Forest canopy gap size affects regeneration potential

of interior Douglas-fir

by

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Abstract

There is growing concern about the long term productivity of forests in British Columbia due to changing climatic conditions. Interior Douglas-fir, an economically and culturally valuable conifer species, has recently had inconsistent regeneration success in the dry climatic regions of its distribution due to high summer soil surface temperatures, drought and growing season frost. Seeds of interior Douglas-fir germinate after mixed severity disturbances, but their survival appears to depend on the size of disturbance gaps, environmental resources and conditions, and colonization by mycorrhizal fungal symbionts. In two separate experiments that differed in climate (very dry, hot and dry, cool Interior Douglas-fir (IDF) subzones), and disturbance agent (natural and harvested), I sowed interior Douglas-fir seed into different sized forest canopy gaps. In both experiments, I tested the effects of canopy gap size and access to mycorrhizal networks on seedling performance (establishment, growth, water use efficiency, foliar nutrition, mycorrhizal colonization) and environmental resources and conditions (light, temperature, soil moisture). In the first experiment, regeneration failed in all canopy gap sizes and network treatments due to the harsh climatic conditions. There, neither protection in small gaps nor access to mycorrhizal networks were sufficient to create favourable regeneration conditions. In the second experiment, where the climate was cooler and wetter, seedling survival reached 74% in harvested gaps that were 80 – 300 m^2 in area, corresponding with greater soil moisture availability. Gaps of $20 - 80 m^2$ were too small to initiate gap-phase regeneration, however, as indicated by low seed emergence and slow height growth rates. Gaps >300 m^2 resulted in high emergence but low survival (26 %) due to low soil moisture availability. Access to mycorrhizal networks had minor effects on mycorrhizal colonization and water use efficiency. My study shows that regeneration potential of interior Douglas-fir is severely limited by the very dry, hot climate in the low elevation IDF forests, but can be increased in wetter, cooler climates with forest harvesting practices that create moderately sized canopy gaps.

Preface

Contributions by Matthew Zustovic:

This thesis is an original, unpublished product of the author, Matthew Zustovic. The overall project was identified and designed by Dr. Suzanne Simard and Dr. Bill Mohn as part of an NSERC Strategic Project Grant. Assistance in the early stages was provided by researcher Dr. Toktam Sajedi. The specific experiments herein were designed by Matthew Zustovic and Dr. Suzanne Simard in conjunction with committee members, Dr. William Mohn and Dr. Jolie Meyer-Smith, and Research Associate, Dr. Brian John Pickles. Matthew Zustovic established and led both the field experiment and sample processing with the exceptions of microwave digestion/ICP analysis, performed by the British Columbia Ministry of Environment Analytical Laboratory, and mass spectrometry, conducted by the Stable Isotope Facility at UBC-Vancouver. Statistical analyses were conducted by Matthew Zustovic with suggestions from Dr. Suzanne Simard and Dr. Brian John Pickles.

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For interior Douglas-fir trees everywhere

Chapter 1: Introduction

Interior Douglas-fir (*Pseudotsuga mensiezii* var glauca) is economically and culturally valuable in the Interior Douglas-fir (IDF) biogeoclimatic zone of southern interior British Columbia, Canada, and the forests have been heavily used for timber production, cattle grazing, urban and rural development, and recreation. However, interior Douglas-fir has been notoriously difficult to regenerate in its lower elevation ranges in recent years because of changing climatic conditions. High summer temperature extremes can cause fatal drought stress to new recruits while cold temperatures can cause frost damage to seedling roots (Griesbauer and Green 2010). In the coming years, these climate extremes will become more frequent and intense as the current climatic envelope for interior Douglas-fir migrates northward and to higher elevations (Hamann and Wang 2006). There is an increasing probability that more drought and heat resistant species from lower elevation ecosystems, such as pinegrass (Calamagrostis rubescens) and cheat grass (Bromus tectorum), will invade these higher elevation forests and compete with interior Douglas-fir seedlings for limited resources like water. Many attempts to facilitate regeneration of interior Douglas-fir have been made through adjustments to forest harvesting and regeneration practices (Nitschke 2005, Long 2009, Day et al. 2011), but how these forest practices interact to affect establishment and survival, especially under changing climatic conditions, is poorly understood.

1.1 Interior Douglas-fir (Pseudotsuga menziesii var. glauca)

Interior Douglas-fir is widely distributed in western North America. It ranges from northern Mexico (19 °N) to the north of British Columbia, Canada (55 °N), and across a variety of soil moisture and nutrient regimes. Interior Douglas-fir is very adaptable to this high environmental variability because of the species' high genetic diversity (Krutovsky *et al.* 2009). At upper elevations where precipitation is high and temperatures are low, summer frost damage to roots limits the species distribution. Soil surface temperatures of -5 °C can incur frost damage and be fatal to seedlings within their first year of establishment (Griesbauer and Green 2010). At low elevations, interior Douglas-fir growth is limited by low soil moisture and high soil surface temperatures. At temperatures greater than 50 °C, seedlings suffer from desiccation (Waring and Schlesinger 1985).

Seed production of interior Douglas-fir is variable with possibly one or two viable seed crops per decade. Of the seeds that do fall, up to 95 % die due to herbivory from birds, small mammals, and insects (Huggard *et al.*2005). Interior Douglas-fir seeds are small, wind dispersed, and adapted to stay dormant until environmental conditions are suitable for germination and emergence. Those seeds that are not eaten require exposed mineral soil and a stratification period where temperatures reach 2 °C for a certain number of days in order to break seed dormancy. The longer the chilling period for stratification, the lower the heat sum requirements are for germination (Sorenson 1991). Light, soil moisture, and soil temperatures all become important drivers of plant growth after emergence (Simard *et al.* 2003).

Many studies have found survival in the hot dry interior to be less than 50 % (Newsome *et al.* 1991, Simard *et al.* 2003). These results have forest managers and ecologists researching the best possible practices to ensure adequate regeneration of these forests. Partial cutting, which includes various methods to create various sized canopy gaps for achieving multiple ecosystem objectives, has been a favorable tool in recent years (Vyse *et al.* 2006). Leaving seed trees throughout cut blocks also increases the chance of natural regeneration, but in most logged areas, regeneration of interior Douglas-fir has been facilitated by planting 1 year-old greenhouse-grown seedlings. Site preparation using screefing sometimes improves establishment, but planted seedlings often fail due to poor root growth and low available soil moisture.

Interior Douglas-fir is a shade tolerant conifer species that prefers to grow in full light conditions (Vyse *et al.* 2006). Increases in light levels usually correspond with increases in

growth and survival; however, many studies have identified moisture as the key limiting factor in dry ecosystems (Bingham and Simard 2013). Growth of interior Douglas-fir is limited by drought stress as stomatal closure reduces photosynthesis and evapotranspiration.

1.2 Ecology and silviculture of the IDF

The forest types of British Columbia have been classified using the Biogeoclimatic Ecosystem Classification (BEC) system (Lloyd *et al.* 1990). BEC zones have been delineated using precipitation, temperature, and elevation data. There are 14 major BEC zones, each further split into subzones based on regional climatic variability, which are in turn characterized at the site level according to soil moisture and soil nutrient regimes. Indicator plants characterize soil moisture and soil nutrient status. As the climate changes, the geographic distribution of the BEC zones are predicted to change (Hamann and Wang 2006). Maximum and minimum temperatures are becoming more extreme, and one consequence is that the average climate conditions of some zones are shifting northward and upward in elevation (Hamann and Wang 2006). This has raised much concern about long term survival of species that have adapted to current conditions. Will tree species migrate to areas with favorable climatic conditions, and will they be able to persist in areas that no longer have the climate conditions suitable for survival and growth?

One of these zones is the IDF zone. It spans mid to low elevations in the southern interior of British Columbia between the Cascade and the Rocky Mountains. The IDF forests stretch far past this range south into Washington and Oregon and are characterized by extensive stands of interior Douglas-fir, the climax tree species. The dominant climate factor for the IDF zone is the rain shadow created by the Cascade Mountains, causing warm, dry summers and cool winters. Mean annual precipitation is 300 to 750 mm, 20 to 50 % of which falls as snow, which limits tree growth. The subzone of the IDF that is most limited by water is the very dry, hot subzone where temperatures reach physiological extremes in the summers.

These forests occur at low elevations above the Ponderosa Pine or Bunchgrass zones. The forests naturally have high cover of the native pinegrass, which competes for resources with interior Douglas-fir trees (Flemming *et al.* 1994). Fire disturbances in the dry climatic regions of the IDF were historically very frequent (Perry *et al.* 2011), which burned the grasses and exposed mineral soils, thus creating suitable conditions for interior Douglas-fir germination. With the long history of fire suppression in the area, however, grass growth dynamics have likely changed.

Fire is just one of many disturbance agents in the IDF zone, which is characterized by a mixed severity disturbance regime that also includes insect, disease, wind, and man-made disturbances such as harvesting (Perry et al. 2011). Disturbances happen at varying frequencies and at different scales, which creates a mosaic of forest canopy gaps. Forest gaps are openings in the canopy that are created by dead and fallen trees. Gaps change the availability of resources necessary for seedling growth, such as light and soil moisture; however, the size of the canopy gaps, which affects the abundance of resources, may determine the survival and growth of the seedlings (Klenner *et al.* 2008). Because of greater light penetration, gaps are warmer in the center (Muscolo *et al.* 2014). This is because the increased solar radiation from reduced canopy closure results in increased soil surface temperatures (Malcolm *et al.* 2001). Soil moisture is also greater in gap centers than at gap edges in Douglas-fir forests (Malcolm *et al.* 2001, Gray *et al.* 2002). This leads to higher rates of decomposition and therefore higher nutrient levels (Prescott 2010). Taylor *et al.* (1989) found that C : N ratio was greater in small gaps because of humification and lower in large gaps due to mineralization.

Forest practices in recent years have attempted to emulate natural disturbances with the intention of creating gaps that facilitate regeneration (Long 2009). These have included partial cutting, shelterwood systems, stand thinning, and controlled burns (Day *et al.* 2011). More often than not, these practices come with trade-offs, where one management goal is sacrificed for another such as timber for wildlife habitat. There are also tendencies for high grading to occur,

where the largest trees are selected regardless of their potential to facilitate regeneration through provision of seed, shading or mycorrhizal networks.

1.3 Mycorrhizal facilitation and networking

Interior Douglas-fir seedling establishment success is also affected by whether they are linked into an existing mycorrhizal network (Teste *et al.* 2009, Bingham and Simard 2012, Barker *et al.* 2014). Interior Douglas-fir forms obligate associations with a diverse suite of ectomycorrhizal fungi, where the tree trades photosynthetic carbon for essential limiting nutrients and water the fungi acquire from the soil (Twieg *et al.* 2007). A mycorrhizal network forms when mycorrhizal genets connect the root systems of multiple plants (van der Heijden and Horton 2009). In the interior Douglas-fir forests in British Columbia, mycorrhizal networks have been shown to link all Douglas-fir trees in a stand together, with larger and older trees serving as network hubs (Beiler *et al.* 2010 & 2015). New seedlings establish within the network of the older hub trees, gaining access to larger pools of soil water and nutrients, thus enhancing their survival and growth capacity (Teste *et al.* 2009). Douglas-fir seedlings also received carbon, nutrients and water transferred from nearby trees (Schoonmaker *et al.* 2007, Teste *et al.* 2009), although the benefits appear to be reduced in the presence of root competition (Bingham and Simard 2012, Song *et al.* 2015). Mycorrhizae are believed to be crucial in the future adaptive strategies of plants as climate changes (Pickles *et al.* 2012).

The physical location where seedlings establish relative to hub trees or in gaps is important to their success. Seedlings that establish in close proximity to hub trees but outside their crown dripline may be ideally located: they may be able to form extensive mycorrhizal networks that provide resources from the hub tree, while escaping direct competition for light and water from roots and crowns (Teste and Simard 2008; Bingham and Simard 2012). By contrast, seedlings establishing immediately adjacent to large trees may suffer intense intraspecific competition for water and light, while those far away have lower mycorrhizal

colonization rates and must compete interspecifically with understory plants for water and nutrients. If accessing mycorrhizal networks affects regeneration potential of interior Douglas-fir, and if this is influenced by proximity to mature trees and hence disturbance gap size, it is important to incorporate this knowledge into harvesting practises.

1.4 Thesis objectives

The three main questions explored in this thesis are: (1) whether regeneration potential of interior Douglas-fir differs between naturally occurring gaps in a very hot, dry IDF subzone and harvested gaps in a dry, cool IDF subzone, (2) whether there is an optimal gap size to facilitate interior Douglas-fir regeneration, and (3) what role mycorrhizal networks play in gap-phase regeneration.

Chapter 2: Regeneration potential of interior Douglas-fir across different sized forest gaps and mycorrhizal network treatments

2.1 Introduction

Forest regeneration in Canada is under increasing stress with climate change (Schepaschenko et al. 2015). As old forests are being disturbed at unprecedented rates (Allen et al. 2010), seedlings establishing in the new openings are facing hotter, drier and more hostile conditions than previous cohorts. In clearcuts, the stress of climate change is already evident in failures of plantations due to drought, insect outbreaks and disease infestations (Woods and Bergerud 2008; Heineman et al. 2010). The projected long term trend toward increased warming and decreased water availability in Canada's forests (IPCC 2015) suggest that forest regeneration will become increasingly limited, leaving disturbed spaces open for invasion by novel species, and reducing their productive and carbon storage capacity. Scientists predict that boreal and temperate forests of North America may consequently shift to savannahs of mixed grassland and woodland (Schepaschenko et al. 2015). Overcoming survival limitations to promote successful reforestation of tree species for maintaining forest cover will require adaptive shifts in forest management practices (Puettmann and Tappeiner 2013). Whereas clearcutting and planting has been economically expedient and generally successful under earlier favorable climate conditions over vast tracts of Canada (Environment Canada 2014). innovating a range of harvesting disturbances and reforestation techniques will be necessary to increase the adaptive capacity of northern forests under a warming climate. Partial retention harvesting that increases resource supply while leaving biological legacies, for example, may provide an opportunity for seedlings to tap into limited resource pools along with mycorrhizal fungal symbionts known crucial for survival (Barker et al. 2014). How regenerating seedlings will respond to partial harvesting practices under changing climatic conditions is poorly

understood, however. Here we examined the effect of gap size and access to mycorrhizal networks on seedling regeneration in two adjacent interior Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco) forests with different climate regimes in southern interior British Columbia.

Regeneration of interior Douglas-fir forests results from mixed severity disturbances caused by wildfire, insect outbreaks and harvesting in southern interior British Columbia (Klenner et al. 2008, Perry 2011). The natural disturbances create a variety of openings, from single tree-fall gaps to watersheds, with a resulting mosaic of forest gaps of varying shapes, sizes and disturbance histories. Seeds naturally disperse into these openings and are adapted to germinate and grow in the resource-limited environment. Harvesting emulates these disturbances to a degree using clearcutting or partial retention methods, but regeneration has been difficult, particularly in the drier interior Douglas-fir forests, because of high summer soil moisture deficits and winter frost damage (Vyse et al. 2006, Griesbauer and Green 2010). Conditions for interior Douglas-fir regeneration are expected to become even more difficult with increasing frequency and intensity of climate extremes, with potential forest losses at lower elevations, but migrations northward and to higher elevations (Hamann and Wang 2006). Natural regeneration of interior Douglas-fir occurs when seeds disperse and germinate in disturbed gaps of various sizes (Huggard et al. 2005; Vyse et al. 2006; Huggard and Arsenault 2009). The size of the canopy gaps affects availability of light, soil water and nutrients necessary for seedling survival and growth. Therefore, the size of the canopy gaps, through their effects on resource availability, may determine the performance of the seedlings (Klenner et al. 2008). Interior Douglas-fir seedling establishment success is also affected by whether they are linked into an existing mycorrhizal network (Teste et al. 2009, Bingham and Simard 2012, Barker et al. 2014).

The physical location where seedlings establish relative to hub trees or in gaps is important to their success. Seedlings that establish in close proximity to hub trees but outside

their crown dripline are ideally located: they are able to form extensive mycorrhizal networks that provide resources from the hub tree, while escaping direct competition for light and water from roots and crowns (Teste and Simard 2008; Bingham and Simard 2012). By contrast, seedlings establishing immediately adjacent to large trees may suffer intense intraspecific competition for water and light, while those far away have lower mycorrhizal colonization rates and must compete interspecifically with understory plants for water and nutrients.

The objective of this study is to determine whether the potential for natural regeneration success of interior Douglas-fir is affected by forest gap size and access to mycorrhizal networks. To achieve this, regeneration potential of directly seeded interior Douglas-fir was evaluated across three gap sizes (small, medium, and large) and three mycorrhizal network treatments (no network, network, network with roots). Regeneration potential was evaluated based on rates of seedling emergence, survival, nutrient content, and growth rates from the sown seed. The effects of gap size and mycorrhizal network access were tested in two separate experiments: the first was a "natural gap experiment" conducted at a hot, dry low elevation interior Douglas-fir forest where canopy gaps had naturally formed due to water limitations and natural disturbances; the second was a "harvested gap experiment" conducted at a cooler, wetter and higher elevation interior Douglas-fir forest that had been partially harvested one year previously creating a range of canopy gap sizes. Sites were chosen because of their elevation, proximity to the IDF/grassland interface, and timing of recent harvesting practises. We sought to compare the seedling regeneration potential between these forests for gaining insights into impacts warmer temperatures and lower growing season precipitation may have on seedling establishment success. Three hypotheses were tested: (1) regeneration potential would be lower in the naturally occurring than harvested canopy gaps because of more extreme resource limitations at the lower elevation forest, even though these seedlings may be better adapted to the natural than human-caused disturbances, (2) regeneration potential would be greatest in medium sized gaps because of an optimal combination of resource availability (light, water and

nutrients), and (3) regeneration potential would be greatest where Douglas-fir seedlings have access to mycorrhizal networks, but this would be reduced where access to networks was accompanied by root competition from neighbors.

2.2 Methods

Study area

Study sites were located near Kamloops, British Columbia, Canada (50°50'32 – 50°54'02 N, 120°18'03 – 120°33'52 W) and spanned in elevation from 870 to 1260 m (Table 1). The harvested gap experiment was located at the upper end of the elevation range and was replicated in three separate blocks that had been selectively harvested to salvage Douglas-fir trees attacked by the Douglas-fir bark beetle (*Dendroctonus pseudotsugae*) in 2009-2010, resulting in a range of canopy opening sizes. Of the three blocks, the Lower Sawmill (LSM) site was located approximately 10 km north of the Lac du Bois Grasslands Protected Area and was harvested in 2010; the Upper Sawmill (USM) site was located approximately 16 km north of Lower Sawmill site and was harvested in 2009; and the O'Connor Lake (OC) site was located 16 km North of Kamloops along the North Thompson River and was harvested in 2009. None of the harvested sites had been site prepared, but some gaps contained the remnants of burned slash piles. The natural gap experiment was also located near O'Connor Lake but was at the low end of the elevation range.

The harvested gap experiment was on mesic sites and located in the Cascade Dry, Cool IDF variant (IDFdk2), where mean annual precipitation is 623-843 mm, MAT is 4.1°C, and mean January and growing season temperatures are -11.1°C and 11.3°C, respectively (Lloyd *et al.* 1990). The natural gap experiment was located on mesic sites within the Thompson Very Dry, Hot IDF biogeoclimatic variant (IDFxh2), where mean annual precipitation is 295-452 mm and mean annual temperature (MAT) is 4.8°C, averaging -13.4°C in January and exceeding 13.1°C in summer months (Lloyd *et al.* 1990) although current temperatures can be much higher. Site-

specific climate estimates for the natural and harvested gap experiments were derived from Climate BC (Table 2). Soils in both experiments were luvisols and brunisols with clay loam texture (Canadian System of Soil Classification 1998). The dominant tree species in both experiments was interior Douglas-fir, with minor amounts of interior spruce (*Picea glauca x engelmannii*) and lodgepole pine (*Pinus contorta* var. *latifolia*) at higher elevations, ponderosa pine (*Pinus ponderosa*) at lower elevations, and small patches of trembling aspen (*Populous tremuloides*) and paper birch (*Betula papyrifera*) throughout. Understory shrub and herb species included bald hip rose (*Rosa gymnocarpa*), birch-leaved spirea (*Spirea betulifolia*), silky lupine (*Lupinus sericeus*), heart-leaved arnica (*Arnica cordifolia*), and bull thistle (*Cirsium vulgare*). Grasses included pinegrass, bluebunch wheatgrass (*Agropyron spicatum*), and cheatgrass. Red-stemmed feather moss (*Plerozium shreberi*) was abundant on moist microsites. Shrub cover tended to greater and grass cover lower in the harvested than natural gap experiment.

Experimental design and treatments

The harvested gap experiment was a 3x3 factorial design, with three gap sizes and three mycorrhizal network treatments. These treatments were replicated three times at each of the three replicate sites (3 gap sizes x 3 network treatments x 3 blocks (sites) x 3 within-site replicates=81 experimental units) in a randomized block design. The natural gap experiment was also a 3x3 factorial design with three gap sizes and three network treatments, but these treatments were replicated nine times within the O'Connor Lake site (3 gap sizes x 3 network treatments x 9 within-site replicates=81 experimental units) in a completely randomized design.

Gap size was characterized by gap diameter, which was measured as the shortest distance between trees from edge to edge. The gaps fell into three categories as follows: small gaps of 5 – 10 m diameter (approx. $20 - 80 m^2$), medium gaps of 11 - 20 m (approx. $80 - 300 m^2$), and large gaps of 21 m and wider (approx. $300 - 2500 m^2$). At the center of each gap, a 1 x 1 m plot was screefed with a planting shovel and 10 interior Douglas-fir seeds were sown

into one of the three mycorrhizal network treatments (no network, network, and network plus roots). These treatments were distinguished by the presence/absence and pore size of nylon mesh bags (Plastok®(Meshes and Filtration) Ltd.) fitted into excavated holes in the soil 20cm deep and 15cm in diameter. In the no network treatment, seeds were sown into nylon mesh bags with a 0.5 µm pore size, which was small enough to exclude mycorrhizal hyphae and roots but still allow free movement of water and solutes. In the network treatment, seeds were sown into mesh bags with a 35 µm pore size, which permitted passage of mycorrhizal hyphae and water, but not plant roots. In the network and roots treatment, soil was excavated in a similar manner but replaced without a mesh bag, thus allowing seedlings full access to the mycorrhizal network and roots of surrounding trees and plants. In each mycorrhizal network treatment, 10 interior Douglas-fir seeds (seedlot no. 39330, Tree Seed Center, Ministry of Forests and Range, Surrey, British Columbia, Canada) were sown just below the soil surface. The seeds were prestratified by the Tree Seed Centre and then soaked in water for 24 hours before planting. Seeds were sown between May 29 and June 2, 2011.

Environmental responses

Available light in the gaps was measured using a Nikon D50 digital camera with a Sigma 8mm fisheye lens and tripod. Gap Light Analyzer (GLA) methods and software were used to calculate total solar radiation (% full light) (Frazer *et al.* 1999). The canopy images were taken 50 cm above the seedling located in gap centers during the summer of 2014. Light was measured only in the harvested gap experiment. Soil moisture content was determined at the center of each gap using a Dynamax ML2 Theta Probe (Delta-T Devices Ltd.), which measures changes to the dielectric constant of the soil as a proxy for volumetric soil moisture content (m^3/m^3) . Two measurements were taken at the beginning of each month in the 2013 growing season at approximately 15 cm from the seedling in north and south directions. These

measures were averaged to obtain monthly average soil moisture content. Soil moisture was measured in both the natural and harvested gap experiments.

Regeneration potential responses

Emergence rate (%) of the 10 sown seeds per experimental unit (gap) was determined at the end of the growing season in 2011 in both the natural gap experiment (n=81) and the harvested gap experiment (n=81). In May of 2012, after 1 year of growth, each experimental unit was culled to the single strongest (target) seedling. Culled seedlings were transplanted to experimental units with no seedling emergence or no survivors by the end of the first year. Height and survival of the target seedling were monitored monthly in the 2012 and 2013 growing seasons. In September of 2013, all target seedlings were tallied for survival rate (%) and then destructively sampled to determine biomass of tissue fractions. Seedlings were cut just above the root collar and placed in a moist Ziplock © bag. If the roots were in a nylon mesh bag, the entire bag was excavated and the root system extracted. If there was no mesh bag, the immediate root zone was excavated. All samples were stored at 4°C until returned to the lab for analysis.

Because of low survivorship in the natural gap experiment, seedling biomass was measured only in the harvested gap experiment. Stems were separated from needles and stem length was measured (cm). Roots were rinsed of soil particles. All fine root tips were examined for mycorrhizal colonization and visually morphotyped using dissecting and compound microscopes according to Goodman *et al.* (1998), and this data was used to calculate the Shannon-Weiner Diversity Index, Simpson's Diversity Index, and percent root colonization. All tissue samples were dried at 105°C for 48 h and the dry weights recorded (g).

Dried seedling stems were assessed for natural abundance δ^{13} C as a proxy for water use efficiency (Farquhar and Richards 1984). Stems were ground using a mortar and pestle, and weighed subsamples were placed into tin capsules. Samples were sent to the UBC Stable

isotope Facility where a mass spectrometer was used to combust the samples and measure the ${}^{13}C/{}^{12}C$ ratio. This ratio is also known as $\delta^{13}C$ and the standard used for analysis is Vienna-PeeDee Belemnite (‰).

Statistical analysis

All statistical analyses were performed using R version 3.0.2 (R Core Team, 2013). A linear mixed effects model (Ime) and generalized linear model (glm) was used from the R package (nlme) for planned comparisons. Graphs were created from the R package (ggplot2). Gap size (3 levels) and access to mycorrhizal networks (3 levels) were fixed effects factors and as the harvested gaps had three sites, site was used as a random effect. All data with noted exceptions met assumptions of equal variance using Levene's test and normality using the Shapiro-Wilk test and no data transformations were used. Post-hoc testing was conducted using the bonferonni-fdr correction. Non-metric multidimensional scaling (NMDS) was used to characterize species assemblages of mycorrhizal morphotypes. In the natural gap experiment, emergence and survival were too low and did not have enough samples for parametric statistics.

2.3 Results

Natural gaps had a 2.3 % total emergence rate and no emergence occurred in large gaps (Table 3) and therefore had too low sample size for parametric statistics. Of the 900 seeds sown in the harvested gaps, 272 emerged for an overall emergence rate of 33.6 % (Table 3). Emergence was lowest in small harvested gaps (24.8 %) compared to medium (37.4 %) and large (38.5%) gaps (n = 81, p < 0.0001) (Table 4) (Figure 2). Emergence tended to decrease with gap size where seedlings were isolated from mycorrhizal networks, but increased with gap size where they did have access to mycorrhizal networks (n = 81, p < 0.001) (Table 4) (Figure 2).

Of the 90 seedlings monitored in the natural gaps, only six survived for a total survival rate of 6.7 % (Table 5). There were no surviving seedlings in large natural gaps and therefore, did not meet the assumptions for parametric statistics. A total of 90 seedlings were monitored for survival through the harvested gap experiment, of which 39 (48.1 %) survived over the three year study period (Table 5). Survival was significantly affected by gap size (n = 81, p = 0.0470) (Table 4). Medium sized gaps had a higher average survival rate (74.0 %) than small (40.7 %) or large gaps (29.6 %) regardless of mycorrhizal network treatment (Figure 3).

Mean soil moisture was variable across all sites and treatments (Table 6). Gap size effects were detected in the harvested gaps (p = 0.0152) but not mycorrhizal network treatment (p = 0.4136) (Table 7). Average soil moisture was greatest in medium sized gaps (Figure 4). In natural disturbance gaps, soil moisture was also highest in medium sized gaps (Figure 4), however, results were not significant (p = 0.4782) (Table 8). Soil moisture content in harvested gaps was higher than in natural gaps (Figure 4).

Available light in harvested gaps was greater in large (64%) than either medium (51%) or small sized gaps (45%), which did not differ from each other (n = 81, p < 0.001) (Table 9) (Figure 5). Variability in available light decreased from small gaps (range 5-80% full sunlight), to large gaps, as did the frequency of low light conditions. Available light increased linearly with gap area, regardless of mycorrhizal network treatment (n=81, p <0.001) (Table 10) (Figure 6).

Mean annual temperature in harvested gaps was lowest in small gaps and greatest in large gaps (4.92 and 6.47 °C respectfully) (Table 11). Medium and large sized gaps had equally high average summer temperatures (12.90 and 12.38 °C respectfully) compared to small sized gaps (10.58 °C) and average winter temperatures were similar for all three gap sizes (Table 11). Large gaps had the highest maximum and lowest minimum temperatures (23.75 and – 0.26 °C) (Table 11). No parametric statistics were run on temperature data as sample sizes were too small.

Growth response variables had variable sample sizes (Table 12) due to high mortality. Natural abundance δ^{13} C values in the woody stem tissues of interior Douglas-fir seedlings was not significantly affected by gap size or access to mycorrhizal networks; however, the interaction term was significant (n = 37, p <0.0043) (Table 13). Where seedlings had access to mycorrhizal networks without interference from roots, seedling had more positive δ^{13} C values in small and medium sized gaps than large gaps (Figure 7). Where seedlings were isolated from mycorrhizal networks, or where roots and networks were allowed to intermingle, δ^{13} C values generally increased with gap size (Figure 7).

Natural abundance δ^{13} C was postively linearly related to available light (n = 37, p = 0.0032) (Table 14) and this was true across all mycorrhizal network treatments (Figure 8). By contrast, δ^{13} C was not related to soil moisture availability (n=35, p=0.9079) (Table 14) (Figure 8).

Seedlings were significantly shorter in small gaps than medium or large harvested gaps (n = 39, p = 0.0313) (Table 15) (Figure 9). However, seedling length did not differ between small and large gaps due to the high variability in large gaps (Figure 9).

Of the foliar nutrient ratios tested, C: N differed among mycorrhizal network treatments (n = 35, p = 0.0301) (Table 16). Average foliar C: N content ratio was significantly lower in seedlings with access to mycorrhizal networks and unrestricted root interaction than seedlings with no mycorrhizal network access (Figure 10). Seedlings that had access to mycorrhizal networks with no root interaction had similar average foliar C : N content ratio to seedlings with no network access, but were not significantly different from the other two treatments (Figure 10).

Mycorrhizal diversity including Shannon diversity, species richness, and root tip colonization were not affected by harvested gap size or mycorrhizal treatment (n = 35, p < 0.05) (Table 17). Non – metric multidimensional scaling showed that there were strong correlations between mycorrhizal species assemblages and gap size (Figure 11). Environmental variables

show that mycorrhizal species abundance in large gaps was correlated strongly with increasing gap size, medium gaps were correlated with increasing moisture, and small gaps were correlated with increasing seedling stem weight (Figure 11).

2.4 Discussion

Seedling emergence and survival were dramatically lower in the natural gap experiment (2.3% and 6.7%, respectively) than the harvested gap experiment (30.2% and 46.9%, respectively), and this was associated with higher surface soil temperature and lower soil moisture availability at the lower elevation experiment, paralleling climate differences between experiments. The extremely low emergence and survival rate in the natural gap experiment suggests the regeneration capacity of these arid forests will likely decline even further if temperature warms and precipitation declines with projected climate change. In the harvested gap experiment, seedlings performed best overall where they were establishing in medium size gaps with access to mycorrhizal networks, and this was related to greater soil moisture content and water use efficiency as well as the assemblage of the mycorrhizal fungal community. These results imply that partial retention harvesting practices can be designed to optimize seedling water relations for greater regeneration success in the interior Douglas-fir forests of British Columbia.

Natural and harvested gaps

The seedling survival rate in the harvested gap experiment was consistent with historical rates for interior Douglas-fir in the dry forests of British Columbia, where survival rates below 50% are common (Simard *et al.* 2003, Griesbauer and Green 2010). However, the low emergence and survival observed in the natural gap experiment were far below expected rates, which would lead us to accept our first hypothesis that seedlings would regenerate poorly in the

drier and hotter climate. Although 95 % of seed mortality before emergence is caused by herbivory from ants, birds, and small mammals in dry interior Douglas-fir forests (Huggard et al. 2005), this factor was controlled in our study by use of protective mesh covering seedlings during the emergence stage. Thus, the low emergence in the natural gap experiment may better be explained by microclimatic conditions. Mean annual temperature at the natural gap experiment was over twice that of the harvested gap experiment while the snowpack was 75% lower and growing season precipitation 10% lower (Table 1). This was reflected in more extreme soil surface summer and winter temperatures in the natural gaps, which may have had lethal effects on emerging cotyledons. Higher temperatures usually lead to earlier emergence rates as the seed can attain its heat-sum requirements sooner (4500 degree days) (Bloomberg 1979), but less snow pack also results in drier soils over an earlier and longer growing season. Sorensen (1991) found that the longer the chilling period for stratification, the lower the heat sum requirements were for germination, but since our seeds were pre-stratified, we assume that the causes of low germination and survival were from the lack of soil moisture and high surface soil temperatures (Newsome et al. 1991, Hermann and Lavender 1999). Once germination has occurred, light, temperature, soil moisture, and soil nutrients are known to limit seedling survival (Simard et al. 2003).

The lower soil water availability in the natural than harvested gap experiment can be explained by lower summer and winter precipitation, but the natural gap site also had consistently steep slopes, with up to 40% gradient and a dominantly south-facing aspect compared to north-facing aspect and 28% maximum slopes of the harvested gaps. Steep slopes can amplify moisture limitations caused by low precipitation because water easily flows down slope before percolating through the soil column. The south-facing aspect also exposed seedlings to longer periods of full sun and high temperatures, further depleting soil moisture. Moreover, perimeter trees in the steep southerly slopes would have cast less shade than those in the harvested gaps, thus providing less protection against the hot sun. In the natural gaps,

the theta probe was hitting zero often and I believe the reason for consistently low soil moisture readings was the fact that there was too little precipitation to keep the soils moist.

Aside from experimentally sown seed, naturally regenerating seedlings were sparse in the natural gap experiment, despite the presence of many gap disturbances and parent trees. Many natural gaps at the lowest elevation were regenerating with ponderosa pine, which is adapted to more open canopies and warmer temperatures (Vyse *et al.* 2006). Our natural gap experimental results agree with Griesbauer and Green (2010) that low elevation interior Douglas-fir forests are at greatest risk for crossing ecological thresholds and may be early indicators of tree species distribution shifts with climate change.

Gap size

Greater emergence and three-year survival rates in the medium than small or large size gaps in the harvested gap experiment supports our second hypothesis that regeneration potential would optimize at intermediate disturbance levels. Gap size, and hence proximity of surrounding perimeter trees, significantly affected light availability, soil moisture content and soil surface temperature as expected (Muscolo *et al.* 2014), with medium size gaps producing an appropriate suite of resources for increased regeneration potential.

In contrast to medium harvest gaps, small gaps of area $20 - 80 m^2$ were not large enough to initiate gap phase regeneration, because of low light availability caused by interception by the surrounding forest canopy (Vyse *et al.* 2006). Even though there were some instances of high light levels (>80% full sun) in small gaps, contributing to increased variation in light availability, the average light in small gaps was low. Vyse *et al.* (2006) showed light availability can range from 5 - 80 % full sun in small patch cuts in interior Douglas-fir forests because of the influence of basal diameter of surrounding perimeter trees, and this likely also explains the large variation we saw in small gaps. Light is a key resource affecting seedling growth and survival (Vyse *et al.* 2006), and it likely accounts for the low germination and survival

rates observed in small gaps. Seedlings were also shorter in small than large gaps, agreeing with strong correlations found by Vyse *et al.* (2006) between seedling height and light availability.

Light availability to seedlings was greater and less variable in large than smaller harvested gaps due to the greater distance from perimeter trees (Vyes *et al.* 2006). Without shade, the center of the large gaps more frequently experienced full light conditions, and this was associated with greater seedling emergence rates. Burton and Leadem (1994) also found that germination success of 14 tree species, including interior Douglas-fir, increased with light availability in a greenhouse experiment. Interior Douglas-fir is a shade-tolerant species (Carter and Klinka 1992), and is adapted to growing under a wide range of light levels (Hermann and Lavender 1990). While small gaps should have been sufficient to satisfy light requirements by interior Douglas-fir, naturally regenerating recruits were rare, suggesting resource requirements were not met for germination and survival.

Soil moisture content was also influenced by gap size and hence proximity of perimeter trees (Gray *et al.* 2002), and was lower in small harvested gaps compared to medium size gaps. Surrounding trees, understory plants, and grasses acquire water with their roots and release it into the atmosphere through evapotranspiration (Flemming *et al.* 1994), creating water demand and reducing soil moisture availability in the gap (Malcom *et al.* 2001). The greater density and closer proximity of nearby perimeter trees in small gaps would have reduced availability of water to seedlings, thus reducing emergence and survival rates. In large gaps, in spite of greater emergence under the higher light conditions, seedlings did not survive long. The low survivorship likely resulted from very low soil moisture content in the large gaps, in keeping with Vyse *et al.* (2006). Many studies have found that soil moisture content in gaps >21 m in diameter than in 11 - 20 m gaps, likely caused by the higher soil surface temperatures and evaporation.

The resulting drought stress in large harvested gaps may explain the greater variability in stem length than in small or medium size gaps.

Mycorrhizal networks and growth potential

Mycorrhizal network treatment interacted with gap size to affect seedling survival, where survival decreased with gap size where seedlings were restricted from forming mycorrhizal networks with perimeter trees, but peaked in medium gap sizes where seedlings could link into a mycorrhizal network. This finding provides partial support for our third hypothesis that regeneration potential would be greatest where Douglas-fir seedlings have access to mycorrhizal networks, provided competition from mature tree roots is low. Teste et al. (2009) found that survival of interior Douglas-fir germinants increased by 25% where they had access to mycorrhizal networks of nearby trees compared to where they had no network access, which agreed with our results in large by not small gaps. Teste and Simard (2008) found that performance of seedlings with access to mycorrhizal networks depended on distance from mature trees, with low survival rates <5 m from the bole due to competition for light and water. The low survival we observed in small gaps where seedlings had access to mycorrhizal networks suggests that competition with mature trees surpassed the resource acquisition benefits of the network. Higher survival of seedlings without network access in small compared with large gaps suggest that the cost of forming mycorrhizal associations may limit establishment of seedlings under marginal conditions (Teste et al. 2009, Bingham and Simard 2012).

Natural abundance of δ^{13} C increased with gap size where seedlings had access to mycorrhizal networks with root presence, suggesting assimilation of δ^{13} C increased under favorable gap size and networking conditions. Vyse *et al.* (2006) similarly found increasing δ^{13} C values in interior Douglas-fir seedlings with canopy openness, and they suggested this could be explained by lower stomatal conductance. Higher δ^{13} C values can result from photosynthetic

efficiency increases with greater light and nitrogen availability (Virgona and Farquhar 1996) or from improved water use efficiency where biomass accumulates at lower stomatal conductance rates (Dawsen *et al.* 2002). As δ^{13} C values were strongly correlated with light rather than soil moisture content in our study, we assume that δ^{13} C values increased due to increased photosynthetic efficiency. Access to mycorrhizal networks and roots appeared to augment this increased photosynthetic efficiency, possibly through increased nitrogen supply by mycorrhizas and root turnover.

Mycorrhizal fungal diversity on regenerating seedlings in harvested gaps was not affected by either gap size or access to mycorrhizal networks. However, the mycorrhizal community assemblage varied with gap size either because of difference in proximity to perimeter trees or soil moisture availability. Moisture conditions are known to affect mycorrhizal fungal community composition of interior Douglas-fir, where dry conditions can limit seedling ability to host certain species of fungus and wet conditions can promote rapid colonization of another (Bingham and Simard 2012). The independence of seedling mycorrhizal fungal diversity from the mycorrhizal network treatment effects resulted from the inclusion of field soil in mesh bags, which would have served to inoculate seedlings equally across all treatments as found in Teste *et al.* (2009) and Simard and Bingham (2013).

2.5 Conclusions

In conclusion, we found that creation of medium size gaps with partial harvesting and provision of access to mycorrhizal networks can improve seedling establishment and survival in dry, cool interior Douglas-fir forests. Regeneration conditions are still favorable in these forests, and modifications of gap size and conservation of mutualistic symbionts during harvesting appear sufficient to ensure good regeneration success. However, none of these techniques provided seedlings with sufficient advantage to successfully establish in the lower elevation dry,

hot interior Douglas-fir forests. There, naturally occurring gaps proved to be hostile environments for seedling establishment due to high soil surface temperatures and low soil moisture availability. It is possible that the period of our study was particularly climatically harsh, but climate projections suggest these conditions will only become more limiting with time. Based on the failure of new regeneration, we therefore predict that the lower elevation forests will gradually transition to grasslands in time, regardless of timber management efforts. Table 1. Temperature and precipitation variables including mean annual temperature (MAT), mean warmest month temperature (MWMT), mean coldest month temperature (MCMT), mean annual precipitation (MAP), mean annual summer precipitation (MSP), and precipitation as snow (PAS) for natural and harvested gap sites collected from Climate BC.

	Harvested gaps	Natural gaps
Mean annual temperature (MAT)	4.6	12.3
(°C) Mean warmest month temperature (MWMT) (°C)	15.8	27.4
Mean coldest month temperature (MCMT) (°C)	-7.3	- 0.6
Mean annual precipitation (MAP) (mm)	384	384
Mean annual summer precipitation (MSP)	178	161
Precipitation as snow (PAS) (mm)	123	30

	Site	n	Elevation (m)	Aspect	Slope (%)	Latitude (N)	Longitude (E)
Harvested gaps	Upper Sawmill	27	1220 - 1260	N – NE	0 - 12	50°52'05" – 50°52'28"	120°33'20" – 120°33'52"
	Lower Sawmill	27	990 - 1098	Ν	0 – 25	50°50'32" – 50°50'58"	120°29'12" – 120°29'37"
	O'Connar Lake	27	920 – 1230	Ν	0 – 28	50°53'.35" – 50°54'02"	120°21'09" – 120°21'44"
Natural gaps	O'Connar Lake	81	870 - 1100	S - SE	0 – 40	50°52'10" – 50°52'57"	120°18'03" – 120°19'44"

Table 2. List of site characteristics including elevation range (m), aspect, slope range (%), latitude (N) and Longitude (E) of the four sites observed in the harvested ad natural gap studies.

		Harvested gaps		Natural gaps	
		#	%	#	%
Small	Mycorrhizal network with roots	18	20.0	3	3.3
	Mycorrhizal network	20	22.2	0	0.0
	No network	29	32.2	8	8.0
	Total	67	24.8	11	4.0
Medium	Mycorrhizal network with roots	38	42.2	3	3.0
	Mycorrhizal network	34	37.8	0	0.0
	No network	29	32.2	5	5.0
	Total	101	37.4	8	2.0
Large	Mycorrhizal network with roots	41	45.6	0	0.0
	Mycorrhizal network	39	43.3	0	0.0
	No network	24	26.7	0	0.0
	Total	104	38.5	0	0.0
Total		272	30.2	19	2.3

Table 3. Emergence rates by total number (#) and percentage (%) for the effects of harvested and natural forest gap size and access to mycorrhizal networks where emergence is of the 90 seeds sown within that.
Table 4. General linear mixed model results for the effects on the number of emerging seedlings (out of 10) and surviving seedlings due to harvested forest gap size (small, medium, and large), access to mycorrhizal network treatment (mycorrhizal network with roots, mycorrhizal network, and no network), and the interaction of size and treatment. (n = 81, $p^{**} < 0.05$)

	<i>x</i> ²	df	p-value
Gap size	91.9060	2	<0.0001**
Mycorrhizal network treatment	30.2861	2	<0.0001**
Gap size x treatment	81.0487	4	<0.0001**
Gap size	5.4836	2	0.0470**
Mycorrhizal network treatment	1.2071	2	0.5469
Gap size x treatment	5.5409	4	0.0877
	Gap size Mycorrhizal network treatment Gap size x treatment Gap size Mycorrhizal network treatment Gap size x treatment	x2Gap size91.9060Mycorrhizal network treatment30.2861Gap size x treatment81.0487Gap size5.4836Mycorrhizal network treatment1.2071Gap size x treatment5.5409	x^2 dfGap size91.90602Mycorrhizal network treatment30.28612Gap size x treatment81.04874Gap size5.48362Mycorrhizal network treatment1.20712Gap size x treatment5.54094

		Harv	Harvested gaps		al gaps
		#	%	#	%
Small	Mycorrhizal network with roots	3	33.3	1	1.1
	Mycorrhizal network	3	33.3	0	0.0
	No network	5	55.6	2	2.2
	Total	11	40.7	3	3.3
Medium	Mycorrhizal network with roots	8	88.9	1	2.2
	Mycorrhizal network	7	77.8	0	0.0
	No network	5	55.6	2	2.2
	Total	20	74.1	3	3.3
Large	Mycorrhizal network with roots	3	33.3	0	0.0
	Mycorrhizal network	3	33.3	0	0.0
	No network	1	11.1	0	0.0
	Total	7	25.9	0	0.0
Total		38	46.9	6.0	6.7

Table 5. Survival rates by total number (#) and percentage (%) for the effects of harvested and natural disturbance forest gap size and access to mycorrhizal networks where survival is of the 9 seedlings established within that treatment.

Table 6. List of means, standard deviations, and maximum and minimum values for harvested forest gap size available light (% full sun) and volumetric soil moisture (m^3/m^3) to describe changes to the environmental conditions of the gap due to gap size and mycorrhizal network treatment.

				Lower S	Sawmill	Upper Sa	awmill	O'Conna	ar Lake
	Mycorrhizal			Light	Soil	Light	Soil	Light	Soil
Gap	network			(% full	water	(% full	water	(% full	water
size	treatment	n		sun)	(m^3/m^3)	sun)	(m^3/m^3)	sun)	(m^3/m^3)
Small	Mycorrhizal	3	Mean	55.726	0.099	53.418	0.135	39.781	0.060
	network		SD	2.897	0.027	18.155	0.097	13.433	0.021
	with roots		Min.	58.822	0.130	74.256	0.210	50.034	0.082
			Max.	53.082	0.076	41.016	0.025	24.575	0.039
	Mycorrhizal	3	Mean	28.497	0.121	44.736	0.157	52.433	0.122
	network		SD	23.932	0.001	24.297	0.044	20.394	0.096
			Min.	56.100	0.122	72.320	0.188	70.345	0.188
			Max.	13.560	0.121	26.508	0.126	30.238	0.011
	No network	3	Mean	70.038	0.131	47.863	0.114	39.346	0.121
			SD	13.010	0.033	13.299	0.050	12.253	0.001
			Min.	81.778	0.154	62.196	0.172	52.873	0.122
			Max.	56.050	0.108	35.922	0.086	28.991	0.121
Medium	Mycorrhizal	3	Mean	73.302	0.154	52.685	0.166	40.705	0.163
	network		SD	19.278	0.069	18.690	0.044	7.473	0.081
	with roots		Min.	87.034	0.195	64.670	0.214	48.335	0.256
			Max.	51.263	0.075	31.150	0.126	33.399	0.104
	Mycorrhizal	3	Mean	37.134	0.144	53.441	0.172	69.604	0.261
	network		SD	11.945	0.036	17.635	0.081	5.878	0.160
			Min.	44.791	0.176	70.324	0.245	75.138	0.440
			Max.	23.370	0.106	35.139	0.085	63.433	0.132
	No network	3	Mean	56.017	0.166	68.930	0.213	41.595	0.180
			SD	10.552	0.067	13.839	0.076	4.824	0.062
			Min.	64.110	0.234	81.411	0.266	46.633	0.247
			Max.	44.083	0.099	54.047	0.159	37.017	0.126
Large	Mycorrhizal	3	Mean	81.053	0.112	55.417	0.085	42.277	0.102
	network		SD	6.120	0.064	9.893	0.043	12.942	0.027
	with roots		Min.	88.060	0.167	66.791	0.111	52.212	0.121
			Max.	76.750	0.042	48.815	0.035	27.641	0.083
	Mycorrhizal	3	Mean	69.469	0.136	59.161	0.105	61.655	0.128
	network		SD	16.859	0.061	9.326	0.009	4.910	0.031
			Min.	79.924	0.203	69.049	0.111	66.926	0.163
			Max.	50.020	0.082	50.522	0.099	57.212	0.104
	No network	3	Mean	65.353	0.163	33.366	0.094	48.988	0.166
			SD	6.299	0.010	8.476	0.037	14.224	0.166
			Min.	71.279	0.174	40.438	0.133	61.108	0.166
			Max.	58.738	0.155	23.971	0.059	33.329	0.166

Table 7. General linear mixed model results for the effects on soil moisture (m^3/m^3) due to harvested forest gap size (small, medium, and large), access to mycorrhizal network treatment (mycorrhizal network with roots, mycorrhizal network, and no network), and the interaction of size and treatment. (n = 72, P^{**} < 0.05)

	<i>x</i> ²	df	p-value
Gap size	8.3725	2	0.0152**
Mycorrhizal network treatment	1.7658	2	0.4136
Gap size x treatment	0.6717	4	0.9548

Table 8. General linear mixed model results for the effects on soil moisture (m^3/m^3) due to natural disturbance forest gap size (small, medium, and large), access to mycorrhizal network treatment (mycorrhizal network with roots, mycorrhizal network, and no network), and the interaction of size and treatment. (n = 67, P^{**} < 0.05)

	f-value	df	p-value
Gap size	0.7468	2	0.4782
Mycorrhizal network treatment	0.7835	2	0.4614
Gap size x treatment	0.4614	4	0.7638

Table 9. Analysis of variance results for harvested forest gap size (small, medium, and large) with elevation included as a covariate and the effects on available light (% full sun). (n = 81, P^{**} < 0.05)

34.1723 1.9900	2 1	< 0.0001** 0.1583
	34.1723 1.9900	34.172321.99001

Table 10. Linear regression results for the effects of harvested forest gap area (m^2) on available light (% full sun). (n = 81, P^{**} < 0.05)

	<i>x</i> ²	df	p-value
Gap area (m^2)	27.5690	2	< 0.0001**

Table 11. List of descriptive statistics of soil surface temperature variables derived from harvested forest gap data measured from August 2012 to August 2013 including mean annual temperature (°C), average summer temperature (°C), average winter temperature (°C), maximum summer temperature (°C), and minimum winter temperature (°C) across small, medium, and large gap sizes (n = 6).

	Small	Medium	Large
	°C	°C	°C
Mean annual soil surface temperature	4.92	5.85	6.47
Average summer soil surface temperature	10.58	12.90	12.38
Average winter soil surface temperature	0.45	0.67	0.37
Maximum summer soil surface temperature	17.95	18.99	23.75
Minimum winter soil surface temperature	-0.01	0.26	-0.26

Table 12. List of means, standard deviations, and maximum and minimum values for seedling growth variables and natural abundance $\delta^{13}C$ to describe changes to seedling growth and Carbon usage due to harvested forest gap size and access to mycorrhizal networks.

Gap	Mycorrhizal	n		Stem	Stem	Needle	Root	Total	Natural
size	network			length	weight	weight	weight	biomass	$\delta^{13}C$
	treatment			(cm)	(g)	(g)	(g)	(g)	abundance
									(‰ VPDB)
0	NA	_		7 000	0.000	0.000	0.045	0.400	00.040
Small	Mycorrnizal	5	Mean	7.380	0.029	0.093	0.045	0.169	-30.646
	network		SD	2.942	0.005	0.142	0.028	0.154	0.405
	with roots		Min.	10.800	0.035	0.346	0.078	0.437	-30.140
		~	Max.	3.900	0.024	0.015	0.012	0.051	-31.020
	Mycorrhizal	3	Mean	5.466	0.031	0.018	0.046	0.086	-29.823
	Network		SD	3.156	0.004	0.011	0.028	0.048	0.930
			Min.	8.500	0.036	0.026	0.063	0.120	-29.090
	N I / I	~	Max.	2.200	0.028	0.010	0.014	0.052	-30.870
	No network	3	Mean	5.100	0.028	0.026	0.028	0.085	-30.916
			SD	1.473	0.004	0.000	0.000	0.002	0.306
			Min.	6.000	0.033	0.027	0.029	0.087	-30.730
	•••	_	Max.	3.400	0.024	0.026	0.028	0.084	-31.270
Medium	Mycorrhizal	7	Mean	9.280	0.027	0.061	0.125	0.213	-30.932
	network		SD	3.099	0.005	0.047	0.103	0.149	1.130
	with roots		Min.	14.200	0.033	0.127	0.277	0.434	-29.560
		_	Max.	6.900	0.019	0.010	0.020	0.062	-32.650
	Mycorrhizal	7	Mean	8.671	0.030	0.054	0.054	0.140	-29.901
	Network		SD	1.947	0.004	0.036	0.061	0.074	0.933
			Min.	10.300	0.036	0.121	0.190	0.286	-28.370
		_	Max.	5.300	0.025	0.017	0.015	0.069	-31.280
	No network	8	Mean	7.862	0.030	0.068	0.124	0.229	-30.290
			SD	3.045	0.003	0.053	0.115	0.166	0.908
			Min.	12.200	0.036	0.185	0.284	0.502	-28.800
	•• ••		Max.	4.400	0.026	0.022	0.010	0.081	-31.400
Large	Mycorrhizal	1	Mean	4.800	0.032	0.030	0.035	0.097	-29.160
	network		SD	na	na	na	na	na	na
	with roots		IVIIN.	4.800	0.032	0.030	0.035	0.097	-29.160
		~	Max.	4.800	0.032	0.030	0.035	0.097	-29.160
	Mycorrnizal	3	Mean	8.300	0.032	0.095	0.118	0.246	-31.053
	Network		SD	5.204	0.000	0.114	0.157	0.271	0.552
			Min.	14.300	0.033	0.227	0.300	0.559	-30.560
	NI / 1	~	Max.	5.000	0.032	0.026	0.015	0.074	-31.650
	No network	3	Mean	12.066	0.031	0.112	0.178	0.322	-28.880
			SD	6.050	0.003	0.079	0.129	0.205	1.050
			Min.	16.000	0.034	0.184	0.309	0.520	-28.200
			Max.	5.100	0.027	0.026	0.051	0.110	-30.090

Table 13. Analysis of varience results for the effects on Natural abundance $\delta^{13}C$ in stem tissues of seedlings growing in different sized forest gaps (small, medium, and large) and in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, and no network), and the interaction of gap size and treatment. (n = 41, p** < 0.05)

	<i>x</i> ²	df	p-value
Gap size	3.5798	2	0.1669
Mycorrhizal treatment	2.4506	2	0.2936
Gap size x treatment	15.1907	4	0.0043**

	f - value	p - value
Available light (% full sun)	10.000	0.0032**
Volumetric soil moisture content (m^3/m^3)	0.0136	0.9079
Foliar nitrogen content (g)	0.2645	0.6103

Table 14. Linear regression results showing the relationship between natural abundance δ^{13} C (‰ V-PDB) of needle tissues of interior Douglas-fir seedlings and available light (% full sun), soil moisture content (m^3/m^3), and foliar nitrogen content (g). (n = 41, p** < 0.05)

Table 15. Analysis of variance results for the effects on stem length (cm), stem weight (g), needle weight (g), root weight (g), total biomass (g), and root: shoot ratio (g) of interior Douglasfir seedlings grown in different sized harvested forest gaps (small, medium, and large), in different mycorrhizal treatments (mycorrhizal network with roots, mycorrhizal network, and no network), and the interaction of gap size and treatment. (n = 41, p** < 0.05)

	Size	Treatment	Size*Treatment
	р	Р	Р
Stem length (cm)	0.0313**	0.5678	0.2274
Stem weight (g)	0.2548	0.7519	0.6905
Needle weight (g)	0.2298	0.3865	0.6503
Root weight (g)	0.7001	0.7489	0.9507
Total biomass (g)	0.2748	0.6977	0.5905
Root : Shoot ratio (g)	0.6723	0.6688	0.7562

	Size	Treatment	Size*Treatment
	Р	Р	Р
Al (g)	0.2317	0.7561	0.7936
B (g)	0.3433	0.8933	0.6652
C (g)	0.2371	0.9487	0.6515
Ca (g)	0.6880	0.9367	0.4002
Cu (g)	0.2071	0.8335	0.4992
Fe (g)	0.2083	0.9450	0.7873
К (g)	0.1772	0.8229	0.7073
Mg (g)	0.1651	0.7952	0.6055
Mn (g)	0.3963	0.7801	0.1985
N (g)	0.2295	0.9409	0.5060
P (g)	0.1790	0.6239	0.6482
S (g)	0.7787	0.2790	0.4050
Zn (g)	0.2028	0.9462	0.2981
C:N	0.1259	0.0301**	0.1132
N:P	0.5334	0.4780	0.8574
N:K	0.2955	0.7120	0.5434
N:Mg	0.4008	0.4536	0.4843
N:Ca	0.7695	0.9200	0.6887
N:S	0.1745	0.5306	0.7147

Table 16. Analysis of variance results for the effects on the foliar nutrient content (g) and ratios due to forest gap size (small, medium, and large), access to mycorrhizal network treatment (mycorrhizal network and roots, mycorrhizal network, and no network), and the interaction of size and treatment. (n = 35, $P^{**} < 0.05$)

Table 17. Analysis of variance results for the effects on Shannon diversity index, species richness, and percent root colonization of ectomycorrhizal fungal species on the fine root tips of interior Douglas-fir seedlings grown in the center of different sized forest gaps (small, medium, and large), in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, and no network) and the interaction of gap size and treatment. (n = 35, p** < 0.05)

	Size	Treatment	Size*Treatment
	р	р	р
Shannon Diversity	0.2615	0.5897	0.1824
Species Richness	0.1798	0.2731	0.1434
Percent root colonization	0.3461	0.4256	0.9154



Figure 1. Google map (© 2015 Google) image of Kamloops, BC, Canada, with three sites in red from the harvested gap study (Upper Sawmill, Lower Sawmill, and O'Connor Lake) and one site in black from the natural gap study.



Figure 2. Average emergence rate of interior Douglas-fir seedlings growing in the center of different sized harvested and naturally occurring forest gaps (small, medium, and large) and in different treatments for access to mycorrhizal networks (mycorrhizal network with roots, mycorrhizal network, and no network). Error bars represent 95% confidence intervals and different lower-case letters indicate averages that have a significant difference greater than p = 0.01. (n = 9 for each treatment level)



Figure 3. Average survival rate of interior Douglas-fir seedlings growing in the center of different sized harvested and naturally occurring forest gaps (small, medium, and large) and in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, and no network). Error bars represent 95% confidence intervals and different lower-case letters indicate averages that have a significant difference greater than p = 0.01. (n = 9 for each treatment level)



Figure 4. Average soil moisture content (m^3/m^3) available for seedlings growing in different sized harvested and naturally occurring forest gaps (small, medium, and large) and in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, and no network). Error bars represent 95% confidence intervals and different lower-case letters indicate averages that have a significant difference greater than p < 0.01. (Harvested gaps: n = 24 for small, 27 for medium, and 21 for large gap sizes) (Natural Gaps: n = 24 for small, 27 for medium, and 21 for large gap sizes)



Figure 5. Average available light (% full sun) to seedlings growing in in the center of different sized harvested forest gaps (small, medium, and large) with error bars representing 95% confidence intervals. Different lower-case letters indicate averages that have a significant difference greater than p = 0.05. (n = 27 for each gap level)



Figure 6. Available light (% full sun) to seedlings growing in the center of harvested forest gaps of varying size (m^2) and in different treatments for access to mycorrhizal networks (Mycorrhizal network with roots, mycorrhizal network, and no network) with a calculated regression line for the relationship. (n = 81, p = 0.0244)



Figure 7. Average natural abundance $\delta^{13}C$ (‰ V-PDB) of seedlings grown in different sized forest gaps (small, medium, and large) and in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, and no network). Different lower-case letters indicate averages that have a significant difference greater than p = 0.01. (n = 11 for small, 22 for medium, and 7 for large mycorrhizal treatment levels)



Figure 8. Natural abundance $\delta^{13}C$ (‰ V-PDB) across varying levels of available light (% full sun), soil moisture (m^3/m^3), and foliar nitrogen content (g) of seedlings growing in the center of harvested forest gaps with calculated regression lines for the relationships. (n=41 for each regression)



Forest gap size

Figure 9. Average stem length (cm) of seedlings grown in different sized harvested forest canopy gaps (small, medium, and large) with error bars representing 95% confidence intervals. Different lower-case letters indicate averages that have a significant difference greater than p = 0.01. (n = 11 for small, 22 for medium, and 7 for large mycorrhizal treatment levels)



Figure 10. Average C : N ratio in foliar tissues of seedlings grown in different mycorrhizal network treatments (mycorrhizal network with roots, mycorrhizal network, no network) with error bars representing 95% confidence intervals. Different lower-case letters indicate averages that have a significant difference greater than p = 0.05. (n = 12 for small, 13 for medium, and 12 for large mycorrhizal treatment levels)



Figure 11. NMDS ordination of ectomycorrhizal morphotype communities on fine roots of interior Douglas-fir seedlings grown in small, medium, and large size gaps. Arrows represent the environmental variable in ordination space, where the direction represents the strongest correlations and the length represents the magnitude of the relationship. Only significant environmental variables (P<0.05) are shown. The oval overlays represent centroid data for gap sizes and suggest similar community assemblages.

Chapter 3: Conclusions

As we witness hotter and drier conditions in interior Douglas-fir ecosystems as well as higher magnitudes and severities of disturbances, we can expect seedling mortality to increase for species such as interior Douglas-fir in the lower elevations of their historical range. Using climate models, we can identify which areas are most likely to experience these extreme conditions and which forests are most at risk (Hamann and Wang 2006). Our interaction with these ecosystems will therefore have large consequences and it is important that we consider shifting from forest management, where we gain economic value from these forests, to a forest stewardship approach, where add value to the system and maintain it. The Opax Mountain Silviculture Systems Project provided a robust look at interior Douglas-fir regeneration including canopy gap size effects in dry forests (Huggard *et al.* 2005) and multiple studies have examined seedling benefits from mycorrhizal networks (Bingham and Simard 2012). This paper integrates these important regeneration factors and provides evidence of a gap size threshold where increased light no longer benefits tree growth and survival suffers due to lack of soil moisture. I also provide evidence of regeneration failure of interior Douglas-fir at elevations near the interface of the IDF zone with the PP and BG zones.

3.1 Review of objectives

The objective of this study was to determine whether the regeneration potential of interior Douglas-fir was affected by forest gap size and access to mycorrhizal networks. I tested three main hypotheses: (1) regeneration potential would be lower in the naturally occurring than harvested canopy gaps because of more extreme resource limitations at the lower elevation forest, even though these seedlings may be better adapted to the natural than human-caused disturbances, (2) regeneration potential would be greatest in medium sized gaps because of an optimal combination of resource availability (light, water and nutrients), and (3) regeneration

potential would be greatest where Douglas-fir seedlings have access to mycorrhizal networks, but this would be reduced where access to networks was accompanied by root competition from neighbors.

3.2 Summary of main findings

Hypothesis 1: Natural vs. harvested gaps

I found lower regeneration success in natural gaps than in harvested gaps. Low germination and survival in the natural gaps was due to lower available soil moisture. This was mainly driven by the climate of the low elevation site, where temperatures were high and precipitation low. For this reason we accept our first hypothesis, that regeneration success was low due to climate, regardless of variation in disturbance severity (i.e., gap size).

Hypothesis 2: Forest gap size

Interior Douglas-fir seedlings that grew in forest gaps of $20 - 80 m^2$ had lower available light and lower soil moisture content compared to gaps larger than $300 m^2$. Light and moisture are believed to be the reason for the low emergence and survival witnessed in small sized gaps. Interior Douglas-fir seedlings grown in small gaps also had the shortest stem length compared to larger sized gaps, suggesting that not only do these trees exhibit low emergence and survival, but those that do survive have stunted shoot growth.

Interior Douglas-fir grown in large gaps had higher available light than smaller sized gaps; however, the increase in solar radiation also increased evaporation and root competition, creating low soil moisture conditions. The high available light also increased temperature which is important for seedling germination and explains the high emergence rate seen in large gaps; however, high available light also decreased soil moisture, explaining the low water use efficiency of seedlings growing in large gaps. The lowered water use efficiency and greater available light decreased survival in larger gaps. Although larger gaps produced some of the

tallest seedlings, the variance in height was large and the average height was not much greater than medium sized gaps.

Interior Douglas-fir seedlings grown in medium sized gaps $(80 - 300 m^2)$ had moderate levels of available light. As with the large sized gaps, higher light levels in the medium sized gaps increased temperatures and led to higher emergence rates. Soil moisture availability was highest in medium sized gaps, which led to greater water use efficiency and increased survival rates. Medium gaps also produced consistently taller seedlings than small sized gaps. This data tells us that medium sized gaps created optimal conditions for interior Douglas-fir regeneration under current climatic conditions and we therefore accept our second hypothesis.

Hypothesis 3: Mycorrhizal networks

The mycorrhizal network effects were complex. I found mycorrhizal networks affected emergence rate, and when interacting with gap size, they also affected survival. Emergence increased with gap size for seedlings that had access to mycorrhizal networks, but survival was highest in medium sized gaps. These findings provide partial support for our third hypothesis that regeneration potential would be greatest where Douglas-fir seedlings have access to mycorrhizal networks, provided competition from mature tree roots is low. The low survival we observed in small gaps where seedlings had access to mycorrhizal networks suggests that competition with mature trees surpassed the resource acquisition benefits of the network. Higher survival of seedlings without network access in small compared with large gaps suggest that the cost of forming mycorrhizal associations may limit establishment of seedlings under marginal conditions.

Water use efficiency was greatly affected by the interaction of gap size and mycorrhizal network access, where natural abundance of δ^{13} C increased with gap size where seedlings had access to mycorrhizal networks with root presence. This result suggests photosynthetic efficiency or water use efficiency increased under favorable gap size and networking conditions.

Low sample sizes for large gaps made the results somewhat difficult to interpret, however, the increased drought stress in large gaps in the no network treatments could have been caused by the bags ability to limit root egress. In the mycorrhizal network treatment, the network would still be interacting with the surrounding plants and available water may have been used by some of the surrounding plants and grasses.

Mycorrhizal fungal diversity varied with gap size either because of differences in proximity to perimeter trees or soil moisture availability. Moisture conditions are known to affect mycorrhizal fungal community composition of interior Douglas-fir, where dry conditions can limit a seedling's ability to host certain species of fungi, whereas wet conditions can promote rapid colonization of others.

3.3 Contributions to the field of study

Climate projections have indicated that IDF forests will be dealing with climate extremes outside of their natural range of tolerance, but we have not seen exactly what this means in the field. This study adds to the growing body of evidence that climate change has the potential to reduce regeneration potential in the lower and drier ranges of the species, and we must therefore address how to manage these changes in the coming years. Forest managers and ecologists have struggled with regeneration in these areas but despite the many innovative silviculture techniques, we still see very low regeneration (Griesbaur and Green 2010). By mimicking natural disturbances to initiate gap-phase regeneration, we may leave the forest with a legacy better suited to interior Douglas-firs adaptive strategies. Regardless, efforts should be made to decrease harvesting in areas of extreme risk.

3.4 Study limitations

Low survival was the key limitation to this study creating small sample sizes and reducing our statistical power. In the case of the natural gaps, the sample size was too low to

run parametric statistics. Low survivorship in large gaps for both studies limited the sample sizes for many of the seedling growth responses. Another limitation was the short duration of the study. One more year of growth may have increased seedling biomass enough to detect gap size and mycorrhizal network effects.

Another limitation was that the complex interactions between gap size, gap shape, and aspect that were not fully taken into account in the experiment. These large scale features should be accounted in future studies as I can influence water balance budgets for plants.

When planning a study involving the dry interior forests of British Columbia, it is important to anticipate very low survival and this should be reflected in the amount of replication. Even though we used nine replicates per treatment in the natural gap study, it was still not enough to ensure usable data for parametric statistics. Survival studies looking at ecosystem thresholds should incorporate wetter ecotones, preferably along moisture, elevation, and temperature gradients to ensure some survival in these harsh conditions. It would also be beneficial to format this data into a standardized data set so that multiple studies could be looked at over time to average the changes in rates of survival over time. In this scenario, had we not had the harvested gap experiment to compare to, the resources used to set-up and run the natural gaps would have gone to waste.

3.5 Applications and further research

The IDF is a complex adaptive system. Many management practices appear poorly aligned with the nature of this complexity (Huggard *et al.* 2005). The main objective has been timber harvesting, but it is evident that interior Douglas-fir is not regenerating as expected in dry ecosystems. Timber harvesting, although drastically reduced, is still happening in much of the dry IDF forests and it is important that we attempt to leave legacies in the forest that will facilitate their persistence in these areas. This research can be used by forest managers that are worried about the success of planted seedlings at reaching free- to-grow standards. If

harvests are designed in a way that is beneficial to naturally regenerating seedlings, with some shade from surrounding trees and space to thrive outside of their dripline, there is a possibility that natural regeneration could succeed if the planted seedlings fail. By mimicking natural disturbances to initiate gap-phase regeneration, we may succeed in leaving legacies better suited to interior Douglas-firs adaptive strategies.

When designing our studies and harvesting practices it will be important to use complex adaptive management strategies in order to prepare for all possible outcomes. This study has shown that our expectations for survival in some ecosystems are too high and we will need to monitor survival in these areas to determine regeneration rates. With low regeneration success, we need to look at alternate economic uses for these forests such as recreation in order to limit our disturbance practices especially in areas of great concern. Using the BEC zone classification system will also be important to identify areas of concern as the hottest and driest subzones have already been identified and will probably be the first indicators of forest health with changing climate.

Observing all plant communities and their interactions with water relations will be an important next step in gap dynamics. How pinegrass' competitive effects were not taken into account in this study and future studies should try to incorporate other strong competitors for water resources and how their source/sink contributions influence water accessibility over different time scales.

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