measurements were taken on an individual species basis. Seedlings that died during the 3-month course of the measurements were removed from the dataset in the months in which they were dead (n=47 removed). Data were reconfigured using the R package “reshape2” (Wickham 2007).

Multiple linear regressions

Multiple linear regressions using backwards stepwise model selection and Type 3 analyses of variance (ANOVA’s) were utilized to determine which environmental variables significantly predict response variables for each individual species. First, a linear regression model using all explanatory variables was run for each of the 5 seedling species. The full model was used to determine stronger and weaker predictor variables and backwards stepwise exclusion of the weaker (higher AIC scores) explanatory variables was used to identify variables which could be removed from the model. Backwards exclusion from the initial full and reduced linear regression models (Tables S4-18) was repeated until the AIC score was no longer lowered by the removal of further variables. Type 3 ANOVA was chosen as a conservative method of determining significance to concentrate on explicit variation in each explanatory variable. The final models were then run to determine the estimates and p-values for the remaining variables. The function "stepAIC" in the package "MASS" was utilized for this analysis (Venables et al. 2002). In significant categorical predictors, Tukey's Honest Significant Difference (Tukey HSD) tests were used to determine significance between groups.

For each center seedling, basal area increment (mm^2) (BAI) was calculated using root collar diameter (mm) measurements from 2019 and 2020 by subtracting the circular volume in 2019 from the circular volume in 2020. This provides volume change for the diameter of the seedling over a year of growth. BAI and change in height (ΔHt) were used as dependent variables. Explanatory variables used in these analyses include: canopy openness %, soil moisture %, vegetation cover and height above or below the seedling gap size, and meaningful interactions between these variables. Interactions include vegetation cover and height with soil moisture and light, light and gap size, and soil moisture and light.

Center seedlings that had been replanted in March 2020 were removed from the dataset because their growth measures and ages would not be comparable to those originally planted. Seedlings that did not survive through both rounds of measurement were also not included because of insufficient data to calculate the change in height or basal area increment. The final number of seedlings for each species included in the growth analysis were red alder – 181, western redcedar – 187, western hemlock – 136, grand fir – 170, and Douglas-fir – 149. Response variables (height and basal area increment) were transformed when necessary to meet assumptions of the analysis.

All analyses were completed using R version 3.5.1 (R Development Core Team, 2012). Other R packages utilized in these analyses include "dplyr", "fBasics", "car", and "vegan" (Wickham, 2021; Fox, 2019; Wuertz, 2020; Oksanen, 2019).

Results

Light and Soil Moisture between Gap Size and Row

The light environment differed significantly between all gap sizes except 0.05 ha to 0.1 ha ($p = 0.43$) and 0.1 ha to 0.5 ha ($p = 0.057$; Figure 4 & 7A). Average canopy openness in the smallest gap size (0.05 ha) was 39.63% and the largest gap size (0.50 ha) was 44.55%. Soil moisture between gap sizes was not significantly different ($p > 0.05$; Figure 5). However, soil moisture was statistically higher in row A and all other rows due to the bottom position and shallow slope of row A ($p < 0.05$; Figure 6). Average soil moisture in rows was A - 22.07%; B - 17.78%; C - 17.61%; and D - 17.1%.

Mortality

Mean final mortality rates for red alder was 6.9%, western redcedar 5.0%, western hemlock 27.9%, grand fir 8.1%, and Douglas-fir 26.8% (Table 1). Mortality rates were significantly higher in Douglas-fir and western hemlock compared to red alder, western redcedar, and grand fir ($p < 0.05$; Table 1). Mortality was highest in Douglas-fir at 26.8% and lowest in western redcedar at 5.0% (Table 1). Row A had the highest mortality rates for Douglas-fir, grand fir, and western hemlock while red alder saw highest morality in row D and western redcedar in row C (Table 1).

Seedling survival is negatively impacted by both vegetation height and soil moisture, though responses are not consistent across species. Generalized linear models indicated red alder survival was significantly reduced by the height of the surrounding vegetation ($p < 0.05$; Table 2). Survival of western redcedar, similar to red alder, was reduced by the height of the surrounding vegetation and soil moisture ($p < 0.05$; Table 2). Survival of western hemlock was also significantly lower on wetter sites and where the height of the surrounding vegetation was above the seedlings ($p < 0.05$; Table 2). Survival of grand fir was significantly lower on wetter sites ($p < 0.05$; Table 2). Survival of Douglas-fir was lowered by higher soil moisture, greater light, and the greater height of the surrounding vegetation ($p < 0.05$; Table 2; Figure 7C). For all species predicted by vegetation height, the estimates are negative which suggests that seedling survival is negatively impacted when the height of the vegetation is above the height of the seedling. The estimates for soil moisture are also negative, indicating that across the study site, soil moisture was too high for all conifer species' survival (Table 2). Notably, survival of red alder was not significantly predicted by soil moisture ($p > 0.05$).

Chlorophyll Fluorescence Over Drought Period

The *Fv/Fm* ratios of chlorophyll fluorescence show decreasing physiological stress as soils dried from July to September. Red alder had a significant increase in fluorescence ratio between July-August and July-September and western hemlock between July-September ($p < 0.05$; Figure 8). Red alder *Fv/Fm* ratio was significantly higher than grand fir in July ($p < 0.05$; Figure 8), indicating a much higher stress on photosystems of grand fir early in the summer. No other groups were significantly different.

Seedling Growth

A backwards exclusion stepwise model building process was used to describe significant predictors of seedling BAI and ΔHt. Complete stepwise analyses for each growth metric by species is listed in supplemental materials (Tables S9 – 18). The final multiple linear regression models from backwards stepwise model selection using Type III ANOVAs (Tables 3-7) are used to describe significant predictors of seedling BAI and ΔHt. Results were summarized by species as analysis was conducted on a species basis. Red alder seedlings showed more BAI and ΔHt growth than all 4 conifer species (RA>WC>GF>WH>DF); differences in growth are complicated by differences in relation to light, soil moisture, and vegetation competition which are described by the ANOVA models.

Red alder

Red alder BAI was increased by increasing soil moisture, increasing light, and gap size ($p < 0.05$). BAI increased as gap size increased, with the largest average BAI in the largest gap size (0.5ha) though Tukey HSD tests indicate no significant differences between groups. Red alder BAI was decreased by the interaction between light and vegetation height ($p < 0.05$). Individual linear regressions show BAI increases when light levels are high and when vegetation is below the height of the seedling ($p < 0.01$; Table 3). The interaction of light and vegetation height is negative, suggesting a more complex relationship (Table 3). Red alder BAI was also reduced by the interaction between soil moisture and light ($p < 0.01$); BAI is greatest at high light and low soil moisture and at low light and high soil moisture (Figure 9). BAI is smallest in both low light and moisture as well as at both high light and moisture (Figure 9).

Red alder height was increased by increasing light and reduced by browse ($p < 0.05$). This significant reduction in height from browse is predominantly caused by the number of seedlings where a large section of the top was snapped off likely due to ungulate damage. A high percentage, 42.5%, of red alder were browsed during the study (Table 8).

Western redcedar

Western redcedar BAI was reduced by soil moisture, vegetation height, the dominant species of surrounding vegetation, and the interaction between light and gap size but was increased by browse ($p < 0.05$) (Table 4). As soil moisture increases, the BAI of western redcedar significantly decreases but the estimate suggests the effect is small ($p < 0.05$) (Table 4). When the height of the surrounding vegetation is above the height of the center seedling, the BAI is reduced ($p < 0.05$). All orders of dominant understory vegetation led to reductions in BAI for western redcedar, most significantly by *Ericales* which includes common species such as red huckleberry and salal ($p < 0.05$) (Table 4). The BAI of western redcedar was largest in the second smallest gap size (0.1ha) and smallest in the smallest (0.05ha) gap size (Figure 7B), though Tukey HSD tests indicate no significant differences between groups. BAI generally increases as light increases although the second smallest gap size has a higher average BAI for western redcedar than the two largest gap sizes (0.25 & 0.5ha).

The height of western redcedar was decreased by soil moisture and influenced by the interaction between vegetation cover and light ($p < 0.05$) (Table 4). Average height of western redcedar increased as vegetation cover increased until 100% coverage, where height was then lowest. Vegetation cover also increases as light increases until 100% coverage where light was then lowest. This interaction between vegetation cover and light leads to increases in height until it decreases at full vegetation coverage in low light conditions.

It is also notable that browse significantly increases the BAI of western redcedar but does not statistically impact height.

Western hemlock

Western hemlock BAI was decreased when the height of the surrounding vegetation was above the height of the seedling ($p < 0.01$) (Table 5). BAI also increased by increasing gap size.

BAI was largest in the largest gap size (0.5ha) and smallest in the smallest gap size (0.05ha), though Tukey HSD tests indicate no significant differences between groups. Western hemlock showed significant differences in BAI by vegetation cover ($p < 0.05$; Table 5), however the response is not linear. BAI increases as vegetation cover increases up until the cover is 100% where the BAI then decreases (Figure 7D). Tukey HSD tests suggest BAI at vegetation cover of 75% is significantly different than BAI at 100% coverage in ($p < 0.05$). The regression coefficients are positive and the values follow the same trend (Table 5).

Change in height is also significantly predicted by height of competing vegetation, with growth reduced by tall understory plants ($p < 0.05$) (Table 5). Western hemlock height in reduced by ungulate browse and when surrounding vegetation is above the height of the seedling ($p < 0.05$) (Table 5). The pattern of height in response to vegetation cover is identical to the pattern for BAI and the estimates are all positive, though there are no significant differences between groups using a Tukey HSD test. Change in height is also increased by increasing gap size, similar to BAI, though a Tukey HSD test yielded no significant differences between gap sizes.

Grand fir

Grand fir BAI is increased by increasing soil moisture and increasing light, though it is reduced by the interaction between these variables ($p < 0.01$) (Table 6). BAI of grand fir is greatest when light is high and soil moisture is moderate (Figure 10). BAI is lowest at low light and low soil moisture conditions (Figure 10).

BAI is reduced by the interaction between vegetation cover and soil moisture ($p < 0.05$) (Table 6). As soil moisture increases, both vegetation cover and BAI increase though as vegetation cover increases, BAI decreases. BAI increases with 50% and 75% vegetation cover, but not 25% and 100% vegetation cover; the vegetation cover and soil moisture terms are significant for all vegetation cover values indicating the effect of soil moisture on BAI is in part dependent on the understory cover.

Change in height for grand fir increases as soil moisture increases ($p < 0.05$) (Table 6).

Douglas-fir

Douglas-fir BAI is increased by gap size and reduced by vegetation taller than the seedlings ($p < 0.05$) (Table 7). BAI is largest in the largest gap size (0.5ha) and smallest in the smallest gap size (0.05ha), though Tukey HSD tests indicate no significant differences between groups. When the height of the surrounding vegetation is higher than the height of the seedling, the BAI is reduced. Vegetation cover is marginally significant and positively associated with BAI at ≤75% vegetation cover.

Change in height of Douglas-fir was only significantly predicted by a negative interaction term soil moisture:light, but the effect was small ($p < 0.05$) (Table 7). Change in height is greatest at high light and low to moderate soil moisture while change in height is least in both low light and soil moisture (Figure 11).

Competition from Surrounding Seedlings

There were no statistically significant results from the generalized linear models or the multiple linear regressions in relation to the species of surrounding seedlings for survival or growth of the center seedling ($p > 0.05$).

Discussion

Impacts of Gap Size

As gap size increases, the availability of light and the openness of the canopy increases (Muscolo et al. 2007; Galhidy et al. 2006; Van Couwenberghe et al. 2010; Morgan et al. 1997). In our study, the largest gap size had the highest average amount of light and the smallest gap size had the lowest (Figure 6). In contrast to light, previous studies have suggested that soil moisture decreases as gap size increases (Muscolo et al. 2007; Morgan et al. 1997). Our study, however, found no significant differences in soil moisture between gap sizes, most likely due to the northern aspect of the sites. Soil moisture was higher on the downward slope position of the study site (Galhidy et al. 2006; Clinton et al. 2003). Vegetation cover also differed significantly between gap sizes; within the largest gap size, vegetation cover was lower than all other plots (Vilhar et al. 2015; Galhidy et al. 2006; Modrow et al. 2020; Pavlovic et al. 2006). In contrast, a study in the Dinaric Alps suggested that gaps with diameters larger than the stand height showed increased vegetation cover (Vilhar et al. 2015; Naaf et al. 2007; Walters et al. 2016; Kern et al. 2013). It is possible that the type of vegetation could impact the amount of vegetation coverage among different gap sizes due to differences in the environmental tolerance of understory vegetation. Vegetation in our study is typical of Douglas-fir forests including salal (*Gaultheria shallon*), trailing blackberry (*Rubus laciniatus*), sword fern (*Polystichum munitum*), and red huckleberry (*Vaccinium parvifolium*), and is well adapted to understory conditions which may have led to an increase in vegetation cover in small gaps (Spies et al. 1989). Our environmental conditions and vegetation response to gap size were inconsistent with the literature, with the exception of increasing light with increasing gap size (Muscolo et al. 2007; Morgan et al. 1997, Vilhar et al. 2015; Galhidy et al. 2006).

Though there are notable differences in environmental characteristics between gap sizes, our study found no differences in mortality among gap sizes. Previous studies have suggested gap size increases seedling height, diameter, and overall growth though this was possibly due to the impact of gap size on environmental conditions at specific study sites (Morrissey et al. 2010; Runkle et al. 1987; Gray et al. 1996; Harrington et al. 2006).

Gap size was significant for seedling growth in red alder, western hemlock, Douglas-fir, and as an interaction with light for western redcedar (Tables 3-5 & 7). Red alder, western hemlock, and Douglas-fir all increased in basal area increment as gap size increased (Tables 3, 4, & 7). Western hemlock also increased in height as a result of gap size (Table 5). It is likely that the increase in light within the largest gap and the decrease in vegetation cover led to this improved growth of the seedlings (Coates et al. 1999; Maas-Hebner et al. 2005). Western redcedar was significantly predicted by the interaction between light and gap size in terms of BAI (Table 4). Generally, western redcedar BAI increased as gap size increased though there was a notable jump in BAI in the second smallest gap size (0.1ha) (Figure 7B). This trend suggests that western redcedar is well-suited to intermediate light levels though tolerates the largest gap sizes well as well. Though western redcedar is often categorized as a shade-tolerant species, our study suggests that it grows best in intermediate to high light environments (Minore et al. 1979; Drever et al. 2001; Sajedi et al. 2012).

Seedling Response to Light

In addition to the response of western redcedar to the interaction of light and gap size, red alder, grand fir, and Douglas-fir also saw significant responses to the light environment across the study (Tables 3, 6, & 7). Douglas-fir was the only species in which mortality was negatively affected by light, a result which contrasts with its shade-intolerant status (Drever et al. 2001;

Carter et al. 1992). This may be due to the overwhelming impact of soil moisture on conifer mortality altering the response to light. The result is more surprising given the flat to north facing aspect of the study site. It may also be that early seedling survival benefits from lower light while roots are established. In terms of growth, red alder BAI and change in height both increased as light increased as well as grand fir BAI (Tables 3 & 6). This result is not surprising as red alder is typically a shade-intolerant deciduous species that thrives in post-disturbance high light environments (Chan et al. 2003; Shainsky et al. 1992; Maas-Hebner et al. 2005).

Soil Moisture as a Predictor of Conifer Mortality and Growth

The most common significant predictor of mortality in our study was soil moisture. Soil moisture was linked to higher likelihood of mortality in all four conifer species but not in red alder. Previous studies of Douglas-fir establishment have suggested even small reductions in soil moisture throughout the summer can lead to decreases in seedling volume growth in their first and second seasons (Gonzalez-Benecke et al. 2018; Chan et al. 2003); including on a nearby south facing aspect (Cockle et al. 2011). In our study, the conifers were likely experiencing water logging of the heavy clay soils that did not dry completely even at the peak of summer drought (Web Soil Survey, 2021). Though high soil moisture through early-August is often beneficial for seedling survival, consistent flooding through the winter and maintenance of moisture through the summer led to mortality in conifers (Gonzalez-Benecke et al. 2018; Drever et al. 2011). Interestingly, soil moisture was not a predictor of mortality for red alder. In a previous study, it was determined that red alder growth was superior to that of Douglas-fir under full light and non-limited water conditions though, under water stress, red alder growth responded negatively whereas Douglas-fir did not (Chan, S.S. et al. 2003; Shainsky et al. 1992; Gonzalez-Benecke et al. 2018).

Chlorophyll fluorescence *Fv/Fm* improved throughout the growing season for all species, although only 2 statistically significant differences between species and within months by species were found. Red alder saw significant increases in fluorescence between July and August and July and September. The only difference between species within months was between red alder and grand fir in July, where red alder had higher fluorescence values. The pattern of increasing fluorescence is likely due to reduced soil moisture over the summer drought period. For each species, chlorophyll fluorescence, a measure of the efficiency of photosystem II, increases between July and September, though not statistically significant (Maxwell et al. 2000). Studies in similar conifers have suggested that chlorophyll fluorescence provides information about the health and efficiency of the needle (Khan et al. 2000). The pattern of increased chlorophyll fluorescence over the summer suggests that as the soils dry out, seedling photosynthesis potential increased, thereby increasing growth and survival increases. The soils were likely too moist for many seedlings over the course of the year which led to low fluorescence values in early July.

Soil moisture was also a significant predictor for growth in all species in this study as a singular variable and in interaction terms. Red alder BAI increased with increasing soil moisture; a result consistent with red alder's lack of response in mortality to high levels of water logging across the site (Table 3) (Chan et al. 2003; Shainsky et al. 1992; Maas-Hebner et al. 2005). Similarly, grand fir also saw increases in BAI and change in height as soil moisture increased (Table 6). This suggests that grand fir benefits from high soil moisture levels until extreme water logging causes early mortality in the seedling (Coates et al. 1999). On the contrary, western redcedar BAI and change in height were both reduced by high levels of soil moisture (Table 4). Previous literature typically categorizes western redcedar as a highly moisture tolerant species though this situation in our study likely went beyond its range of tolerance (Minore et al. 1979, Drever et al. 2001; Sajedi et al. 2012). This indicates that western redcedar may be more sensitive to high soil moisture conditions in this gap setting.

Red alder, grand fir, and Douglas-fir growth were significantly predicted by the interaction of light and soil moisture (Tables 3, 6, & 7; Figures 9-11). At low light and low soil moisture, growth rates were reduced which suggests these species are not suited for growth near gap edges with limited water availability (Chan et al. 2003; Maas-Hebner et al. 2005). Red alder saw increases in BAI at high light and low soil moisture conditions as well as in low light and high soil moisture conditions (Figure 9B). Interestingly, red alder thrives in more extreme conditions of either light or soil moisture, but fairs poorly in conditions when both are high or low (Figure 9B). Similarly, Douglas-fir had the highest change in height values in high light and low to moderate soil moisture conditions (Figure 11B). Previous studies have suggested that in limited light and moisture conditions, there is little difference in growth rates for red alder and Douglas-fir (Chan et al. 2003); a result that is consistent with our findings that both red alder and Douglas-fir perform poorly in these environments (Figures 9B & 11B). As the gaps in the study site are expanded and light availability increases while soil moisture stays constant, it is likely that red alder will increase in BAI while Douglas-fir increases in height. Grand fir, however, shows highest BAI in high light with moderate soil moisture (Figure 10B). An increase in light availability may lead to increases in BAI but only in areas with sufficient soil moisture.

Possible Evidence of Gap Partitioning

Our study suggests there may be some gap partitioning based on light availability between species with wide-ranging shade tolerances, such as shade-intolerant Douglas-fir and red alder and shade-tolerant western redcedar, western hemlock, and grand fir (Diaci et al. 2008;

Gray et al. 1996; Vepakomma et al. 2012; Van Couwenverghe et al. 2010). This result is relatively novel as other studies have found no evidence of partitioning (Adamic et al. 2017; Wright et al. 1998; Kern et al. 2013). Red alder, a shade-intolerant species, showed a strong growth response to increasing light conditions and faired best in bright environments compared to western redcedar and western hemlock, shade-tolerant species, which showed little response to light (Tables 8-10) (Minore et al. 1979). This suggests that gaps provide suitable environments for both red alder and conifer species and in a natural establishment pattern, this could lead to a division of primarily red alder in the center of gaps and conifers occupying gap edges. This study reports on early seedling responses post planting, years 1 and 2, and growth responses might become more responsive to gap size in future years.

Vegetation and Browse Impacts Inconsistent Across Species

The height of the surrounding vegetation compared to the height of the seedling reduced growth in red alder, western redcedar, western hemlock, and Douglas-fir (Tables 3-5 & 7). In red alder, the interaction of light and vegetation height negatively impacts BAI. When light is high and the height of the vegetation is below the height of the seedling, the BAI of red alder increases. The interaction of these environmental variables is significant partly because vegetation height is a comparative measure with seedling height. As light increases, vegetation height is lower due to the increased growth of red alder in comparison. This does not indicate that the general height of the vegetation is lower in sites with more light, it merely describes the increase in seedling height under high light growing faster than competing vegetation.

Western redcedar, western hemlock, and Douglas-fir were negatively impacted by understory vegetation height which led to a decrease in BAI and change in height (Tables 3, 4, & 7). The height of the vegetation above the height of the seedling likely impacted light availability to the needles, although competition for nutrients was not measured and cannot be ruled out. Similarly, Lorimer (1994) and Davis (1999) found that tall understory vegetation leads to increased mortality in oak seedlings, slower average annual growth, and lower rates of photosynthesis. The impact of competition for light, and possibly nutrients, likely led to a decrease in growth for these conifer species.

Previous studies mostly suggest vegetation control is necessary for efficient seedling growth (Vandenverghe et al. 2006; Lu et al. 2018; Walters et al. 2016), however others have found no difference in stem volume growth across varying vegetation controls scenarios within the first 3 years after planting (Rose et al. 2002). Western hemlock was the only species in our study affected by only vegetation cover (Table 5). Both BAI and height increased as vegetation cover increased up to 75% cover then sharply decreased at 100% cover. Our study suggests that vegetation cover was sometimes beneficial to seedling growth. Western redcedar responded similarly in change in height to the interaction of vegetation cover and light (Table 3). As light increases, vegetation cover increases until 75% coverage. At 100% coverage of vegetation, light levels are typically low; a result associated with high vegetation cover in the smallest gaps with lower light availability. Western redcedar height increases as vegetation cover increases until the 100% coverage as well. This interaction suggests that western redcedar growth also benefits from increased vegetation cover except in conditions with low light and 100% vegetation cover (Drever et al. 2001; Carter et al. 2003).

Vegetation cover also interacts with soil moisture to decrease BAI in grand fir (Table 6). Soil moisture leads to increases in BAI of grand fir but also to increases in vegetation cover. This increase in vegetation cover, in contrast to western hemlock and western redcedar, reduces BAI of grand fir. Grand fir is typically categorized as a shade mid-tolerant and is likely outcompeted by vegetation for light availability in high soil moisture environments (Minore et al. 1979; Coates et al. 1999); our results show optimum BAI growth with high light and intermediate moisture (Figure 10).

Though each species was surrounded by generally the same type of vegetation across the 16 plots, the responses were quite varied. The results suggests that there are many species that respond to interactions with vegetation cover or height to light or soil moisture as opposed to the variables themselves. It is important to recognize both the impacts of the environmental conditions on both the seedlings and their surrounding understory vegetation. Though previous studies often suggest that vegetation negatively impacts seedling survival and growth, our study indicates that this cannot be generalized across all species (Harrington et al. 2006; Kern et al. 2012; Wagner et al. 1991). Western hemlock and western redcedar, for example, grew larger under vegetation cover until it was completely surrounded by competing vegetation, while grand fir growth was reduced by increasing vegetation cover in conjunction with soil moisture (Tables 4-6).

Browse played a key role in growth for 3 of the 5 species with both positive and negative influences on growth. Western redcedar was most heavily browsed at 51% followed by red alder at 42.5% (Table 8). An increase in BAI was associated with browse on western redcedar, though there was no significant decrease in height (Table 3). Western redcedar likely put energy towards growth of the stem or roots which increased BAI, instead of height with repeated ungulate browse (Stroh et al. 2008). Red alder responded in an opposite manner, with browse predicting a decrease in height but no influence on BAI (Table 3). These decreases in height were not surprising as the ungulates in the region tend to completely remove terminal buds and branches from the top of seedlings (Wagner et al. 1991; Maas-Hebner et al. 2005; Kern et al. 2012;

Walters et al. 2016). The influence of browse on seedling growth is an important factor to consider when deciding on the species to plant and how to properly protect them (Maas-Hebner et al. 2005; Naaf et al. 2007).

No Influence of Competition from Surrounding Seedlings

Surrounding seedling species was not a significant predictor for any growth or mortality measure across all 5 species. This is likely due to the size of seedlings at planting and the 1m spacing between seedlings within the pentad design. This will probably change over time as the seedlings get larger and their roots and crowns begin to compete with neighboring seedlings. Of the seedlings planted, red alder often grows the fastest and is on average the largest seedling in the early years. It is possible that red alder will be the first species to shade out other seedlings and lead to decreased growth rates of surrounding conifers. The species with the fastest early growth rates may outcompete their neighboring seedlings. It is also possible that red alder as a nitrogen fixer may increase the growth of neighboring seedlings, thereby facilitating increased growth. Differences in seedling size as well as differential allocation of resources across the gaps will likely create interesting patterns of seedling interactions going forward (Chan et al. 2003).

Limitations

There are a few limitations within our study that could influence the degree to which each species responded to environmental conditions and gap size. The aspect of the experimental site was north where, in the northern hemisphere, light strength and availability is much lower and the temperatures are generally cooler. The difference in initial seedling age and size may have also impacted the survival and growth of certain species (Morrissey et al. 2010). Douglas-fir was planted as the smallest and youngest seedling stocktype (1 year-old plugs) which could decrease survival and the likelihood of determining significant predictors of growth at two years post planting. Previous studies have suggested the importance of stocktype in competitive status of seedlings 5 years after planting which indicates that this may continue to impact the study going forward (Morrissey et al. 2010; Pinto et al. 2011; Pinto et al. 2012; Dumroese et al. 2016).

The impact of gap size on microclimate and seedling development is likely highly site-specific. The mixed nature of the literature on gaps indicates their influence on factors such as forest type, soils, climate, and species composition are wide ranging. This study is solely focused on a lower elevation forest in Western Washington and the results should not be applied too broadly, perhaps best describing responses on fine textured soil types in this region.

Conclusions and Management Implications

In initial survival and growth of Pacific Northwest natives, gap size was influential in growth for 4 of 5 species in the study. Gap size influences the microclimate by causing shifts in average light availability and vegetation cover which likely creates distinctions in growth for these species between gap sizes. These environmental conditions also interact with each other to further impact the early development of seedlings. The most important factor in determining survival for the conifer species tested was soil moisture. These conifers, specifically those with higher mortality rates such as western hemlock and Douglas-fir, are less likely to survive if planted in pockets of high soil moisture or at the bottom of slopes such as in this study. Soil moisture and light were also large contributing factors in the increased growth rates of all species except western hemlock. The interactions between these abiotic factors and vegetation measures also created both positive and negative impacts on seedling growth.

Early vegetation control on planted sites is common in western Washington, however our study found that not all species respond equally to the quantity and height of surrounding understory (Maguire et al. 2009). All species except grand fir would best be planted in sites where the height of the surrounding vegetation was generally lower than the seedlings themselves, similar to Dumroese's (2016) Target Plant Concept in which site characteristics for specific species are vital in reforestation efforts. Vegetation cover led to increased growth of western hemlock and western redcedar until 75% coverage though vegetation cover, in conjunction with soil moisture, also decreased height in grand fir. This suggests that vegetation control could be less intensive in early years of seedling growth for some conifers than is traditionally accepted. The long-term implications of vegetation competition will be better ascertained when seedlings are free-to-grow above competing vegetation—this may take several more years to determine.

Browse, a well-known foe of seedlings in the Pacific Northwest, was highly impactful across the study. The differential impacts of browse on seedlings may lead to potential consequences for establishment and growth in mixed-species plantations. With high browse rates in red alder and western redcedar, other species in mixed plantings such as a Douglas-fir or grand fir may overtop their growth in early years post-planting, though the quick growth of red alder may protect it from this consequence of browse. Protecting against browse can be extremely challenging but future studies in the use of ungulate deterrents may determine the most efficient method of environmental control to increase seedling survival and growth.

Clear-cut forestry practices in the Pacific Northwest are often implemented to favor fast growing shade-intolerant Douglas-fir plantations while mixed-species plantations grown across variable light and soil moisture conditions show differential growth and survival responses of these 5 native species. Gap size is responsible for shifts in environmental conditions which leads to differences in survival and growth of seedlings (Bolton et al. 2011; Wright et al. 1998; Adamic et al. 2017). Management prescriptions using mixed-species plantations should take into account the microclimate of each site before determining the specific mix of species that would best fit the location. The formation of gaps within management plans provides interesting mimics to natural disturbance regimes that may see benefits in wildlife habitat and resilience to future disturbances. In the Pacific Northwest, our study suggests that in the short term, the size of these gaps leads to shifts in the site-specific environmental characteristics and that the success of the stand will be dependent on the individual species' responses to this microclimate. We will continue this as a long-term study to determine if gap size becomes more or less influential over time and how these mixed-species pentads will interact in the future.

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Tables

Table 1: Mortality by species and row arranged from lowest to highest topographic position Row A to D. Rate of mortality for each species of seedling for all rows and for each individual row.

Species	***Row***	***Mortality Rate %***
Red Alder	All Rows	6.9
	Row A	6.3
	Row B	7.3
	Row C	5.7
	Row D	10.3
Western redcedar	All Rows	5.0
	Row A	5.5
	Row B	2.4
	Row C	7.8
	Row D	0
Western hemlock	All Rows	27.9
	Row A	35
	Row B	23.7
	Row C	26.3
	Row D	23.3
Grand fir	All Rows	8.1
	Row A	19.4
	Row B	2.2
	Row C	5.5
	Row D	0
Douglas-fir	All Rows	26.8
	Row A	50
	Row B	18.6
	Row C	22.2
	Row D	9.7

Table 2: Results of Generalized Linear Models for Mortality by Species. Results of generalized linear models including all explanatory variables tested for mortality of each species, the model estimate, standard error, z-value, and p-value. Significant predictors for each species are listed with (*).

Species	*Predictor*	*Estimate*	*Std. Error*	*Z-value*	*P-value*
Red alder	Soil Moisture	-0.044	0.0254	-1.728	0.083
	Light	0.0132	0.0257	0.523	0.601
	VegCov	-14.93	1796.3	-0.008	0.993
	Dominant Vegetation	19.87	3956.2	0.005	0.996
	Gap Size	-0.2231	1.268	-0.176	0.860
	Browse	0.6837	0.6093	1.122	0.262
	Vegetation Height	-2.6464	0.6756	-3.917	8.97 e-05*
Western redcedar	Soil Moisture	-0.0991	0.03250		0.0023*
	Light	-0.2215	0.0309	-0.715	0.474
	VegCov	19.57	4809	0.004	0.997
	Dominant Vegetation	20.57	17730	0.001	0.999
	Gap Size	18.57	1882.9	0.01	0.992
	Browse	0.9307	0.0705	1.32	0.187
	Vegetation Height	-1.9418	0.8045	-2.41	0.015*
Western hemlock	Soil Moisture	-0.14110	0.03022	-5.95	3.03 e-06*
	Light	-0.0089	0.0147	-0.602	0.548
	VegCov	14.57	882.7	0.017	0.987
	Dominant Vegetation	16.57	1073	0.015	0.988
	Gap Size	0.559	0.6268	0.893	0.372
	Browse	0.679	1.107	0.613	0.54
	Vegetation Height	-1.6094	0.3651	-4.408	1.05 e-05*
Grand fir	Soil Moisture	-0.1411	0.0302	-4.669	3.30e-06*
	Light	-0.037	0.0293	-1.561	0.118
	VegCov	17.57	1615.1	0.011	0.991
	Dominant Vegetation	19.57	1075	0.002	0.999
	Gap Size	18.57	1630.6	0.011	0.991
	Browse	-0.2451	1.086	-0.226	0.821
	Vegetation Height	-0.575	0.5275	-1.09	0.276
Douglas-fir	Soil Moisture	-0.09501	0.01915	-4.962	6.98 e-07*
	Light	-0.038	0.0149	-2.543	0.0109*
	VegCov	16.57	1073.1	0.015	0.988
	Dominant Vegetation	1.792	1.780	1.007	0.314
	Gap Size	0.9808	0.677	1.449	0.147
	Browse	0.399	0.8065	0.494	0.621
	Vegetation Height	-1.8833	0.4147	-4.541	5.59 e-06*

*Vegetation Height represents the effect of vegetation cover growing above the height of seedlings

Table 3: Red Alder Reduced Model Results. Final results of red alder basal area increment (BAI) and change in height (ΔHt) growth models after using backwards stepwise model selection. For BAI, significant variables include soil moisture, light, gap size, soil moisture: light interaction, and light: vegetation height interaction. For ΔHt, significant variables include light and browse. VegHt = Vegetation height above or below center seedling. VegCov = Vegetation cover.

Species	*Response*	*Variable*	*Estimate*	*Std. Error*	*F-value*	*P-value*
Red alder	BAI	Soil Moisture	0.031	0.01	8.819	0.003*
		Light	0.021	0.005	19.66	1.64e-05*
		VegHt	0.217	0.266	0.665	0.415
		GapSize	0.067	0.027	6.332	0.0128*
		Soil Moisture:Light	-0.0007	0.0002	11.09	0.001*
		Light:VegHt	-0.014	0.006	4.982	0.027*
		Soil Moisture:VegHt	0.012	0.007	2.933	0.088
	ΔHt	VegCov			1.930	0.107
		Soil Moisture	1.39	5.44	0.796	0.798
		Light	0.865	0.288	8.997	0.003*
		Browse	-23.03	5.79	15.79	0.0001*
		VegHt	-12.75	6.76	3.558	0.061
		VegCov:Soil Moisture			2.09	0.084

Table 4: Western Redcedar Reduced Model Results. Final results of western redcedar basal area increment (BAI) and change in height (ΔHt) growth models after using backwards stepwise model selection. For BAI, significant variables include soil moisture, order of dominant vegetation, browse, vegetation height, and light: gap size interaction. For ΔHt, significant variables include soil moisture and vegetation cover: light interaction. VegHt = Vegetation height above or below center seedling. VegCov = Vegetation cover. DomVeg = Dominant vegetation.

Species	***Response***	***Variable***	***Estimate***	***Std. Error***	***F-value***	***P-value***
Western redcedar	BAI	VegCov			1.929	0.107
		Soil Moisture	-0.007	0.003	4.860	0.0288*
		Light	0.013	0.007	2.836	0.094
		DomVeg⸙			3.223	0.003*
		Browse	0.134	0.046	8.510	0.004*
		VegHt	-0.327	0.114	8.114	0.035*
		GapSize	0.211	0.108	3.827	0.052
		Soil Moisture:VegHt	0.007	0.005	2.293	0.131
		Light:GapSize	-0.005	0.002	4.163	0.043*
	ΔHt	VegCov			3.401	0.011
		Soil Moisture	-0.677	-0.257	6.890	0.009*
		Light	0.239	3.18	0.006	0.940
		Browse	-5.15	2.81	3.359	0.068
		VegHt	-4.49	2.93	2.344	0.127
		VegCov:Light			3.437	0.009*

⸙Significant orders in the category dominant vegetation include Dipsacales, Ericales, Poales, Polypodiales, Ranunculales, and Rosales.

Table 5: Western Hemlock Reduced Model Results. Final results of western hemlock basal area increment (BAI) and change in height (ΔHt) growth models after using backwards stepwise model selection. For BAI, significant variables include vegetation cover, vegetation height, and gap size. For ΔHt, significant variables include vegetation cover, browse, vegetation height, and gap size. VegHt = Vegetation height above or below center seedling. VegCov = Vegetation cover.

Species	*Response*	*Variable*	*Estimate*	*Std. Error*	*F-value*	*P-value*
Western hemlock	BAI	VegCov			4.033	0.007*
		Browse	-33.72	23.88	1.994	0.160
		VegHt	-33.69	8.21	16.86	7.14e-05*
		GapSize	12.64	4.76	7.043	0.009*
	ΔHt	VegCov			4.716	0.0014*
		Soil Moisture	-0.481	0.294	2.678	0.104
		Light	-0.484	0.246	3.863	0.051
		Browse	-34.07	14.76	5.331	0.022*
		VegHt	-24.25	4.92	24.28	2.56e-06*
		GapSize	10.16	2.85	12.72	0.0005*

Table 6: Grand Fir Reduced Model Results. Final results of grand fir basal area increment (BAI) and change in height (ΔHt) growth models after using backwards stepwise model selection. For BAI, significant variables include soil moisture, light, vegetation cover: soil moisture interaction, and soil moisture: light interaction. For ΔHt, significant variables include soil moisture. VegHt = Vegetation height above or below center seedling. VegCov = Vegetation cover.

Species	***Response***	***Variable***	***Estimate***	***Std. Error***	***F-value***	***P-value***
Grand fir	BAI	Soil Moisture	10.12	3.188	10.08	0.0018*
		Light	1.93	0.656	8.627	0.0038*
		VegCov			2.171	0.075
		VegCov:Soil Moisture			3.975	0.0042*
		Soil Moisture:Light	-0.068	0.033	4.301	0.039*
	ΔHt	Soil Moisture	3.05	1.53	3.974	0.048*
		VegCov			2.324	
		Light	-0.56	0.509	1.232	0.268
		VegHt	16.949	14.9	1.293	0.2574
		GapSize	-10.71	7.17	2.229	0.137
		Light:VegHt	-0.5	0.336	2.212	0.139
		VegCov:Soil Moisture			2.205	
		Light:GapSize	0.252	0.163	2.389	0.124

Table 7: Douglas-fir Reduced Model Results. Final results of Douglas-fir basal area increment (BAI) and change in height (ΔHt) growth models after using backwards stepwise model selection. For BAI, significant variables include vegetation height and gap size. For ΔHt, significant variables include soil moisture: light interaction. VegHt = Vegetation height above or below center seedling. VegCov = Vegetation cover.

Species	***Response***	***Variable***	***Estimate***	***Std. Error***	***F-value***	***P-value***
Douglas-fir	BAI	VegCov			2.355	0.057
		VegHt	-0.204	0.068	7.949	0.005*
		GapSize	0.109	0.037	7.894	0.005*
	ΔHt	Soil Moisture	0.033	0019	2.741	0.10003
		Light	0.011	0.008	1.817	0.180
		VegHt	-0.111	0.079	1.974	0.162
		GapSize	0.086	0.045	3.556	0.061
		Soil Moisture:Light	-0.0009	0.0004	4.029	0.047*

Table 8: Browse and average seedling health by species after the second growing season. Percent of seedlings with ungulate browse by species of center seedling. Mean seedling health was calculated from field ranks of individuals from 1-4 (1= few live needles; 2 = most needles are chlorotic with some green; 3 = most needles are green with some chlorotic; 4 = all needles are alive and green).

Species	***Percent Browsed %***	***Mean seedling health***
Red alder	42.5	3.34
Western redcedar	51	3.68
Western hemlock	2.9	2.9
Grand fir	4.7	3.5
Douglas-fir	4.6	2.6

Figures

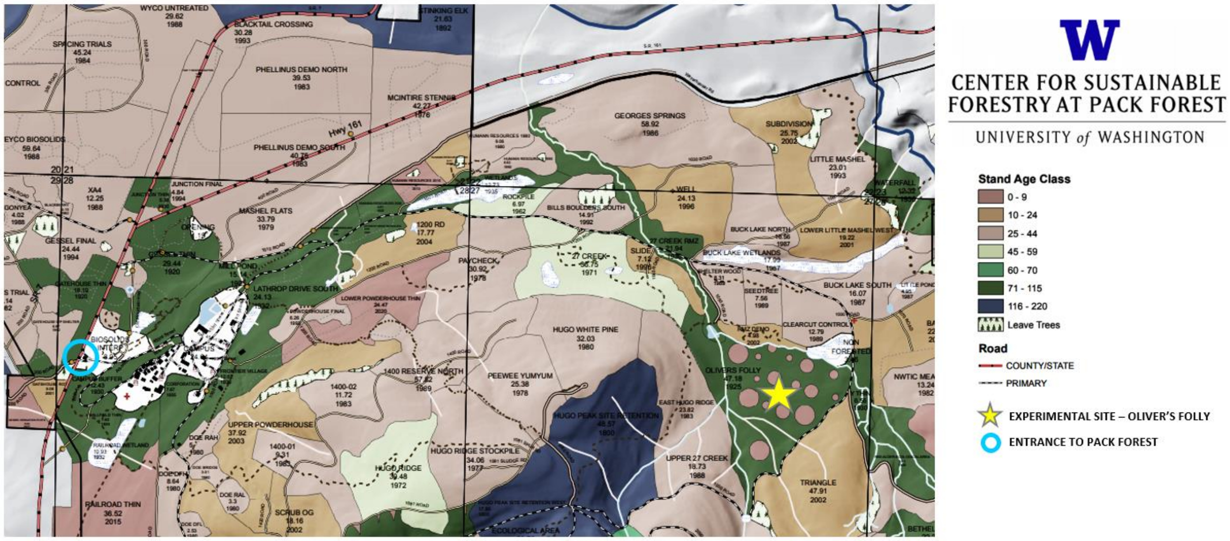

Figure 1: Study site location road and stand map of University of Washington Center for Sustainable Forestry at Pack Forest. Experimental site and entrance to Pack Forest are noted.

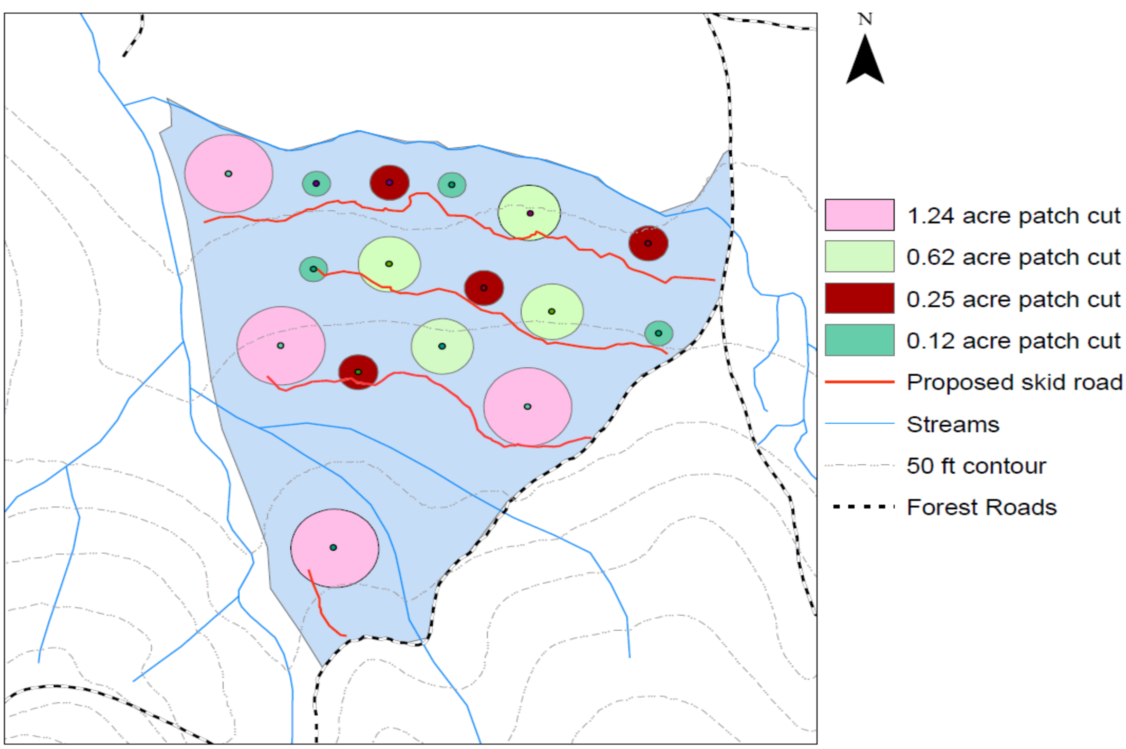

Figure 2: Map of study site gap arrangement and skid roads (red) used in creating gaps. Sixteen plots were clear-cut in 2018 to produce 4 plots at each of the following sizes: 0.05, 0.1, 0.25, and 0.5 ha (1.24, 0.62, 0.25, and 0.12 acres).

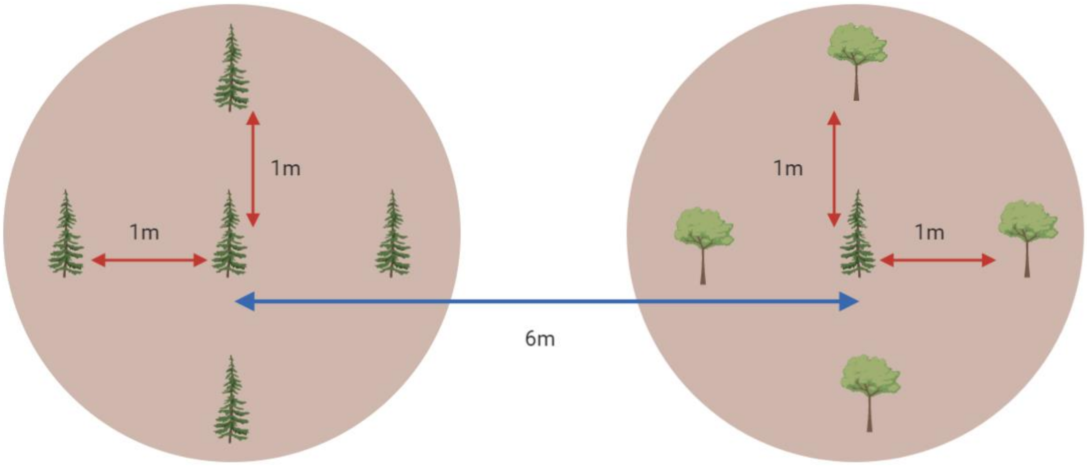

Figure 3: Planting scheme for Oliver's Folly experimental seedlings. Each surrounding seedling is 1m from the center seedling. Center seedlings of each pentad are 6m from each other. Pentad A is a monoculture group with all seedlings of the same species. Pentad B is a mixed group with a different species in the center than the surrounding seedlings. Figure created in BioRender.

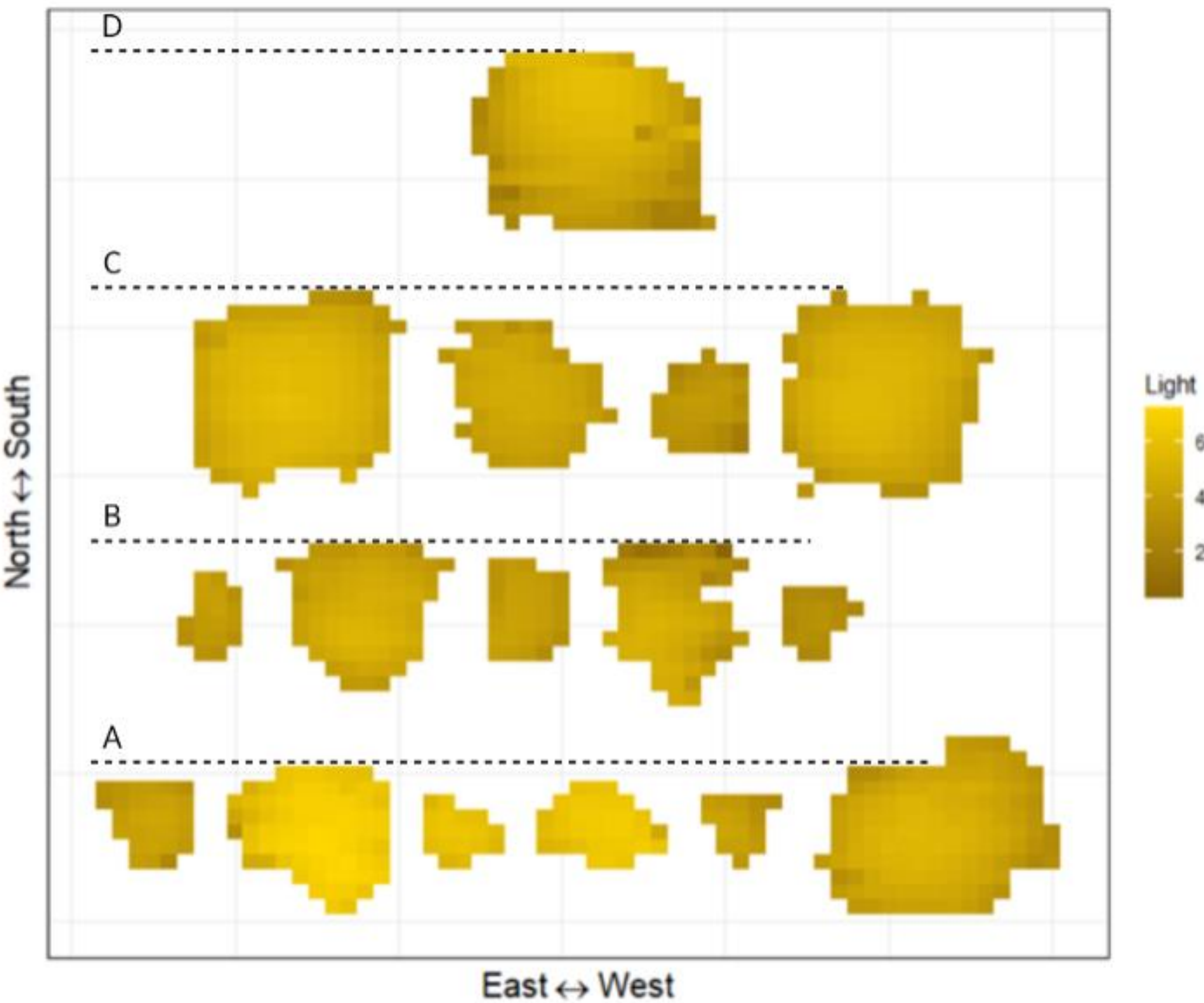

Figure 4: Distribution of light across the 16 plots in Oliver's Folly. Canopy openness values (%) are represented as one square per hemispherical photo taken above a pentad in each plot in the study site. The rows are labelled as A with 6 plots, B with 5 plots, C with 4 plots, and D with 1 plot. The seedlings were planted on a grid system and only in viable locations (without mature trees, logs, or other natural objects) which creates a non-circular pattern for each plot. The dashed lines represent the skid roads that were used in the harvest process which can be sources of light for some plots. Plots in row A are often much lighter than others because the surrounding forest is predominantly composed of deciduous species which had no leaves at the time the hemispherical photos were taken.

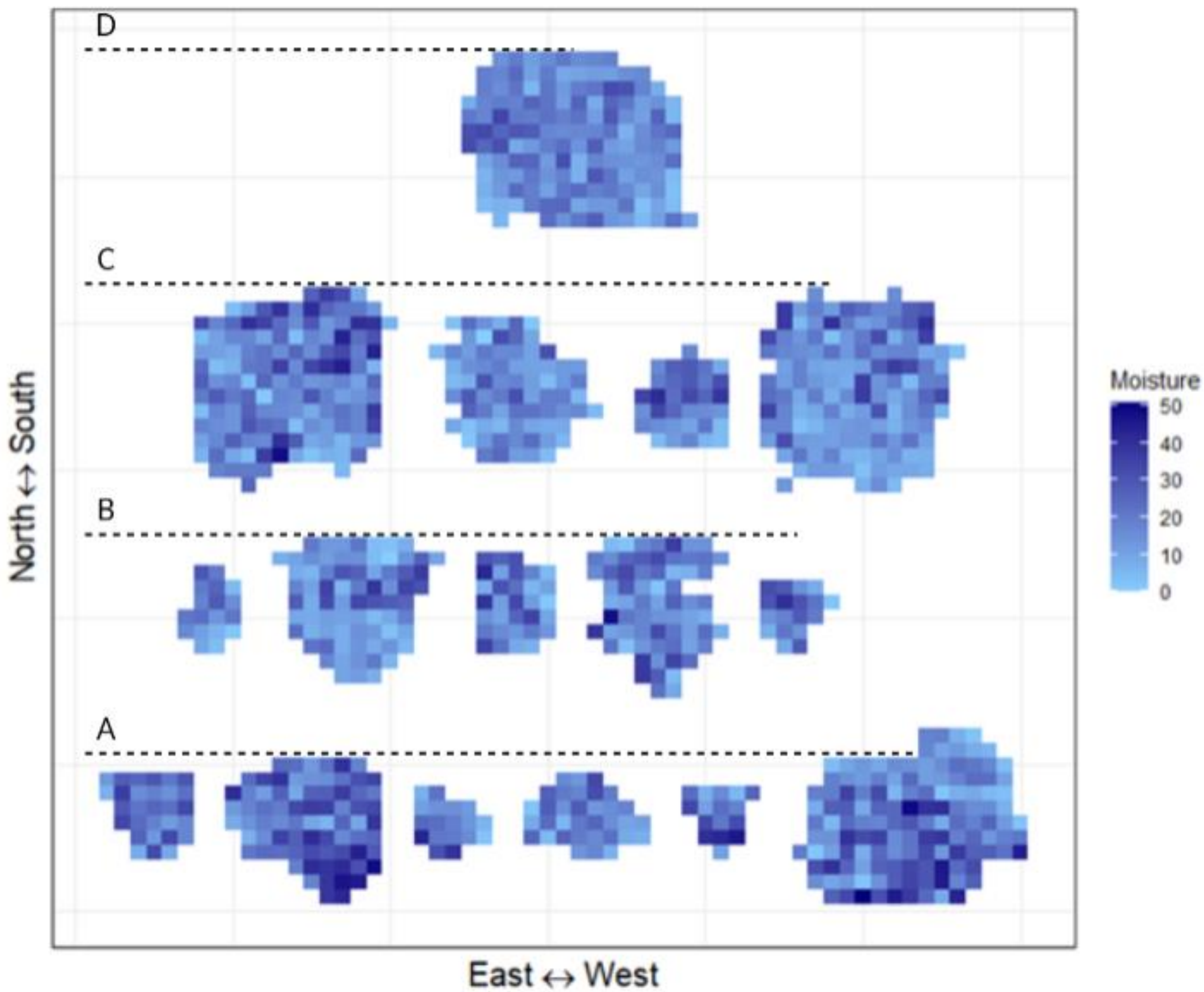

Figure 5: Distribution of soil moisture across the 16 plots in Oliver's Folly. Soil moisture values (%) are represented as one square per moisture measurement taken below the center seedling of a pentad in each plot in the study site in August 2019. The rows are labelled as A with 6 plots, B with 5 plots, C with 4 plots, and D with 1 plot. The seedlings were planted on a grid system and only in viable locations (without mature trees, logs, or other natural objects) which creates a non-circular pattern for each plot. The dashed lines represent the skid roads that were used in the harvest. The region of highest soil moisture is at the bottom of the plot second to the left in row A where a swamp occurs for the fall and winter months.

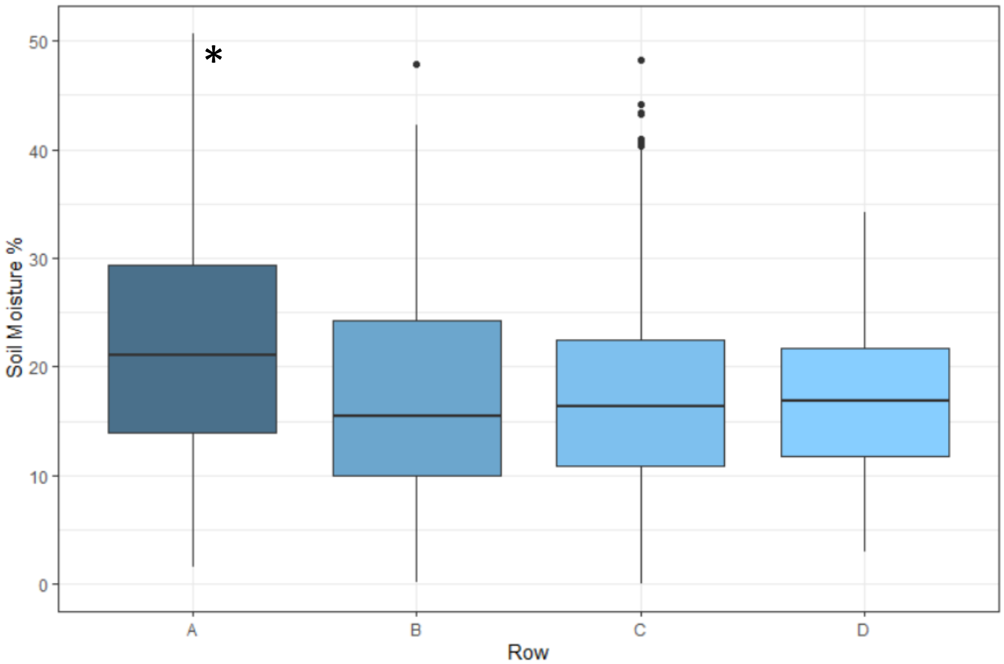

Figure 6: Soil moisture distribution between rows across Oliver's Folly. Row A has significantly higher soil moisture than all other rows ($p < 0.05$). Average soil moisture in row A is 22.07%, B - 17.78%, C - 17.61%, and D - 17.1%.

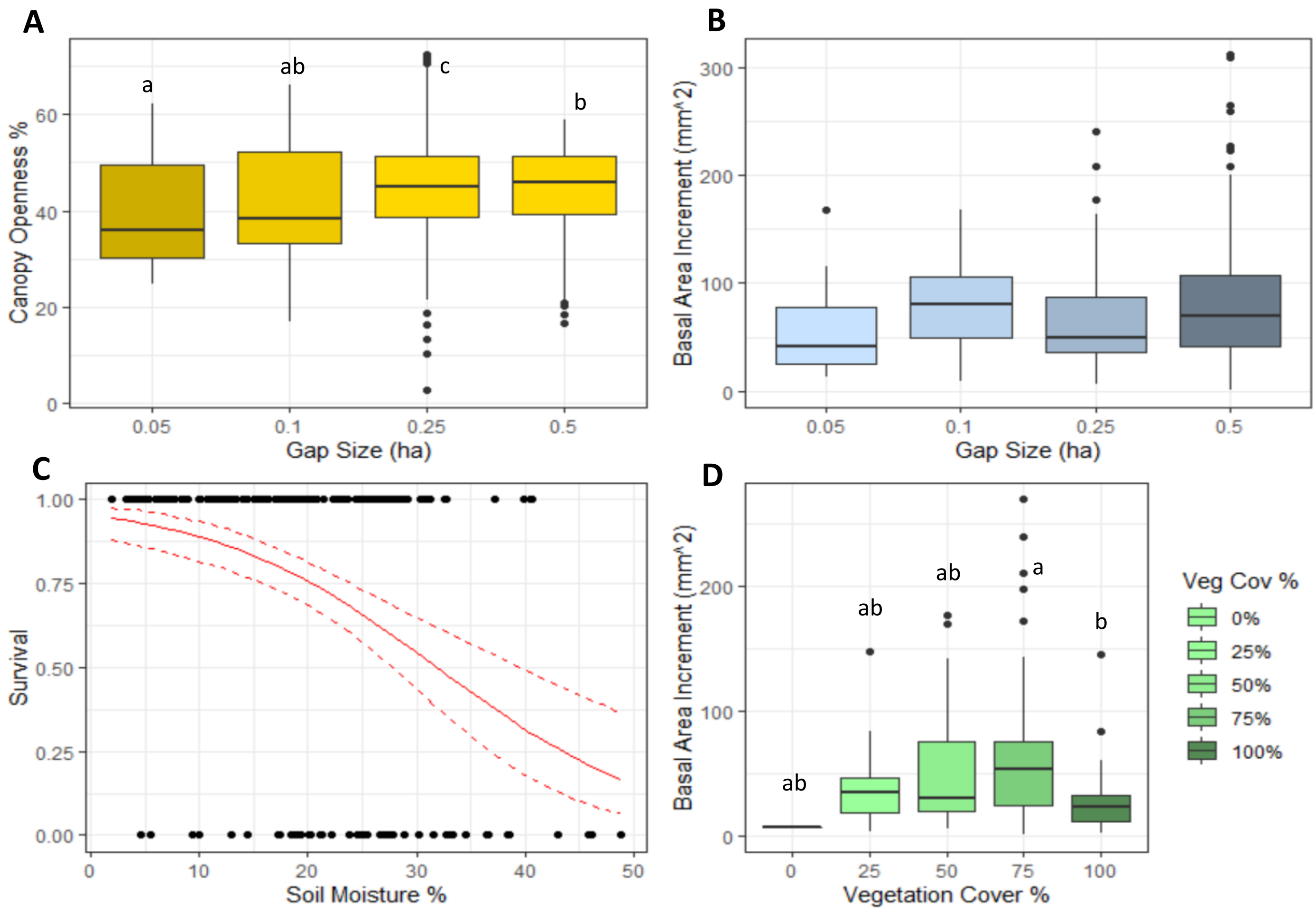

Figure 7: Canopy openness by gap size, basal area increment of western redcedar by gap size, survival of Douglas-fir according to soil moisture, and basal area increment of Western hemlock by vegetation cover. *(A)* Percent of canopy openness by plot size for all pentads within the study site. Significance factors are listed above each box ($p < 0.05$). *(B)* Basal area increment of western redcedar between gap sizes ($p < 0.05$). *(C)* Results of general linear model of Douglas-fir survival against soil moisture ($p < 0.05$). *(D)* Basal area increment of western hemlock by vegetation cover percentage ($p < 0.05$). Cover 75% and 100% are significantly different ($p < 0.05$).

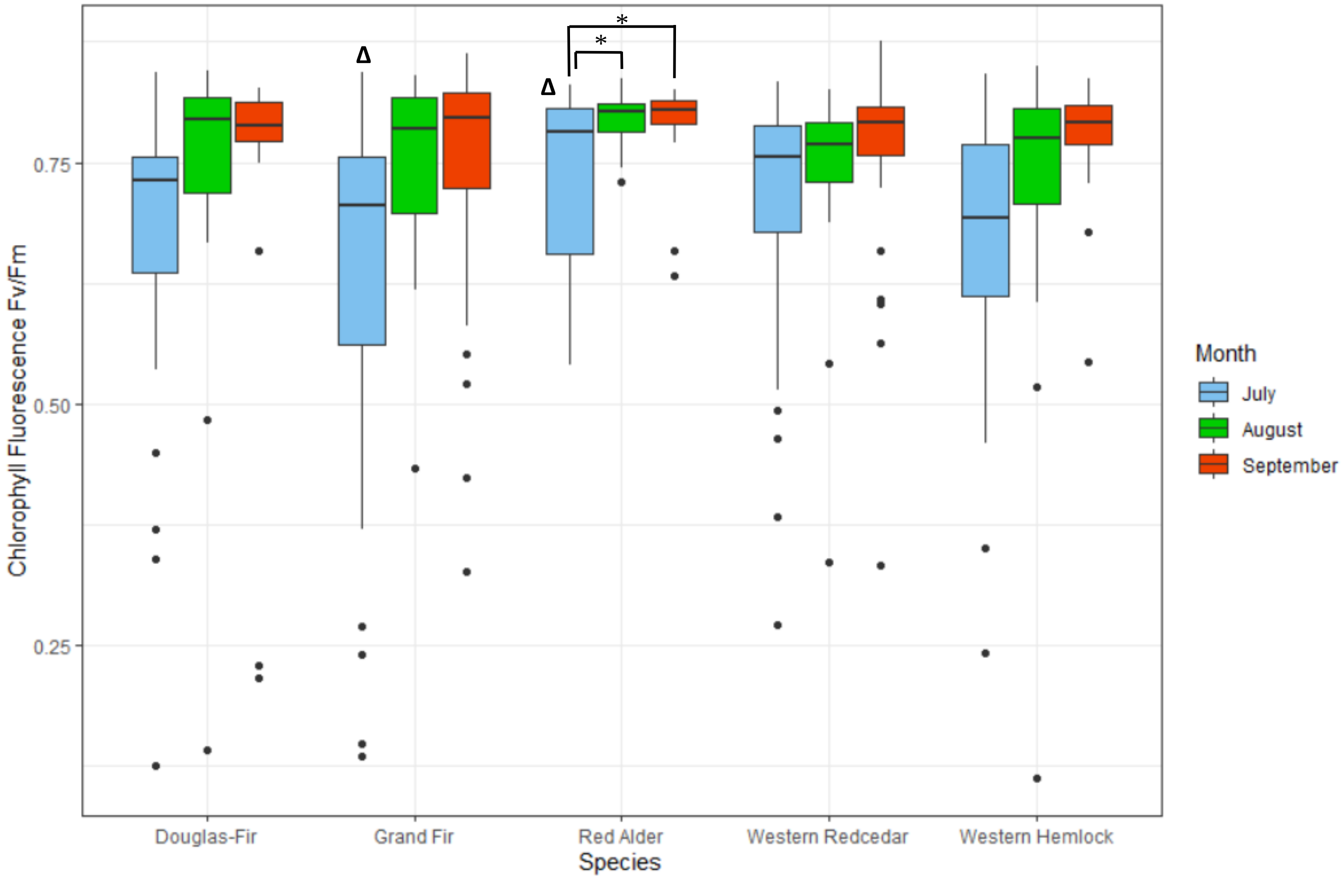

Figure 8: Chlorophyll fluorescence by species over summer months. Chlorophyll fluorescence values in Fv/Fm for each species between July, August, and September 2020. *Red alder fluorescence is significantly difference in July and August and July and September. **Δ** Fluorescence of grand fir and red alder are significantly different in July. Each species sees an average increase in chlorophyll fluorescence over the summer months.

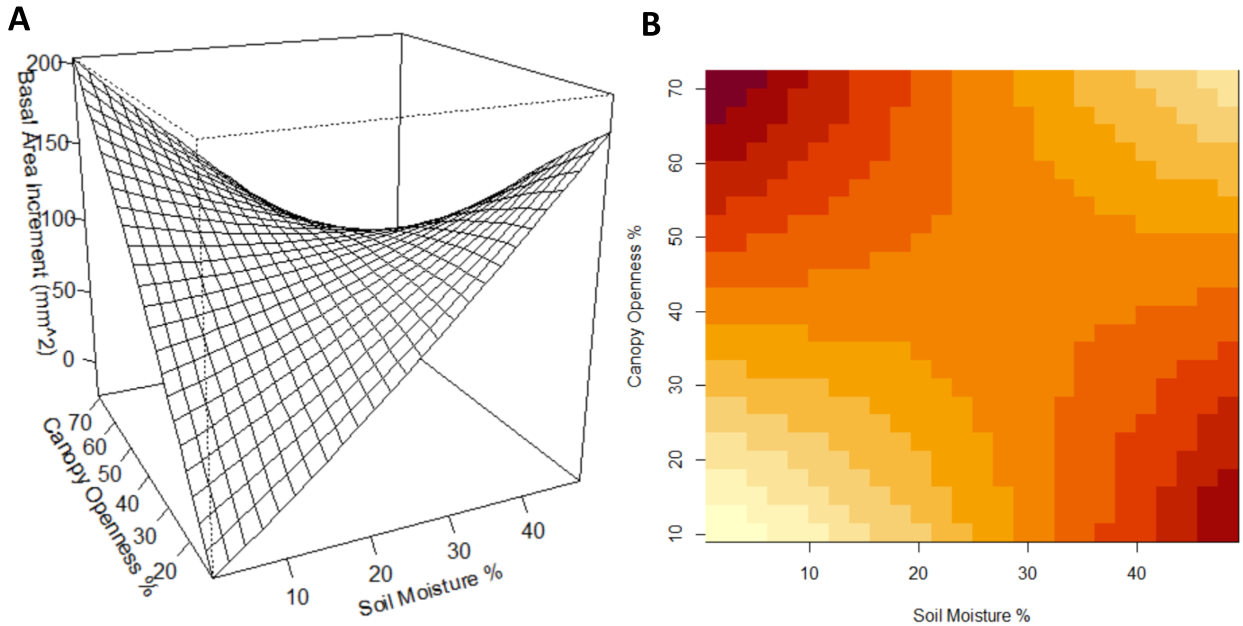

Figure 9: Response Surface of Red Alder Basal Area Increment by Light:Soil Moisture Interaction. Response surface is depicted of basal area increment (BAI) by the interaction of light and soil moisture. (A) Response surface as a plane along the axes of BAI (mm^2), canopy openness %, and soil moisture %. (B) Heat map of BAI by canopy openness % and soil moisture %. Dark red areas indicate high BAI while light yellow areas indicate low BAI. BAI is highest when light is high and soil moisture is low as well as when soil moisture is high and light is low. Figures were created using the R package "rsm" (Lenth 2009).

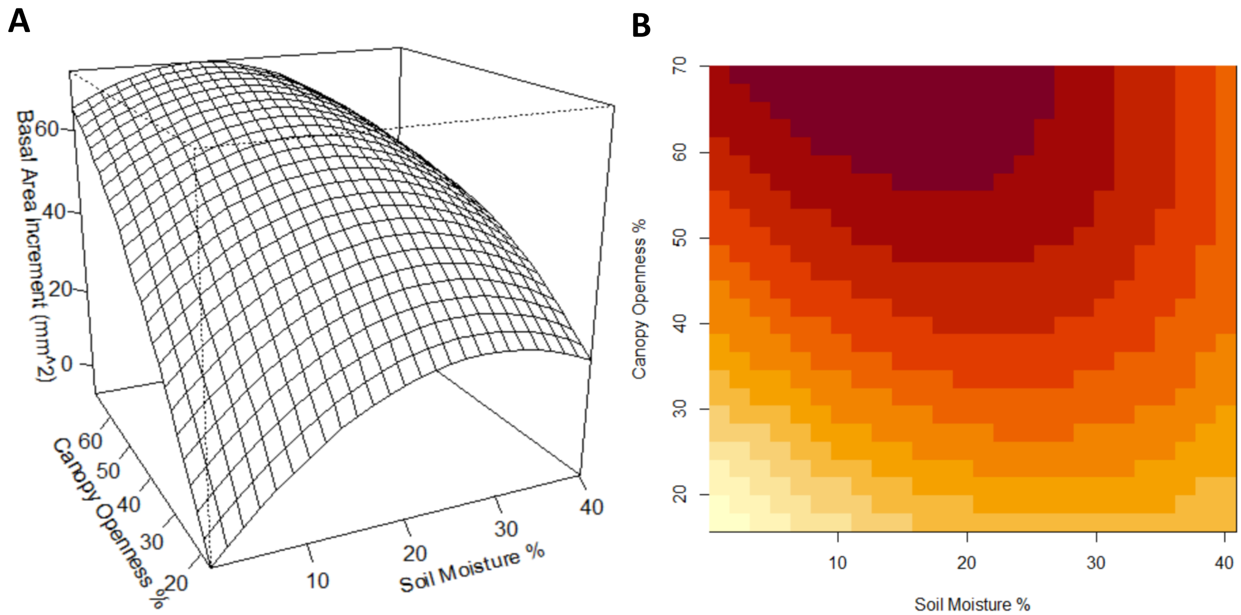

Figure 10: Response Surface of Grand Fir Basal Area Increment by Light:Soil Moisture Interaction. Response surface is depicted of basal area increment (BAI) by the interaction of light and soil moisture. (A) Response surface as a plane along the axes of BAI (mm^2), canopy openness %, and soil moisture %. (B) Heat map of BAI by canopy openness % and soil moisture %. Dark red areas indicate high BAI while light yellow areas indicate low BAI. BAI is highest when light is high and soil moisture is low to moderate. Figures were created using the R package “rsm” (Lenth 2009).

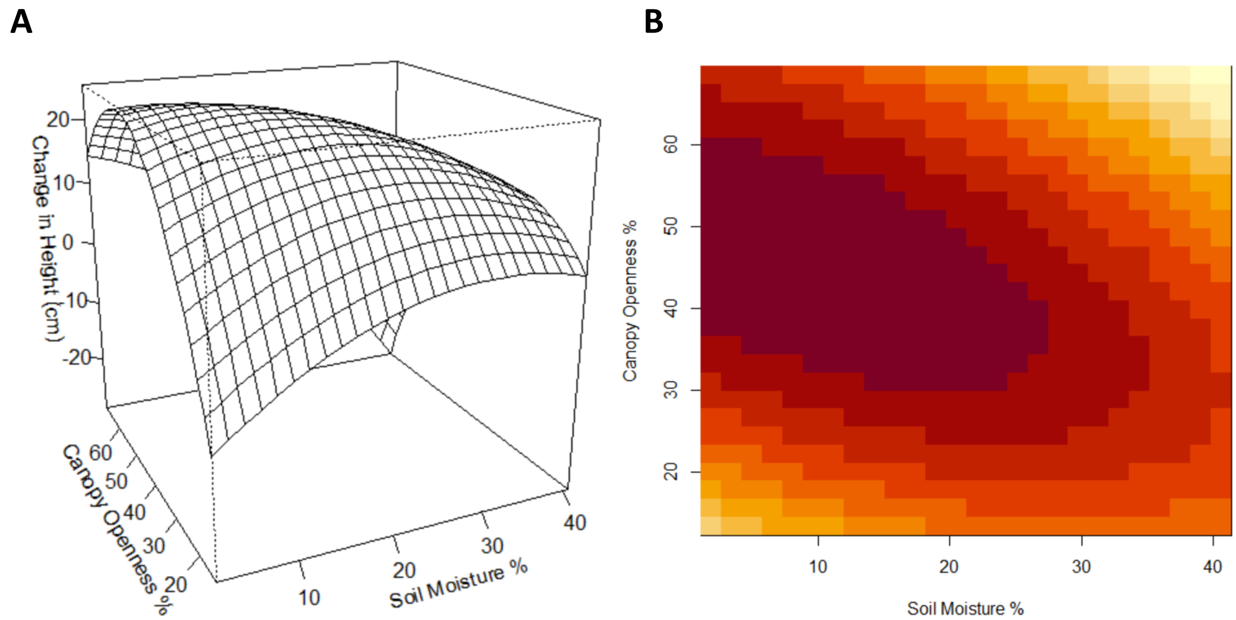

Figure 11: Response Surface of Douglas-fir Change in Height by Light:Soil Moisture Interaction. Response surface is depicted of change in height (cm) by the interaction of light and soil moisture. (A) Response surface as a plane along the axes of change in height (cm), canopy openness %, and soil moisture %. (B) Heat map of change in height by canopy openness % and soil moisture %. Dark red areas indicate high change in height while light yellow areas indicate low change in height. Change in height is highest when light is moderate to high and soil moisture is low to moderate. Figures were created using the R package “rsm” (Lenth 2009).

Supplemental Materials

Table S1: Average seedling size and health by species and gap size. Root collar diameter (mm), height (cm), and average health of seedlings of each species by gap size (ha).

Species	*Gap Size*	*N*	*Root Collar*	*Height*	*Health*
Red alder	0.05	17	11.66	155.1	3.1
	0.1	26	10.77	115.8	3.4
	0.25	54	12.24	140.2	3.4
	0.5	109	12.49	137.8	3.3
Western redcedar	0.05	12	10.87	71.8	3.8
	0.1	25	12.0	79.8	3.8
	0.25	60	11.75	81.5	3.7
	0.5	109	12.07	81.2	3.7
Western Hemlock	0.05	13	6.54	52.5	2.5
	0.1	26	8.75	72.1	2.5
	0.25	59	8.6	76.4	2.8
	0.5	112	9.01	76.1	3.0
Grand fir	0.05	16	9.18	41.1	3.8
	0.1	24	10.34	73.7	3.8
	0.25	59	9.49	54.3	3.5
	0.5	115	10.38	54.1	3.4
Douglas-fir	0.05	12	5.9	40.6	2.1
	0.1	28	6.7	47.4	2.7
	0.25	59	6.92	47.4	2.5
	0.5	116	7.71	51.8	2.8

Table S2: Average environmental conditions by gap size. Soil moisture (%), light (canopy openness %), vegetation cover (%), vegetation height above the height of the seedling (%), and browse (%) by gap size (ha).

Gap Size	*N*	*Soil Moisture %*	*Light %*	*Vegetation Cover %*	*Vegetation Height Above %*	*Browse %*
0.05	70	19.91	39.63	66.8	41.4	25.7
0.1	129	19.78	41.97	72.3	42.6	24
0.25	292	18.89	46.64	68.2	33.6	15.8
0.5	562	18.50	44.55	58.5	53	22.1

Table S3: Average environmental conditions by row. Soil moisture (%), light (canopy openness %), vegetation cover (%), vegetation height above the height of the seedling (%), and browse (%) by row.

Row	***N***	***Soil Moisture %***	***Light %***	***Vegetation Cover %***	***Vegetation Height Above %***	***Browse %***
A	305	22.07	50.12	73.6	42.6	24.9
B	211	17.78	38.64	66.7	40	14.2
C	387	17.61	43.98	59.9	49.9	18.3
D	150	17.09	42.59	47.2	50.7	28

Table S4: Red Alder Full Model Results. Initial results for red alder basal area increment (BAI) and change in height growth full models utilizing all environmental explanatory variables and biologically meaningful interaction terms.

Species	***Response***	***Variable***	***P-value***	***F-value***
Red alder	BAI	VegCov	0.821	0.381
		Soil Moisture	0.845	0.037
		Light	0.572	0.319
		DomVeg	0.525	0.891
		Browse	0.409	0.684
		VegHt	0.373	0.791
		GapSize	0.374	0.792
		VegCov:Light	0.854	0.335
		Soil Moisture:Light	0.0559	3.71
		Light:VegHt	0.036*	4.46
		VegCov:Soil Moisture	0.689	0.564
		Soil Moisture:VegHt	0.204	1.63
		Light:GapSize	0.632	0.230
	ΔHt	VegCov	0.197	1.53
		Soil Moisture	0.922	0.009
		Light	0.957	0.003
		DomVeg	0.151	1.53
		Browse	2.52e-05*	18.95
		VegHt	0.443	0.592
		GapSize	0.428	0.631
		VegCov:Light	0.199	1.52
		Soil Moisture:Light	0.929	0.008
		Light:VegHt	0.145	2.14
		VegCov:Soil Moisture	0.242	1.38
		Soil Moisture:VegHt	0.725	0.124
		Light:GapSize	0.521	0.414

Table S5: Western Redcedar Full Model Results. Initial results for western redcedar basal area increment (BAI) and change in height growth full models utilizing all environmental explanatory variables and biologically meaningful interaction terms.

Species	***Response***	***Variable***	***P-value***	***F-value***
Western redcedar	BAI	VegCov	0.845	0.347
		Soil Moisture	0.377	0.782
		Light	0.866	0.027
		DomVeg	0.023*	2.39
		Browse	0.017*	5.77
		VegHt	0.043*	4.15
		GapSize	0.114	2.52
		VegCov:Light	0.886	0.286
		Soil Moisture:Light	0.762	0.091
		Light:VegHt	0.422	0.646
		VegCov:Soil Moisture	0.218	1.46
		Soil Moisture:VegHt	0.221	1.51
		Light:GapSize	0.104	2.67
	ΔHt	VegCov	0.088	2.06
		Soil Moisture	0.613	0.257
		Light	0.849	0.036
		DomVeg	0.464	0.957
		Browse	0.065	3.44
		VegHt	0.117	2.47
		GapSize	0.608	0.264
		VegCov:Light	0.091	0.044
		Soil Moisture:Light	0.567	0.329
		Light:VegHt	0.591	0.289
		VegCov:Soil Moisture	0.851	0.339
		Soil Moisture:VegHt	0.296	1.09
		Light:GapSize	0.592	0.287

Table S6: Western Hemlock Full Model Results. Initial results for western hemlock basal area increment (BAI) and change in height growth full models utilizing all environmental explanatory variables and biologically meaningful interaction terms.

Species	***Response***	***Variable***	***P-value***	***F-value***
Western hemlock	BAI	VegCov	0.017	3.15
		Soil Moisture	0.819	0.05
		Light	0.535	0.386
		DomVeg	0.870	0.446
		Browse	0.181	1.81
		VegHt	0.66	0.193
		GapSize	0.280	1.17
		VegCov:Light	0.805	0.65
		Soil Moisture:Light	0.860	0.03
		Light:VegHt	0.890	0.191
		VegCov:Soil Moisture	0.735	2.12
		Soil Moisture:VegHt	0.646	0.211
		Light:GapSize	0.714	0.135
	ΔHt	VegCov	0.0235	2.94
		Soil Moisture	0.891	0.018
		Light	0.42	0.654
		DomVeg	0.622	0.759
		Browse	0.043	4.17
		VegHt	0.714	0.134
		GapSize	0.998	0
		VegCov:Light	0.883	0.53
		Soil Moisture:Light	0.705	0.144
		Light:VegHt	0.221	1.51
		VegCov:Soil Moisture	0.819	2.3
		Soil Moisture:VegHt	0.817	0.053
		Light:GapSize	0.294	0.294

Table S7: Grand Fir Full Model Results. Initial results for grand fir basal area increment (BAI) and change in height growth full models utilizing all environmental explanatory variables and biologically meaningful interaction terms.

Species	*Response*	*Variable*	*P-value*	*F-Value*
Grand fir	BAI	VegCov	0.588	0.708
		Soil Moisture	0.110	2.58
		Light	0.848	0.036
		DomVeg	0.178	1.47
		Browse	0.479	0.503
		VegHt	0.171	0.062
		GapSize	0.986	0.0002
		VegCov:Light	0.663	0.6006
		Soil Moisture:Light	0.176	1.85
		Light:VegHt	0.775	0.082
		VegCov:Soil Moisture	0.079	2.14
		Soil Moisture:VegHt	0.522	0.41
		Light:GapSize	0.882	0.022
	ΔHt	VegCov	0.614	0.670
		Soil Moisture	0.132	2.29
		Light	0.427	0.632
		DomVeg	0.563	0.846
		Browse	0.654	0.209
		VegHt	0.076	3.19
		GapSize	0.054	3.77
		VegCov:Light	0.664	0.598
		Soil Moisture:Light	0.177	1.83
		Light:VegHt	0.115	2.51
		VegCov:Soil Moisture	0.400	1.01
		Soil Moisture:VegHt	0.305	1.06
		Light:GapSize	0.026	5.02

Table S8: Douglas-fir Full Model Results. Initial results for Douglas-fir basal area increment (BAI) and change in height growth full models utilizing all environmental explanatory variables and biologically meaningful interaction terms.

Species	*Response*	*Variable*	*P-value*	*F-Value*
Douglas-fir	BAI	VegCov	0.96	0.155
		Soil Moisture	0.979	0.0007
		Light	0.617	0.251
		DomVeg	0.849	0.477
		Browse	0.181	1.80
		VegHt	0.905	0.014
		GapSize	0.571	0.323
		VegCov:Light	0.986	0.087
		Soil Moisture:Light	0.727	0.129
		Light:VegHt	0.561	0.339
		VegCov:Soil Moisture	0.870	0.311
		Soil Moisture:VegHt	0.682	0.168
		Light:GapSize	0.421	0.649
	ΔHt	VegCov	0.553	0.759
		Soil Moisture	0.947	0.004
		Light	0.733	0.116
		DomVeg	0.900	0.362
		Browse	0.378	0.782
		VegHt	0.761	0.093
		GapSize	0.944	0.005
		VegCov:Light	0.923	0.225
		Soil Moisture:Light	0.082	3.07
		Light:VegHt	0.204	1.63
		VegCov:Soil Moisture	0.575	0.727
		Soil Moisture:VegHt	0.229	1.46
		Light:GapSize	0.683	0.167

Table S9: Red Alder Basal Area Increment Backwards Stepwise Regression by AIC. Steps 1-7 of the backwards stepwise regression by AIC of red alder basal area increment (mm^2). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 ***AIC: -366***	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	DomVegOrder	18.032	-373.44
	VegCov:Light	17.323	-372.20
	VegCov:Soil Moisture	17.605	-369.79
	Light:Gap Size	17.202	-367.98
	Browse	17.249	-367.49
	None	17.200	-366.00
	Soil Moisture:VegHt	17.478	-365.10
	Soil Moisture:Light	17.631	-363.52
	Light:VegHt	17.735	-362.46
Step 2 ***AIC: -373***	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + VegCov:Light + Soil Moisture:Light + Light:VegHt + VegCov:Soil Moisture + Soil Moisture:VegHt + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	18.250	-379.27
	VegCov:Soil Moisture	18.413	-377.67
	Light:Gap Size	18.038	-375.39
	Browse	18.098	-374.79
	None	18.032	-373.44
	Soil Moisture:VegHt	18.279	-372.98
	Light:VegHt	18.463	-371.18
	Soil Moisture:Light	18.727	-378.61
Step 3 ***AIC: -379***	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + VegCov:Soil Moisture + Soil Moisture:VegHt + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	18.504	-384.77
	Light:Gap Size	18.278	-380.99
	Browse	18.321	-380.57
	None	18.250	-379.27
	Soil Moisture:VegHt	18.570	-378.13
	Light:VegHt	18.691	-376.96
	Soil Moisture:Light	18.933	-374.62
Step 4 ***AIC: -384***	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt + Light:Gap Size		

	Variable Removed	RSS	AIC
	VegCov	18.643	-391.42
	Light:Gap Size	18.514	-386.68
	Browse	18.608	-385.76
	None	18.504	-384.77
	Soil Moisture:VegHt	18.860	-383.33
	Light:VegHt	19.009	-381.90
	Soil Moisture:Light	19.563	-376.70
Step 5 ***AIC: -391***	BAI ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	18.644	-393.41
	Browse	18.745	-392.43
	None	18.643	-391.42
	Soil Moisture:VegHt	18.960	-390.37
	Light:VegHt	19.136	-388.70
	Soil Moisture:Light	19.798	-382.54
Step 6 ***AIC: -393***	BAI ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	Browse	18.750	-394.38
	None	18.644	-393.41
	Soil Moisture:VegHt	18.960	-392.37
	Light:VegHt	19.142	-390.64
	Gap Size	19.330	-388.86
	Soil Moisture:Light	19.800	-384.52
Step 7 ***AIC: -394***	BAI ~ Soil Moisture + Light + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	None	18.750	**-394.38**
	Soil Moisture:VegHt	19.068	-393.34
	Light:VegHt	10.290	-391.24
	Gap Size	19.437	-389.87
	Soil Moisture:Light	19.952	-385.13

Table S10: Red Alder Change in Height Backwards Stepwise Regression by AIC. Steps 1-8 of the = backwards stepwise regression by AIC of red alder change in height (cm). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 1311	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:Light	169839	1308.8
	Soil Moisture:VegHt	169975	1308.9
	Light:Gap Size	170315	1309.3
	DomVeg	184171	1309.5
	VegCov:Soil Moisture	176316	1309.6
	VegCov:Light	176956	1310.2
	None	169830	1310.8
	Light:VegHt	172343	1311.4
	Browse	192027	1331.0
Step 2 AIC:1309	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov +Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	169977	1306.9
	Light:Gap Size	170322	1307.3
	DomVeg	184218	1307.5
	VegCov:Soil Moisture	176522	1307.8
	None	169839	1308.8
	VegCov:Light	177557	1308.8
	Light:VegHt	172434	1309.5
	Browse	190257	1329.0
Step 3 AIC: 1307	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov +Light:VegHt + Soil Moisture:VegCov + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	170416	1305.4
	DomVeg	184246	1305.5
	VegCov:Soil Moisture	177250	1306.5
	VegCov:Light	177628	1306.9
	None	169977	1306.9
	Light:VegHt	172435	1307.5
	Browse	192179	1327.2
Step 4 AIC: 1305	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov +Light:VegHt + Soil Moisture:VegCov + Gap Size		

	Variable Removed	RSS	AIC
	Gap Size	170957	1304.0
	DomVeg	185330	1304.6
	VegCov:Light	177640	1304.9
	VegCov:Soil Moisture	177940	1305.2
	None	170416	1305.4
	Light:VegHt	172635	1305.7
	Browse	193904	1326.8
Step 5 ***AIC: 1304***	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov +Light:VegHt + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	DomVeg	186110	1303.3
	VegCov:Soil Moisture	178286	1303.6
	Light:VegHt	172786	1303.9
	None	170957	1304.0
	VegCov:Light	177039	1304.3
	Browse	196477	1327.2
Step 6 ***AIC: 1303***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov + Light:VegHt + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	193145	1302.1
	VegCov:Soil Moisture	193587	1302.5
	Light:VegHt	187838	1303.0
	None	186110	1303.3
	Browse	209631	1322.9
Step 7 ***AIC: 1302***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	Light:VegHt	194165	1301.0
	None	193145	1302.1
	VegCov:Soil Moisture	203160	1303.2
	Browse	213670	1318.3
Step 8 ***AIC: 1299***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	None	199275	1299.7
	VegCov:Soil Moisture	209375	1300.7
	VegHt	203573	1301.6
	Light	210141	1307.3
	Browse	218355	1314.3

Table S11: Western redcedar Basal Area Increment Backwards Stepwise Regression by AIC. Steps 1-5 of the backwards stepwise regression by AIC of western redcedar basal area increment (mm^2). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 434	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	12.738	-440.38
	Soil Moisture:Light	12.650	-435.68
	Light:VegHt	12.696	-434.99
	VegCov:Soil Moisture	13.127	-434.75
	Soil Moisture:VegHt	12.768	-433.94
	None	12.642	-433.79
	Light:Gap Size	12.864	-432.53
	Browse	13.123	-428.81
	DomVeg	14.037	-428.22
Step 2 AIC: -440	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:Light	12.744	-442.29
	Light:VegHt	12.798	-441.50
	VegCov:Soil Moisture	13.226	-441.34
	Soil Moisture:VegAB	12.873	-440.42
	None	12.738	-440.38
	Light:Gap Size	13.042	-437.96
	Browse	13.186	-435.92
	DomVeg	14.138	-434.88
Step 3 AIC: -442	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:VegHt	12.801	-443.45
	VegCov:Soil Moisture	13.233	-443.25
	None	12.744	-442.29
	Soil Moisture:VegHt	12.889	-442.18
	Light:Gap Size	13.043	-439.96
	Browse	13.199	-437.73
	DomVeg	14.240	-435.54

Step 4 AIC: -443	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	13.281	-444.57
	None	12.801	-443.45
	Soil Moisture:VegAB	13.018	-442.31
	Light:Gap Size	13.059	-441.72
	Browse	13.291	-438.43
	DomVeg	14.445	-434.86
Step 5 AIC: -447	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	None	13.540	-446.96
	VegCov	14.173	-446.41
	Soil Moisture:VegHt	13.728	-446.38
	Light:Gap Size	13.882	-444.30
	Browse	14.238	-439.56
	DomVeg	15.392	-436.99

Table S12: Western redcedar Change in Height Backwards Stepwise Regression by AIC. Steps 1-8 of the backwards stepwise regression by AIC of western redcedar change in height (cm). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 1104	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	47431	1097.2
	DomVeg	49083	1097.6
	Light:Gap Size	47100	1101.9
	Light:VegHt	47101	1101.9
	Soil Moisture:Light	47113	1102.0
	Soil Moisture:VegHt	47350	1102.9
	None	47011	1103.5
	VegCov:Light	49541	1105.4
	Browse	48077	1105.8
Step 2 AIC: 1097	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size + Light:VegCov		
	Variable Removed	**RSS**	**AIC**
	DomVeg	49788	1092.3
	Light:VegHt	47522	1095.6
	Light:Gap Size	47534	1095.6
	Soil Moisture:Light	47597	1095.9
	Soil Moisture:VegHt	47804	1096.7
	None	47431	1097.2
	Browse	48263	1098.5
	VegCov:Light	49998	1099.1
Step 3 AIC: 1092	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Gap Size + Light:Gap Size + Light:VegCov + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:Light	49836	1090.5
	Light:Gap Size	49922	1090.8
	Light:VegHt	50014	1091.1
	Soil Moisture:VegHt	50038	1091.2
	None	49788	1092.3
	Browse	50734	1093.8
	VegCov:Light	53371	1095.1
Step 4 AIC: 1090	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegHt + Gap Size + Light:Gap Size + Light:VegCov + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**

	Light:Gap Size	49970	1089.0
	Soil Moisture:VegHt	50077	1089.4
	Light:VegHt	50087	1089.4
	None	49836	1090.5
	Browse	50762	1091.9
	VegCov:Light	53139	1094.5
Step 5 AIC: 1089	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegHt + Gap Size + Light:VegCov + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	Gap Size	50042	1087.2
	Light:VegHt	50153	1087.7
	Soil Moisture:VegHt	50255	1088.0
	None	49970	1089.0
	Browse	50860	1090.3
	VegCov:Light	53157	1092.5
Step 6 AIC: 1087	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov + Light:VegHt + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	Light:VegHt	50245	1086.0
	Soil Moisture:VegHt	50280	1086.1
	None	50042	1087.2
	Browse	50976	1088.7
	VegCov:Light	53464	1091.6
Step 7 AIC: 1086	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov + Soil Moisture:VegHt		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	50625	1085.4
	None	50245	1086.0
	Browse	51110	1087.2
	VegCov:Light	54218	1092.2
Step 8 AIC: 1085	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov		
	Variable Removed	**RSS**	**AIC**
	None	50625	1085.4
	VegHt	51331	1086.0
	Browse	51637	1087.1
	VegCov:Light	54767	1092.1

Table S13: Western hemlock Basal Area Increment Backwards Stepwise Regression by AIC. Steps 1-9 of the backwards stepwise regression by AIC of western hemlock basal area increment (mm^2). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 ***AIC: 1080***	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	DomVeg	254702	1070.8
	VegCov:Light	248095	1075.2
	Light:Gap Size	245706	1077.9
	Light:VegHt	245708	1077.9
	Soil Moisture:VegHt	246083	1078.1
	Soil Moisture:Light	246283	1078.2
	None	245701	1079.9
	Browse	249706	1080.1
Step 2 ***AIC: 1066***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegCov + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	259771	1061.3
	Soil Moisture:VegHt	256431	1063.7
	Light:Gap Size	256448	1063.7
	Soil Moisture:Light	256522	1063.8
	Light:VegHt	257477	1064.3
	None	256423	1065.7
	Browse	262523	1066.9
Step 3 ***AIC: 1057***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:Light	262253	1054.8
	Soil Moisture:VegHt	262353	1054.8
	Light:Gap Size	262447	1054.9
	Light:VegHt	263131	1055.2
	None	262172	1056.7
	Browse	267140	1057.3
	VegCov	290544	1062.7
Step 4 ***AIC: 1055***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	262497	1052.9

	Light:Gap Size	262506	1052.9
	Light:VegHt	263150	1053.2
	None	262253	1054.8
	Browse	267239	1055.3
	VegCov	290548	1060.7
Step 5 AIC: 1053	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	262732	1051.0
	Light:VegHt	263317	1051.3
	Soil Moisture	263526	1051.4
	None	262497	1052.9
	Browse	267283	1053.3
	VegCov	290693	1058.8
Step 6 AIC: 1051	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:VegHt + Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:VegHt	263402	1049.3
	Soil Moisture	263687	1049.5
	None	262732	1051
	Browse	267422	1051.4
	Gap Size	273413	1054.4
	VegCov	291029	1056.9
Step 7 AIC: 1049	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light	263449	1047.4
	Soil Moisture	264257	1047.8
	None	263402	1049.3
	Browse	268059	1049.7
	Gap Size	275796	1053.6
	VegCov	294268	1056.4
	VegHt	294269	1062.4
Step 8 AIC: 1047	ΔHt ~ VegCov + Soil Moisture + Browse + VegHt + Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture	264309	1045.8
	None	263449	1047.4
	Browse	268214	1047.8
	Gap Size	276684	1052.0
	VegCov	294300	1054.4
	VegHt	296712	1061.5
Step 9	ΔHt ~ VegCov + Browse + VegHt + Gap Size		

AIC: 1046

Variable Removed	RSS	AIC
None	264309	1045.8
Browse	268426	1045.9
Gap Size	278854	1051.1
VegCov	297662	1054.0
VegHt	299117	1060.7

Table S14: Western hemlock Change in Height Backwards Stepwise Regression by AIC. Steps 1-8 of the backwards stepwise regression by AIC of western hemlock change in height (cm). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 ***AIC: 927***	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size + VegCov:Light + VegCov:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	DomVeg	79712	918.80
	VegCov:Soil Moisture	77439	921.41
	VegCov:Light	78233	922.86
	Soil Moisture:VegHt	76280	924.25
	Soil Moisture:Light	76489	925.19
	Light:VegHt	76986	926.04
	Browse	77005	926.10
	Light:Gap Size	77100	926.27
	None	76277	926.81
Step 2 ***AIC: 919***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt + Light:Gap Size + VegCov:Light + VegCov:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	81299	915.48
	VegCov:Soil Moisture	81649	916.06
	Soil Moisture:VegHt	79721	916.81
	Soil Moisture:Light	79790	916.93
	Light:VegHt	79939	917.19
	Light:Gap Size	80244	917.70
	Browse	80788	918.62
	None	79712	918.80
Step 3 ***AIC: 910***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt + Light:Gap Size + VegCov:Light		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	83907	907.77
	Soil Moisture:Light	81712	908.17
	Soil Moisture:VegHt	81724	908.19
	Light:Gap Size	81968	908.59
	Light:VegHt	82014	908.67
	None	81711	910.17
	Browse	84036	911.98
Step 4 ***AIC: 908***	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:VegHt + Soil Moisture:VegHt + Light:Gap Size		

	Variable Removed	RSS	AIC
	Soil Moisture:Light	83928	905.81
	Soil Moisture:VegHt	84025	905.97
	Light:VegHt	84259	906.34
	Light:Gap Size	84629	906.94
	None	83907	907.77
	Browse	87620	911.66
	VegCov	95049	916.73
Step 5 AIC: 904	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Soil Moisture:VegHt + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	86657	902.16
	Soil Moisture:Light	86700	902.23
	Light:Gap Size	87011	902.71
	None	86452	903.84
	Browse	90028	907.35
	VegCov	99529	914.99
Step 6 AIC: 902	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Soil Moisture:Light + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:Light	86825	900.42
	Light:Gap Size	87210	901.02
	None	86657	902.16
	Browse	90358	905.85
	VegCov	99695	913.22
	VegHt	103588	924.43
Step 7 AIC: 900	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	87409	899.34
	None	86825	900.42
	Soil Moisture	88817	901.51
	Browse	90375	903.87
	VegCov	99733	911.27
	VegHt	103857	922.78
Step 8 AIC: 899	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size		
	Variable Removed	**RSS**	**AIC**
	None	87409	899.34
	Soil Moisture	89267	900.19
	Light	90089	901.44
	Browse	91107	902.97
	VegCov	100496	910.31

Gap Size	96234	910.42
VegHt	104258	921.31

Table S15: Grand fir Basal Area Increment Backwards Stepwise Regression by AIC. Steps 1-9 of the backwards stepwise regression by AIC of grand fir basal area increment (mm^2). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 1237	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	163587	1231.8
	Light:Gap Size	160732	1234.8
	Light:VegHt	160804	1234.9
	DomVeg	174687	1234.9
	Soil Moisture:VegHt	161199	1235.3
	Browse	161310	1235.4
	None	160706	1236.8
	Soil Moisture:Light	168310	1237.1
	Soil Moisture:VegCov	170978	1239.3
Step 2 AIC: 1232	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	DomVeg	177535	1229.7
	Light:VegHt	163607	1229.8
	Light:Gap Size	163629	1229.8
	Soil Moisture:VegHt	163947	1230.2
	Browse	164486	1230.7
	None	163587	1231.8
	Soil Moisture:Light	166042	1232.3
	VegCov:Soil Moisture	179058	1239.1
Step 3 AIC: 1230	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	177549	1227.7
	Light:VegHt	177610	1227.8
	Light:Gap Size	177811	1228.0
	Browse	178059	1228.2
	None	177535	1229.7
	Soil Moisture:Light	181926	1231.8
	VegCov:Soil Moisture	196229	1238.7
Step 4 AIC: 1225	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + Light:Gap Size		

	Variable Removed	RSS	AIC
	Light:VegHt	180943	1222.9
	Light:Gap Size	181084	1223.1
	Browse	181287	1223.2
	None	180866	1224.8
	Soil Moisture:Light	185151	1226.8
	VegCov:Soil Moisture	200355	1234.2
Step 5 AIC: 1223	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Soil Moisture:VegCov + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	181121	1221.1
	Browse	181351	1221.3
	VegHt	182236	1222.1
	None	180943	1222.9
	Soil Moisture:Light	185169	1224.8
	VegCov:Soil Moisture	200466	1232.3
Step 6 AIC: 1221	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	Gap Size	181164	1219.1
	Browse	181660	1219.6
	VegHt	182391	1220.3
	None	181121	1221.1
	Soil Moisture:Light	185845	1223.5
	VegCov:Soil Moisture	201152	1230.9
Step 7 AIC: 1219	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Light:Soil Moisture + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	Browse	181763	1217.7
	VegHt	182413	1218.2
	None	181164	1219.1
	Soil Moisture:Light	185875	1221.5
	VegCov:Soil Moisture	201164	1228.9
Step 8 AIC: 1218	BAI ~ VegCov + Soil Moisture + Light + VegHt + Light:Soil Moisture + Soil Moisture:VegCov		
	Variable Removed	**RSS**	**AIC**
	VegHt	182939	1216.8
	None	181763	1217.7
	Soil Moisture:Light	186611	1220.2
	VegCov:Soil Moisture	201175	1226.9
Step 9 AIC: 1217	BAI ~ VegCov + Soil Moisture + Light + Light:Soil Moisture + Soil Moisture:VegCov		
	None	182939	1216.8

Soil Moisture:Light	188015	1219.4
VegCov:Soil Moisture	201706	1225.4

Table S16: Grand fir Change in Height Backwards Stepwise Regression by AIC. Steps 1-6 of the backwards stepwise regression by AIC of grand fir change in height (cm). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 1053	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	DomVeg	62103	1047.1
	VegCov:Light	59714	1048.5
	VegCov:Soil Moisture	60629	1051.0
	Browse	58728	1051.6
	Soil Moisture:Light	58812	1051.9
	Soil Moisture:VegHt	58828	1051.9
	None	58617	1053.3
	Light:Gap Size	59704	1054.4
	Light:VegHt	59898	1055.0
Step 2 AIC: 1047	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	63534	1043.0
	VegCov:Soil Moisture	64297	1045.0
	Soil Moisture:VegHt	62322	1045.7
	Soil Moisture:Light	62354	1045.8
	Browse	62431	1046.0
	None	62103	1047.1
	Light:VegHt	62940	1047.4
	Light:Gap Size	63128	1047.9
Step 3 AIC: 1043	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Browse	63703	1041.5
	Soil Moisture:Light	63790	1041.7
	Soil Moisture:VegHt	63855	1041.9
	Light:VegHt	64133	1042.6
	Light:Gap Size	64269	1043.0
	None	63534	1043.0
	VegCov:Soil Moisture	66855	1043.7
Step 4 AIC: 1041	ΔHt ~ VegCov + Soil Moisture + Light + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		

	Variable Removed	RSS	AIC
	Soil Moisture:Light	63959	1040.1
	Soil Moisture:VegHt	64040	1040.3
	Light:Gap Size	64321	1041.1
	Light:VegHt	64326	1041.1
	None	63703	1041.5
	VegCov:Soil Moisture	67260	1042.7
Step 5 AIC: 1040	ΔHt ~ VegCov + Soil Moisture + Light + VegHt + Gap Size + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	64213	1038.8
	Light:VegHt	64586	1039.8
	None	63959	1040.1
	Light:Gap Size	64847	1040.5
	VegCov:Soil Moisture	67308	1040.8
Step 6 AIC: 1039	ΔHt ~ VegCov + Soil Moisture + Light + VegHt + Gap Size + Light:VegHt + Soil Moisture:VegCov + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	None	64213	1038.8
	Light:VegHt	65130	1039.2
	Light:Gap Size	65203	1039.4
	VegCov:Soil Moisture	67867	1040.2

Table S17: Douglas-fir Basal Area Increment Backwards Stepwise Regression by AIC. Steps 1-10 of the backwards stepwise regression by AIC of Douglas-fir basal area increment (mm^2). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: 65.2	BAI ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegHt + Gap Size + Light:Gap Size + VegCov:Light + VegCov:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	DomVeg	147.57	54.561
	VegCov:Light	145.32	58.273
	VegCov:Soil Moisture	146.11	59.080
	Soil Moisture:VegHt	144.43	63.355
	Light:VegHt	144.46	63.386
	Soil Moisture:Light	144.47	63.404
	Light:Gap Size	144.83	63.768
	Browse	145.71	64.670
	None	144.27	65.198
Step 2 AIC: 54.6	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	148.86	47.863
	VegCov:Soil Moisture	150.07	49.070
	Soil Moisture:Light	147.71	52.700
	Soil Moisture:VegHt	147.86	52.859
	Light:VegHt	147.93	52.926
	Light:Gap Size	147.97	52.965
	None	147.57	54.561
	Browse	150.36	55.354
Step 3 AIC: 47.9	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	152.40	43.364
	Soil Moisture:Light	148.94	45.939
	Light:VegHt	149.09	46.091
	Soil Moisture:VegHt	149.12	46.122
	Light:Gap Size	149.36	46.361
	None	148.86	47.863
	Browse	151.78	48.750
Step 4 AIC: 43.4	BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + VegHt:Soil Moisture + Light:Gap Size		

Variable Removed	RSS	AIC
Soil Moisture:Light	152.40	41.365
Light:VegHt	152.50	41.455
Soil Moisture:VegHt	152.69	41.645
Light:Gap Size	153.07	42.012
VegCov	160.59	43.165
None	152.40	43.364
Browse	155.00	43.880

Step 5 AIC: 41.4 BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:VegHt + VegHt:Soil Moisture + Light:Gap Size

Variable Removed	RSS	AIC
Light:VegHt	152.50	39.457
Soil Moisture:VegHt	152.69	39.649
Light:Gap Size	153.07	40.020
VegCov	160.63	41.202
None	152.40	41.365
Browse	155.00	41.882

Step 6 AIC: 39.5 BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + VegHt:Soil Moisture + Light:Gap Size

Variable Removed	RSS	AIC
Soil Moisture:VegHt	152.81	37.763
Light:Gap Size	153.10	38.044
VegCov	160.91	39.453
None	152.50	39.457
Browse	155.19	40.069

Step 7 AIC: 37.8 BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Gap Size

Variable Removed	RSS	AIC
Light:Gap Size	153.56	36.497
None	152.81	37.763
VegCov	161.85	38.324
Browse	155.67	38.523
VegHt	160.31	42.901

Step 8 AIC: 36.5 BAI ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size

Variable Removed	RSS	AIC
Light	153.67	34.598
Gap Size	154.31	35.222
None	153.56	36.497
Browse	156.18	37.009
VegCov	163.39	37.736
VegHt	160.91	41.457

Step 9 BAI ~ VegCov + Soil Moisture + Browse + VegHt + Gap Size

AIC: 34.6			
	Variable Removed	**RSS**	**AIC**
	Gap Size	154.57	33.470
	None	153.67	34.598
	Browse	156.21	35.045
	VegCov	164.14	36.421
	VegHt	161.57	40.072
Step 10 ***AIC: 33.5***	BAI ~ VegCov + Soil Moisture + Browse + VegHt		
	Variable Removed	**RSS**	**AIC**
	None	154.57	33.470
	Browse	157.18	33.959
	VegCov	165.75	33.874
	VegHt	161.93	38.398

Table S18: Douglas-fir Change in Height Backwards Stepwise Regression by AIC. Steps 1-9 of the backwards stepwise regression by AIC of Douglas-fir change in height (cm). Each step includes residual sums of squares (RSS) values and AIC scores for each model where the listed variable was removed. Models with the lowest AIC scores were progressed to the next step. Stepwise regression was stopped when the AIC score no longer improved.

Step 1 AIC: -183	ΔHt ~ VegCov + Soil Moisture + Light + DomVeg + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	DomVeg	21.983	-192.61
	VegCov:Light	21.719	-190.21
	VegCov:Soil Moisture	22.135	-187.71
	Light:Gap Size	21.567	-185.13
	Browse	21.695	-184.35
	Soil Moisture:VegHt	21.835	-183.50
	None	21.533	-183.34
	Light:VegHt	21.871	-183.29
	Soil Moisture:Light	22.170	-181.50
Step 2 AIC: -193	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + VegCov:Light + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Light	22.362	-198.36
	VegCov:Soil Moisture	22.257	-197.38
	Light:Gap Size	22.005	-194.48
	Soil Moisture:VegHt	22.248	-193.03
	Browse	22.252	-193.01
	None	21.983	-192.61
	Light:VegHt	22.405	-192.11
	Soil Moisture:Light	22.593	-191.00
Step 3 AIC: -198	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + Soil Moisture:VegCov + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	VegCov:Soil Moisture	23.044	-202.39
	Light:Gap Size	22.423	-200.00
	Soil Moisture:VegHt	22.671	-198.54
	None	22.362	-198.36
	Light:VegHt	22.713	-198.30
	Browse	22.750	-198.09
	Soil Moisture:Light	23.211	-195.44
Step 4 AIC: -202	ΔHt ~ VegCov + Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + VegHt:Soil Moisture + Light:Gap Size		

	Variable Removed	**RSS**	**AIC**
	VegCov	23.748	-206.42
	Light:Gap Size	23.153	-203.77
	Light:VegHt	23.189	-203.57
	Soil Moisture:VegHt	23.312	-202.87
	Browse	23.346	-202.67
	None	23.044	-202.39
	Soil Moisture:Light	22.663	-200.89
Step 5 AIC: -206	ΔHt ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + VegHt:Soil Moisture + Light:Gap Size		
	Variable Removed	**RSS**	**AIC**
	Light:Gap Size	23.969	-207.20
	Light:VegHt	23.972	-207.18
	Browse	23.989	-207.09
	Soil Moisture:VegHt	24.005	-207.00
	None	23.748	-206.42
	Soil Moisture:Light	24.418	-204.75
Step 6 AIC: -207	ΔHt ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + Light:VegHt + VegHt:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	Light:VegHt	24.119	-208.38
	Soil Moisture:VegHt	24.136	-208.28
	Browse	24.165	-208.12
	None	23.969	-207.20
	Soil Moisture:Light	24.570	-205.93
	Gap Size	24.609	-205.72
Step 7 AIC: -208	ΔHt ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture + VegHt:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	Soil Moisture:VegHt	24.252	-209.65
	Browse	24.338	-209.18
	None	24.119	-208.38
	Gap Size	24.764	-206.89
	Soil Moisture:Light	24.915	-206.09
Step 8 AIC: -210	ΔHt ~ Soil Moisture + Light + Browse + VegHt + Gap Size + Light:Soil Moisture		
	Variable Removed	**RSS**	**AIC**
	Browse	24.450	-210.57
	None	24.252	-209.65
	VegHt	24.623	-209.64
	Gap Size	24.927	-208.03
	Soil Moisture:Light	25.091	-207.16
Step 9	ΔHt ~ Soil Moisture + Light + VegHt + Gap Size + Light:Soil Moisture		

AIC: -211

Variable Removed	**RSS**	**AIC**
None	24.450	-210.57
VegHt	24.833	-210.52
Gap Size	25.140	-208.90
Soil Moisture:Light	25.232	-208.42

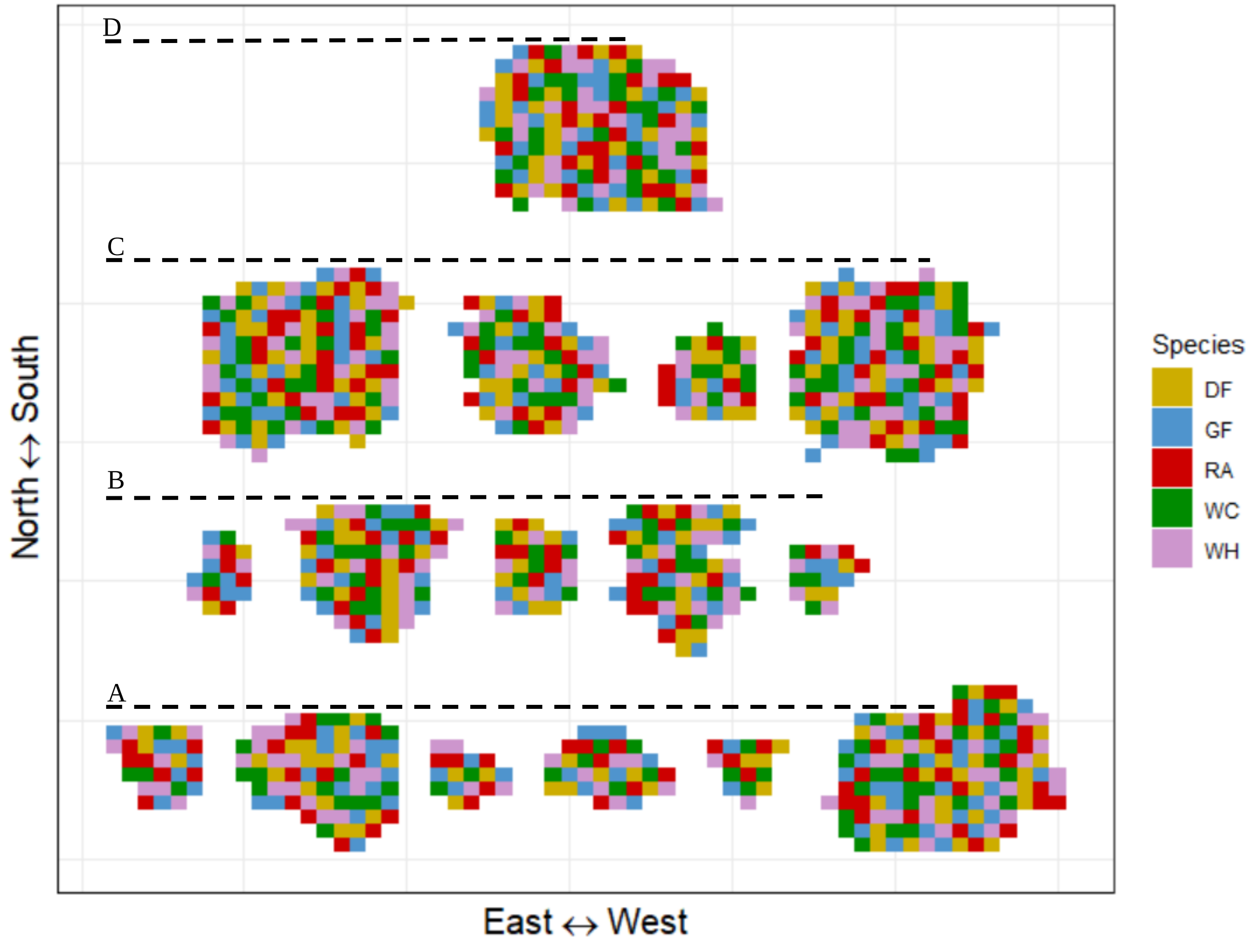

Figure S1: Species distribution of seedlings across the study site. Random distribution of center seedling species across the study site with Douglas-fir (yellow), grand fir (blue), red alder (red), western redcedar (green), and western hemlock (purple).

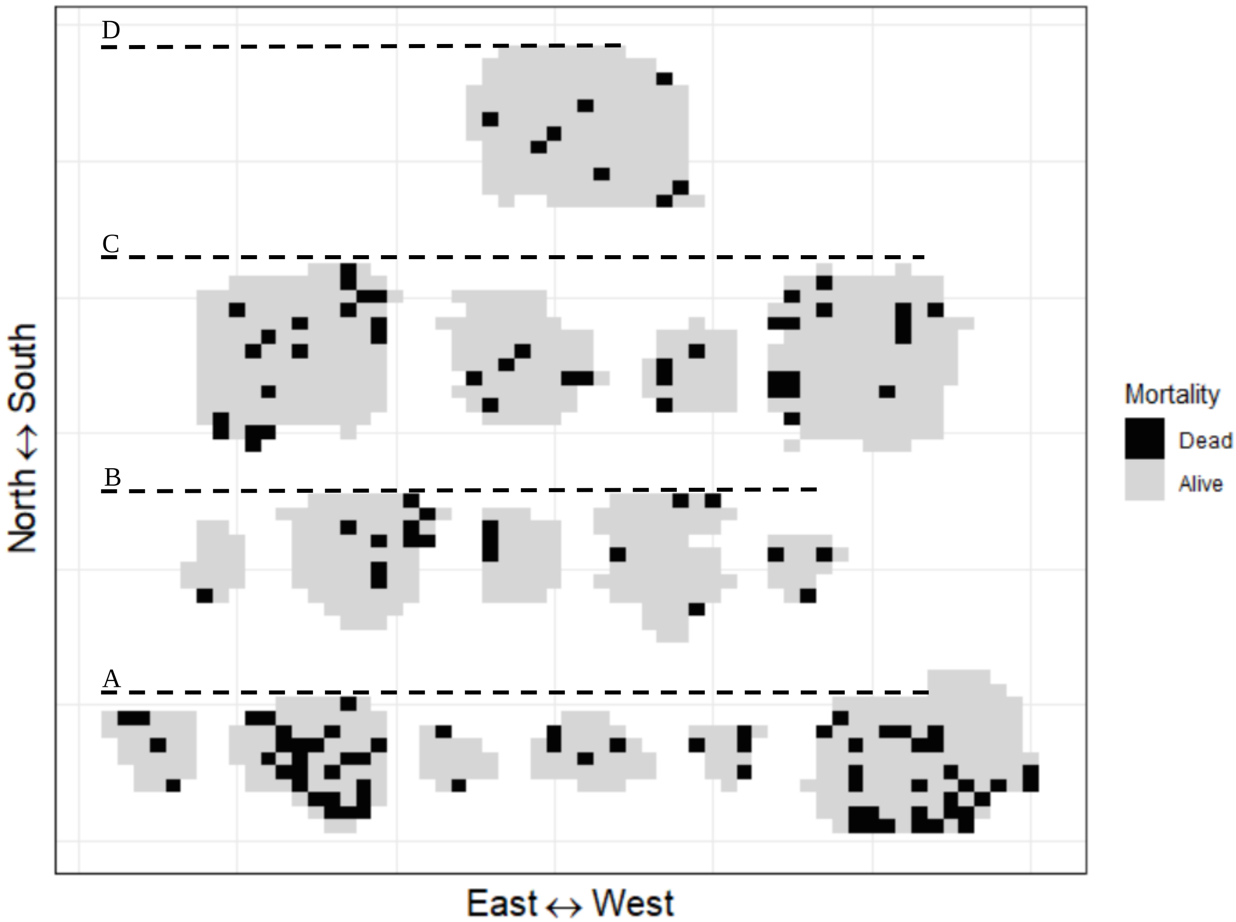

Figure S2: Distribution of seedling mortality across the study site. Seedling mortality through the 2-year experiment is marked in black while surviving seedlings are marked in grey. Mortality was highest in row A.

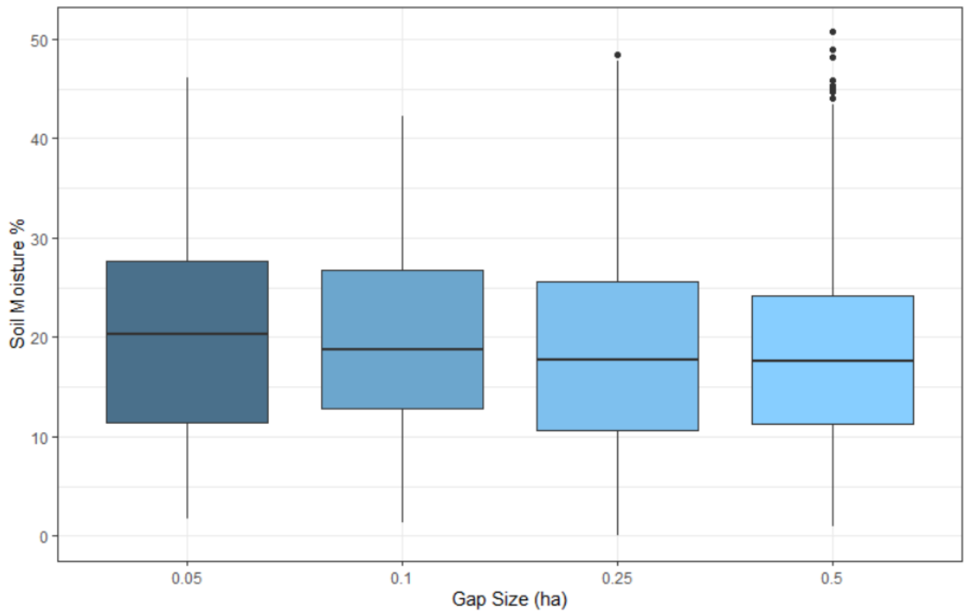

Figure S3: Soil moisture percentage by gap size (ha). Distribution of soil moisture percentage across gap sizes (0.05, 0.1, 0.25, 0.5 ha). The smallest gap size (0.05 ha) has the highest average soil moisture percentage while the largest gap size (0.5 ha) has the lowest.

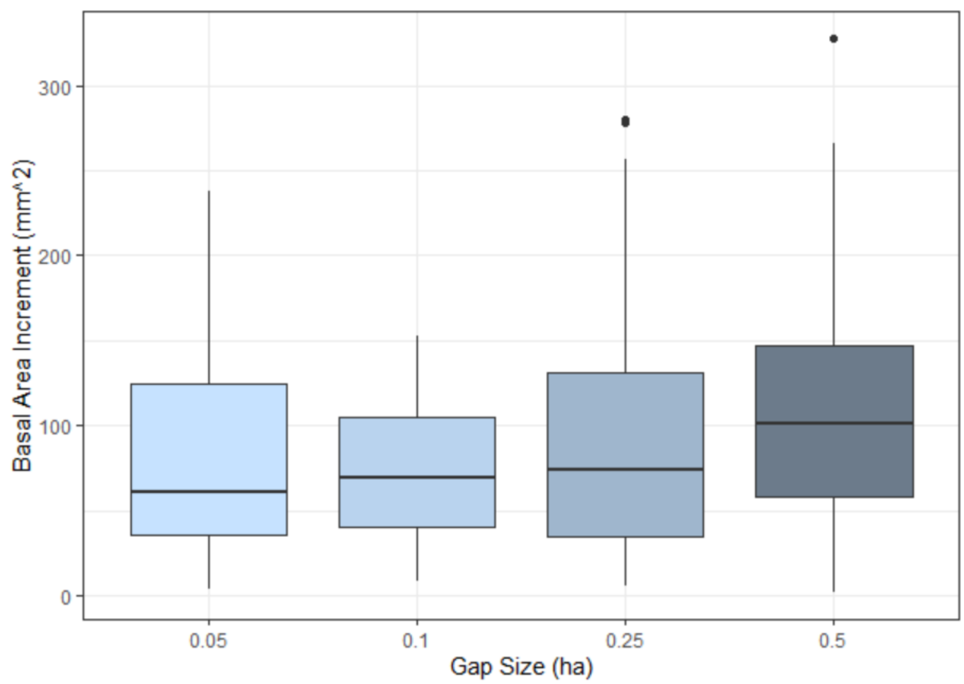

Figure S4: Red alder basal area increment by gap size. Basal area increment (mm^2) of red alder increases are gap size increases from 0.05ha to 0.5ha.

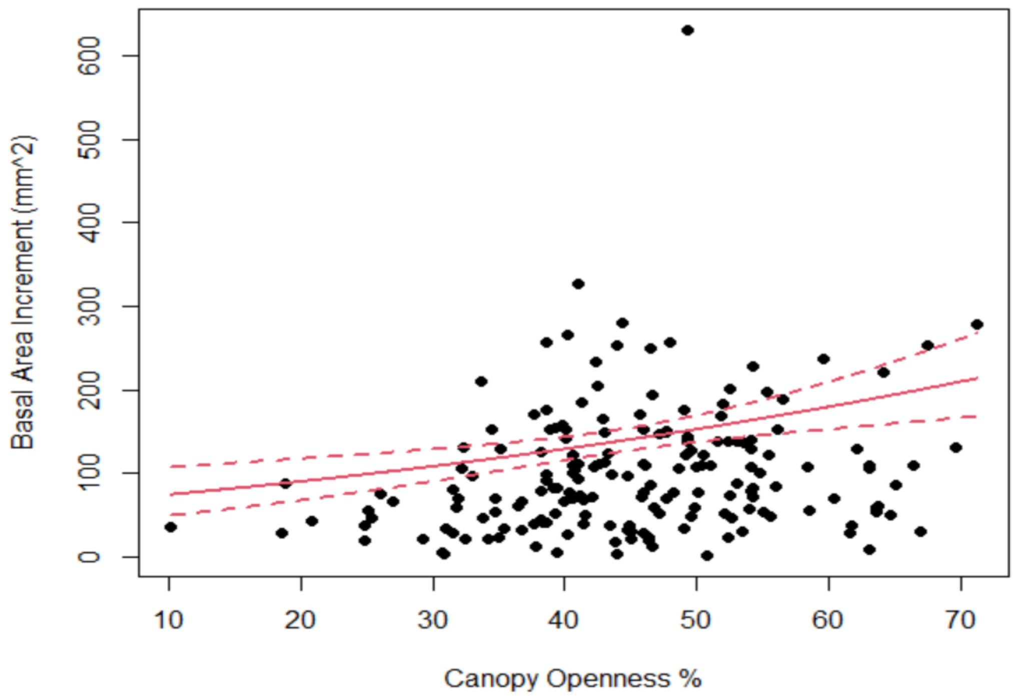

Figure S5: Red alder seedling basal area increment by canopy openness. Basal area increment (mm^2) of red alder increases as canopy openness (light) increases ($p < 0.05$). The solid red line depicts a linear regression while the dashed red lines indicate the 95% confidence interval.

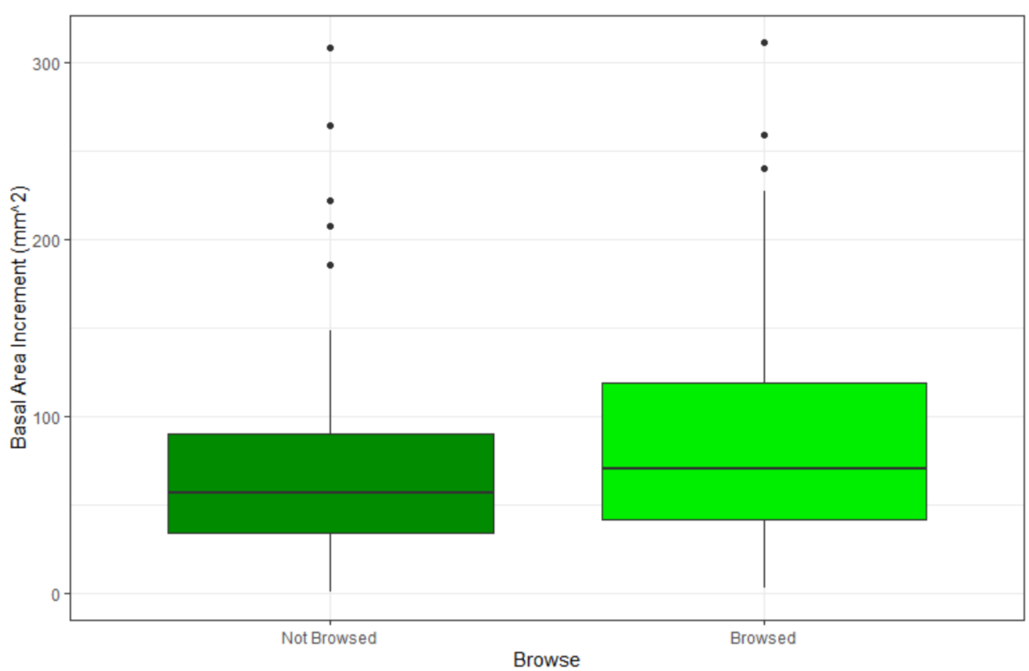

Figure S6: Western redcedar seedling browsed vs not browsed seedlings by basal area increment. Basal are increment (mm^2) is on average higher in browsed seedlings than non-browsed seedlings ($p < 0.05$).

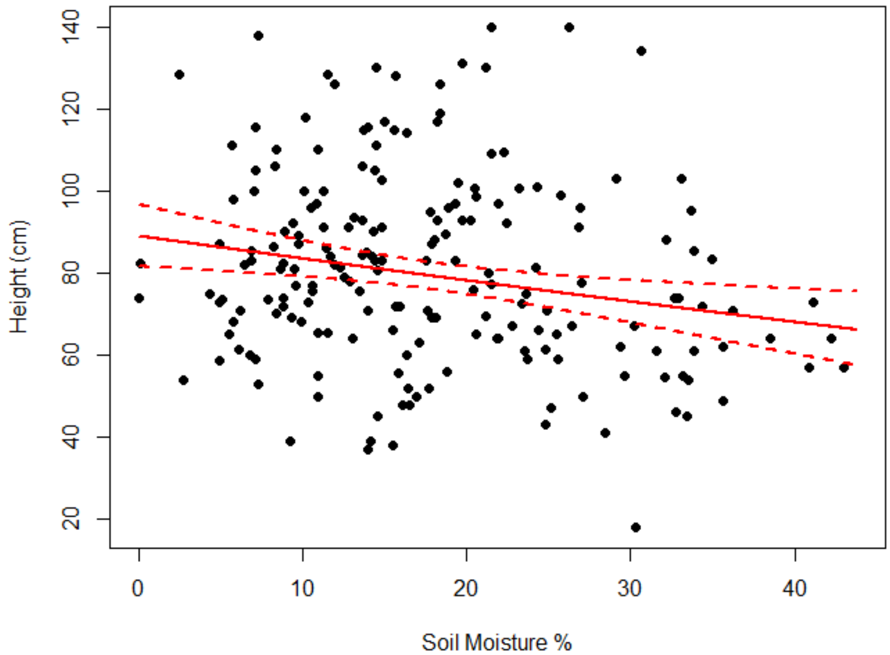

Figure S7: Western redcedar height by soil moisture percentage. Height (cm) of western redcedar seedlings decreases as soil moisture increases ($p < 0.05$). The solid red line depicts a linear regression while the dashed red lines indicate the 95% confidence interval.

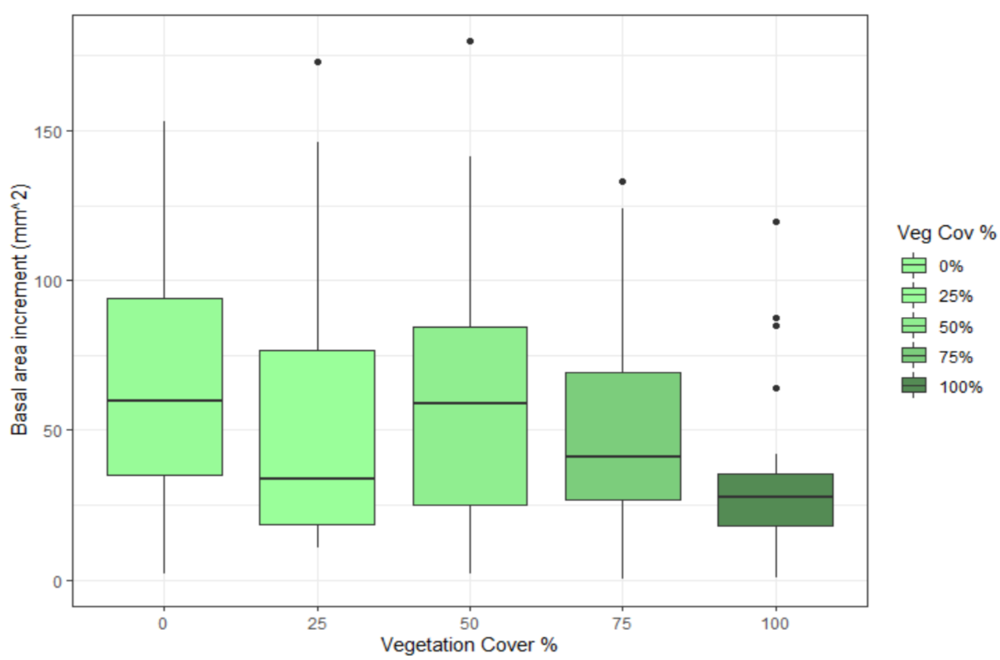

Figure S8: Grand fir basal area increment by vegetation cover. Basal area increment (mm^2) of grand fir generally decreases from 0% vegetation cover to 100% cover with a sharp decrease at 25% cover. Basal area increment then increases again at 50% and declines to 100%.

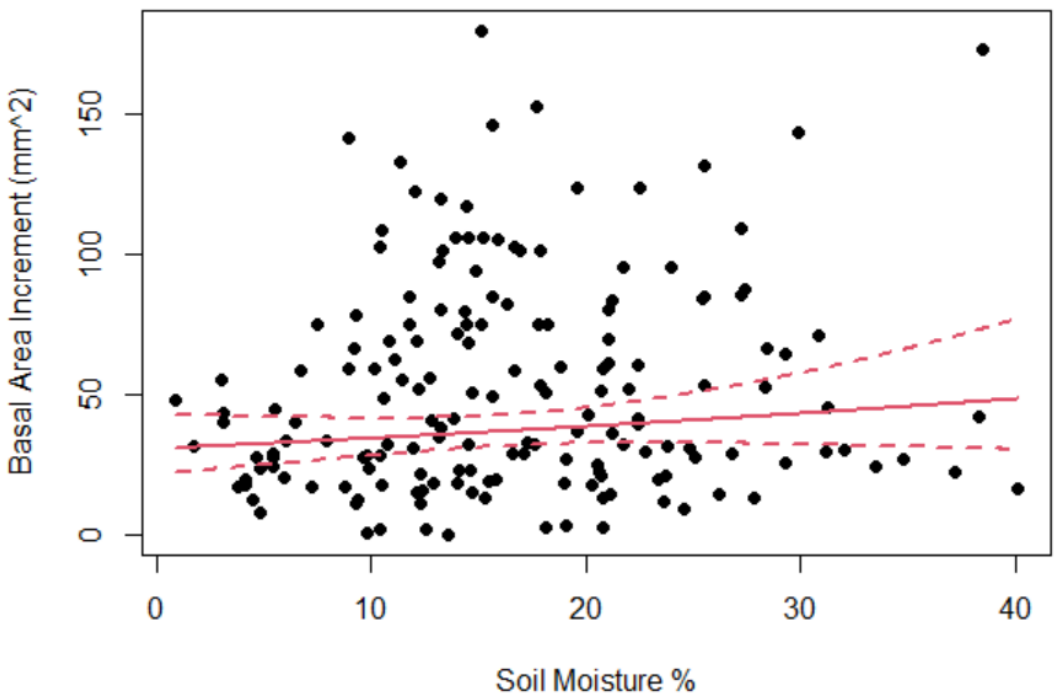

Figure S9: Grand fir basal area increment by soil moisture. Basal area increment (mm^2) of grand fir increases as soil moisture increases.

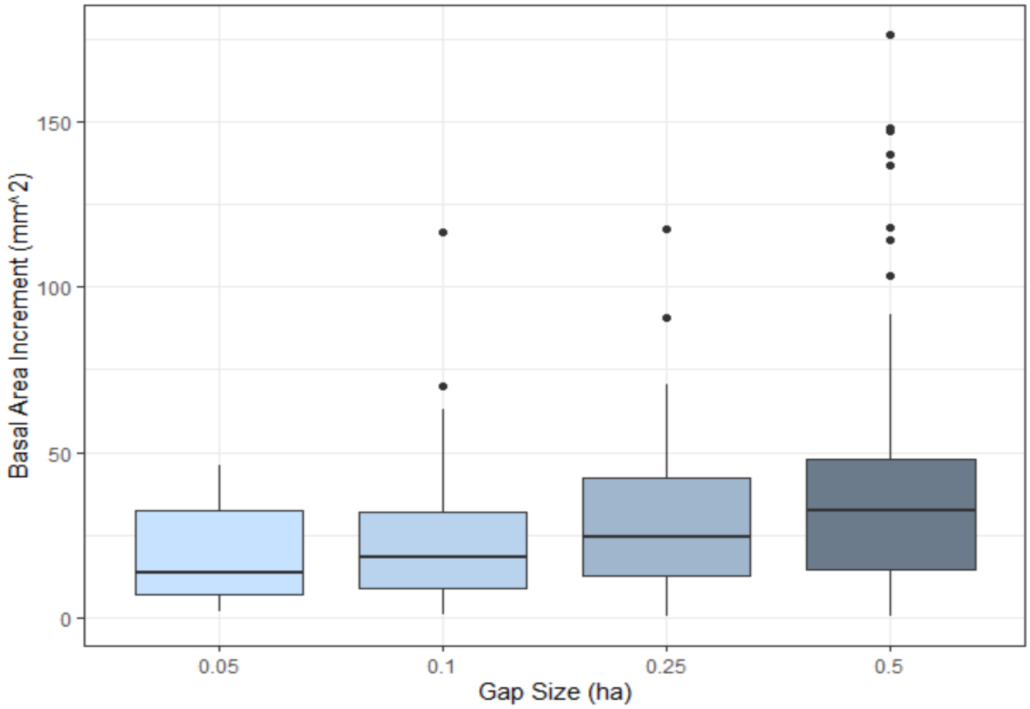

Figure S10: Douglas-fir basal area increment by gap size. Basal area increment (mm^2) of Douglas-fir increases as gap size increases from 0.05ha to 0.5ha.