Tree Regeneration in Single-Tree Selection Gaps in the Mixed Conifer Forests of the Sierra Nevada

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Abstract   Localized loss of canopy by natural or anthropogenic forces creates canopy gaps, providing changes in environmental conditions and influencing species recruitment. While gap dynamics in Eastern deciduous forests and tropical rain forests are well studied, little is known about the effect of gaps in the Sierran mixed conifer forests. Silvicultural implementation of gaps by selective logging could be important for small land-owners by providing a method to create revenue while still maintaining a continuous canopy cover. This study looked at ~0.04 hectare gaps created by single-tree selection in two compartments at University of California Berkeley's Blodgett Forest Research Station. Following creation of gaps, material was piled and burned to create an ash substrate in gap centres. Seedlings in the gaps and in the background of the stand were measured in one compartment a year after the harvest, and in the other compartment three years after harvest. Species, substrate, age, and location were recorded for each seedling. Gaps have higher densities of fir seedlings (Douglas-fir, *Pseudotsuga menziesii*, and white fir, *Abies concolor*) than pine (ponderosa pine, *Pinus ponderosa*, and sugar pine, *Pinus lambertiana*) or incense-cedar (*Calocedrus decurrens*) seedlings. Firs prefer areas with high amounts of bare mineral soil to those with high amounts of litter. There was no clear relationship between gap size and seedling density. This study shows no strong evidence that single-tree selection gaps of this size increase the regeneration of timber species in the Sierra Nevada mixed conifer forest.

Introduction

Disturbances create changes in the type and distribution of species in systems. The type, size, magnitude, and frequency of disturbance regimes strongly influence the structure and composition of the communities (Sousa 1984, Franklin *et al.* 2004). For example Franklin *et al.* (2004) showed that changes in the fire return interval (frequency of disturbance) in chaparral pushed a community previously dominated by obligate resprouting shrubs, to one in which both obligate resprouting and obligate seeding shrubs existed. In forests, the size and type of the disturbance have both been shown to be important in determining the pattern and type of regeneration that takes place (McCarthy 2001, Pham *et al.* 2004). Though shade tolerant tree species can germinate and develop under a closed canopy, shade intolerant species require the increased light that comes from openings that disturbances create in the canopy to germinate and develop (McCarthy 2001). The dependence of shade intolerant species on canopy openings for the establishment of a new generation of individuals makes disturbances very important in determining the structure of forest communities. One way a disturbance may manifest itself in a forest is in the creation of a gap.

A common definition for a gap is "a gap is a 'hole' in the forest extending through all levels down to an average height of two meters above ground" with a diameter significant enough for it to effect forest dynamics (Brokaw 1987). In places where catastrophic disturbances such as stand replacing fire and windthrow events are rare, gap disturbance dynamics can be very important in creating space for new individuals (McCarthy 2001). Unique ground conditions are created in gaps such as increased light, decreased root competition, increased temperature, and soil disturbance (Ritter *et al.* 2005, McClure and Lee 1993). Increased light and other effects of the gap are not limited to the area directly under the hole in the canopy but extend out into the stand under the surrounding trees (Runkle 1982, Canham *et al.* 1990). Increased light penetration can be detected in the surrounding canopy as well as in the center of the gap (Canham *et al.* 1990). Increased light may improve the ability of light-limited species to colonize gaps, but the lower soil moisture content in the high light areas becomes the limiting factor in dry enviornments (Page and Cameron 2006). Disturbance at the ground level exposes bare mineral soil on which trees germinate at higher rates (Valkonen and Maguire 2005). However, not all soil disturbances are necessarily positive to seedlings establishment and growth.

Mycorrhizal-colonized roots have been found to be less common in gaps (Parsons *et al*. 1994), which could lead to reduced nutrient supply for the seedlings.

The processes that create gaps also influence regeneration patterns and stand composition (Hill *et al*. 2005). For example, though both fire and disease kill trees and create gaps of varying sizes, fires remove the organic matter and small unrelated plants that would compete with the seedlings (Schimmel and Granstrom 1996) while soil diseases leave all of these organisms and organic materials behind. Following disease, branches and leaves drop to the ground, creating a thicker layer of organic material over the soil (Franklin *et al*. 1987) in which some tree germination is less favorable (Valkonen and Maguire 2005). In the Sierran mixed-conifer forest, the establishment of conifer seedlings have been found to be unsuccessful in coarse woody debris and to occur in greatest densities in bare mineral soil (Gray *et al.* 2005). Logging, as does other disturbances, changes the distribution and type of soil cover. Logging creates disturbances to the forest floor covering that can range in scale and severity from that of small insects and disease outbreaks to that of catastrophic fires.

Many organizations and individuals manage parts of the Sierra Nevada mixed conifer forests using some type of logging. The logging can be used to achieve many diverse management goals, such as maximizing short term profit, sustaining long term resource availability, reducing fire hazard, improving recreation, and disease prevention in the Sierra Nevada. Many methods of felling and log recovery are used to achieve the different goals. Methods vary from creating many small single tree openings to large 16 hectare open spaces in stands: group selection, single-tree selection, shelter wood, seed tree, and clearcutting are types of harvest systems being used in the Sierran mixed conifer forest and are covered in detail in Helms and Tappeiner (1996). The machines used for felling and removing trees can cause soil compaction which retards tree growth while at the same time opening up patches of bare mineral soil which increases seed germination (Hatchell *et al*. 1970). Activity fuels, the dead plant material added to the forest floor during logging, can be left on the forest floor, burned, or collected for use in co-generation power plants. The type of machinery used and how activity fuels are treated depend on the age, composition, and management goals for the stand being harvested.

Forest management goals for many areas have changed over the years and with this methods have also changed from practices such as clear cutting, even-aged, single species stands, and other practices that do not mimic common natural settings; this has led some foresters to

implement single-tree selection (Coates and Burton 1997). Single-tree selection is a method of logging in which the removal of trees create small gaps while maintaining the overall structure of the stand. The loss of small parts of the stand more closely mimics the natural processes where a mosaic of early and late succession areas compose the forest (Jones 1945). Other advantages of small gaps created by single-tree selection are that they have less chance of colonization by invasive species, allow for multi-aged stands, and retain wildlife habitat (Coates and Burton 1997, Battles *et al*. 2001).

In the gaps created by single-tree selection, regeneration occurs at several different levels which can compete for dominance in the gap. When established trees, suppressed by shade, are released, they may grow quickly due to a significant increase in light availability (Murphy *et al*. 1998, Parish and Antos 2006). In larger gaps this advanced regeneration can be overtopped by faster growing shade intolerant species that seed in after the creation of the gap (Shure *et al.* 2006). Larger gaps let in more light (Canham *et al.* 1990) changing the available resources and the relative success of different species. Both gap size and age has shown to be related to the density of regeneration in some species of eastern North American hardwood forests (McClure and Lee 1992). In group selection gaps in the Sierra Nevada, larger openings have been shown to increase the height growth of seedlings across timber species (York *et al.* 2003). In the undisturbed Sierran mixed conifer forest understory, low soil moisture has been shown to be the main limiting factor for seedling survival (Gray *et al.* 2005). In longleaf pine woodlands single-tree selection has been shown to create conditions adequate to maintain regeneration (Pecot *et al.* 2006). Little data has been collected on single-tree selection in Sierran mixed conifer forest.

The trees in a Sierran mixed conifer forest can be expected to react to gaps as do species in other environments. These species will be influenced by the changed light, moisture, temperature, and biotic conditions in gaps. The dominant tree species in the Sierran mixed conifer forest are: incense-cedar (*Calocedrus decurrens* Florin), Douglas-fir (*Pseudotsuga menziesii* Franco var. *menziesii*), white fir (*Abies concolor* Hildebrand), sugar pine (*Pinus lambertiana* Douglas), and ponderosa pine (*Pinus ponderosa* Lawson).

The species in the study vary in their shade tolerance. Ponderosa pines are the most shade intolerant of the conifer species at Blodgett Forest Research Station (BFRS) (Minore 1988). Since ponderosa pines develop deep taproots very quickly they are tolerant to drought (Page and Cameron 2006). This trait facilitates ponderosa pine's colonization of drier sites, such as the

centers of gaps where light levels are high and soil moisture is diminished (Page and Cameron 2006). Sugar pines are more shade tolerant than ponderosa pines though still relatively shade intolerant when compared with the other tree species found in the Sierra Nevada mixed conifer forest (Minore 1988). Douglas-fir is slightly more shade tolerant than sugar pine. (Minore 1988). Incense cedars are shade tolerant (Gersonde and O'Hara 2005) so they can develop under relatively closed canopies. White fir also has high shade tolerance (Minore 1988). It is present throughout the understory, even in the absence of gaps, due to its ability to tolerate shady conditions (Gersonde and O'Hara 2005).

This study examines seedling establishment of several commercial timber species within and outside of single-tree selection. I ask the following questions:

    i.   Does seedling density differ inside and outside of a gap?

    ii   Does a species' shade tolerance correlate with its distribution of seedlings relative to gaps?

    iii Does gap size effect seedling density?

    iv. Does soil cover affect seedling density?

This study will help show the extent of new trees recruited after harvests in gaps (within the range of sizes examined). A clearer understanding of the regeneration in single-tree selection managed stands of the Sierran mixed conifer forest could increase harvest efficiency while still achieving the same ecological management goals.

 The following are the hypotheses that I will be testing:

    i.   The density of regeneration within the gaps will be higher than the background regeneration of the compartments because of the increased light and bare mineral soil.

    ii. The ratio of shade intolerant to shade tolerant trees will be higher inside the gaps than outside because the lower light levels outside of the gaps will favor shade tolerant species.

    iii. There will be a higher density of seedlings in larger gaps since there will be more light in larger gaps and light is an important limiting factor for some of these species (Minore 1988).

    iv. Based on previous research (Valkonen and Maguire 2005), I predict there will be a higher density of seedlings on the bare mineral and charred soil than on the litter and coarse wood material covered.

These were tested by sampling single-tree selection gaps for conifer seedling regeneration in two stands in the Sierra Nevada of California.

Methods

  Study Site   The study area is a mixed conifer forest at the University of California at Berkeley's Blodgett Forest Research Station (BFRS) on the west side of the Sierra Nevada Range, near the community of Georgetown, California.   The dominant species in this mixed conifer forest are sugar pine, ponderosa pine, Douglas-fir, white fir, incense-cedar, and black oak.

  The research station is composed of 109 compartments. To examine the effects of single-tree selection gaps on regeneration, two compartments (230 and 110) were examined in this study that have been under single-tree selection silviculture since the 1950's and 1970's respectively. Since this management system was applied, each compartment has been harvested approximately once every 10 years (Olsen and Helms 1996). In order to minimize the differences caused by elevation, these compartments, similar in elevation, (both between 1255 meters and 1329 meters above sea level) were selected. To address the effects of time since harvest on recruitment, the two compartments were harvested in different years. Compartment 230 was harvested last in 2004 and compartment 110 was harvested last in 2006 (Table 1).

  Logging Treatment To create the gaps for this study, the single-tree selection gap logging was done using conventional felling (chainsaws). The logs were yarded (taken to the road) using a track laying skidder. Following the logging, the slash was piled by hand or excavator in the center of gaps (avoiding areas of advanced regeneration of ponderosa and sugar pine seedlings) and then burned during the fall, producing the various soil cover types that were investigated.

Table 1 Compartment Sampling

Compartment	Gaps	Permanent Plots	Year Logged
110	39	15	2006
230	34	13	2004

  Sampling Method   To estimate regeneration in single-tree selection gaps while reducing variation by maximizing sample size and minimizing effects of seasonal changes, every gap in both compartments was sampled for presence of tree seedlings between the dates of August 18 and August 26, 2007.   The sampling procedure consisted of running two-meter wide transects along the north-south and

east-west axis crossing the gap-marking stake. Post burning, these gap-marking stakes were placed in the middle of the burn piles, and therefore approximate the center of the gaps. Gap effects may extend beyond the opening in the canopy (Runkle 1982); therefore, transects extend from the pile in the center of the gap to three meters beyond the surrounding trees' dripline so that the full effect of the gap on regeneration would be measured.

To estimate "background" (i.e. non-gap) regeneration samples were taken from existing permanent plots. The background regeneration provides a comparison for the gap data so that the effect of the gap can be measured. Permanent plots, situated on grids in both compartments were placed and maintained by BFRS to aid in the estimation of stand growth. Transects two meters wide by ten meters long were run through the centers of these plots, along the same axis as the transects in the gaps, to serve as data on the background seedling establishment in the stands (Table 1). The same data were collected at the permanent plots as at the gap plots in each compartment. Data from the permanent plots serve as controls to see if the variation between the gap and background is greater than the variation observed in the stand.

To determine the composition of the regeneration in the gaps height, distance from gap center, soil cover type, and species of each seedling more than eight cm tall were recorded for each gap. The length of each transect was also measured to allow the densities of seedlings to be calculated and to account for differences in gap size affecting density of regeneration.

To analyze the effect of soil cover on seedling density total coverage of transects by each soil coverage type was estimated by visual inspection. The four soil cover type classifications used were: bare mineral soil, charred soil, litter, and coarse woody debris. Bare mineral soil was defined as soil that has not been burned and could be easily seen without disturbing any material on the soil. Charred soil was defined as the area covered by the burn pile; this was clearly visible as a different color from the rest of the soil. Litter soil cover was defined as areas where the mineral soil surface was not clearly visible without disturbing the material on the soil surface. Coarse woody material was defined as soil covered by pieces of wood larger than one inch in diameter.

The seedlings were identified by species to determine if shade tolerance affected the distribution and density of the seedlings. Due to the absence of distinguishing characteristics, some ponderosa pine and sugar pine had to be grouped under the classification *Pinus* sp. and some Douglas-fir and white fir had to be grouped together as well which limits the precision in

determine the effect of shade tolerance of seedlings on their distribution. Due to time constraints, trees less than eight cm tall in compartment 230 were counted without concern to species, exact height, or soil cover. Eight cm was chosen as the cut off for these data because all trees under this height appeared to be less than a year old. Location for these seedlings was only recorded as within (below the hole created in the canopy) or beyond the gap (from the drip line to three meters from the drip line) and no gap (permanent plots). Due to this lack of information, data from compartment 230 for first year seedlings could only be used for analysis that does not take into account species. For compartment 110 seedlings less than eight cm tall were counted to species, soil cover type, and within and without the gap. These data were used for all questions except the analysis of distribution of seedlings within the gap.

Statistics Seedlings were analyzed by age classes. Densities of seedlings within gaps and without the gap were analyzed using t-tests assuming unequal variances. Seedling densities between species were analyzed using matched pairs t-tests. A standard regression was run to compare seedling density within the gap to post-gap areas as well as size and seedling density relationships. Due to the non-normal distribution and large number of zeros, correlation between soil cover type and seedling density was analyzed using the nonparametric test Spearman's ρ. Only first year seedlings were analyzed in compartment 110 since these gaps were only one year old. All analysis was run using JMP statistical software (JMP 7.0, SAS, Cary, North Carolina).

Results

Species Composition "Fir" (Douglas fir and white fir) had the highest density within gaps and in the background of the stand for first year seedlings (Fig.1). For second year seedlings, ponderosa pine had the lowest density while incense-cedar and white fir had the highest density of the second year seedlings (Fig. 2). For third year seedlings incense-cedar had the highest density and Douglas-fir had the lowest density in gaps, while ponderosa pine had the lowest density and white fir had the highest density in stand background (Fig. 3).

Pooled Species Densities First year seedlings density was higher in forest compartment 230 (C230) than in forest compartment 110 (C110) (t = 2.398, df = 13.38, p = 0.0159) (Fig. 4). Due to this difference in background regeneration the two forest compartments were analyzed separately. In C110, when all species were pooled together, there was no difference in the density of first year seedlings between background and gap plots (t = -0.959, df = 39.57, p =

0.1716) (Fig. 4). The density of first year seedlings pooled together by species in C230 was higher in gap than in background plots (t = -1.682, df = 44.53, p = 0.0497) (Fig. 4). There was a higher density of second year seedlings in gaps than in the background of the stand when all species where pooled together (t = -1.8436, df = 42, p = 0.0361) (Fig. 5). Third year seedlings showed no significant density difference between background and gap plots when the species were pooled together (t = 0.9466, df = 11.7530, p =0.1815).
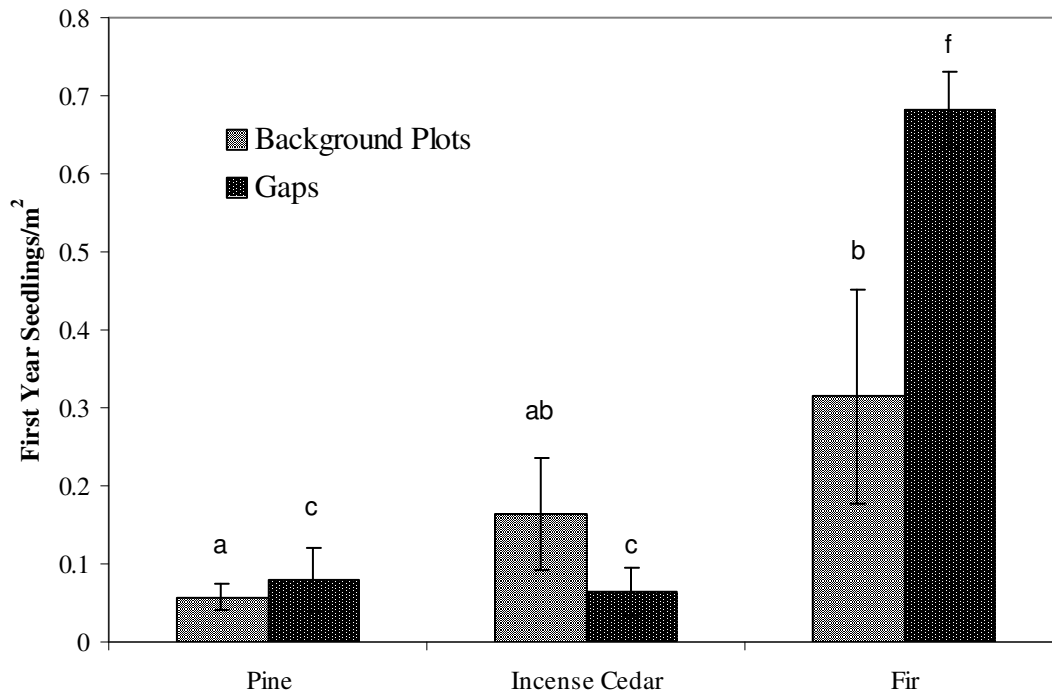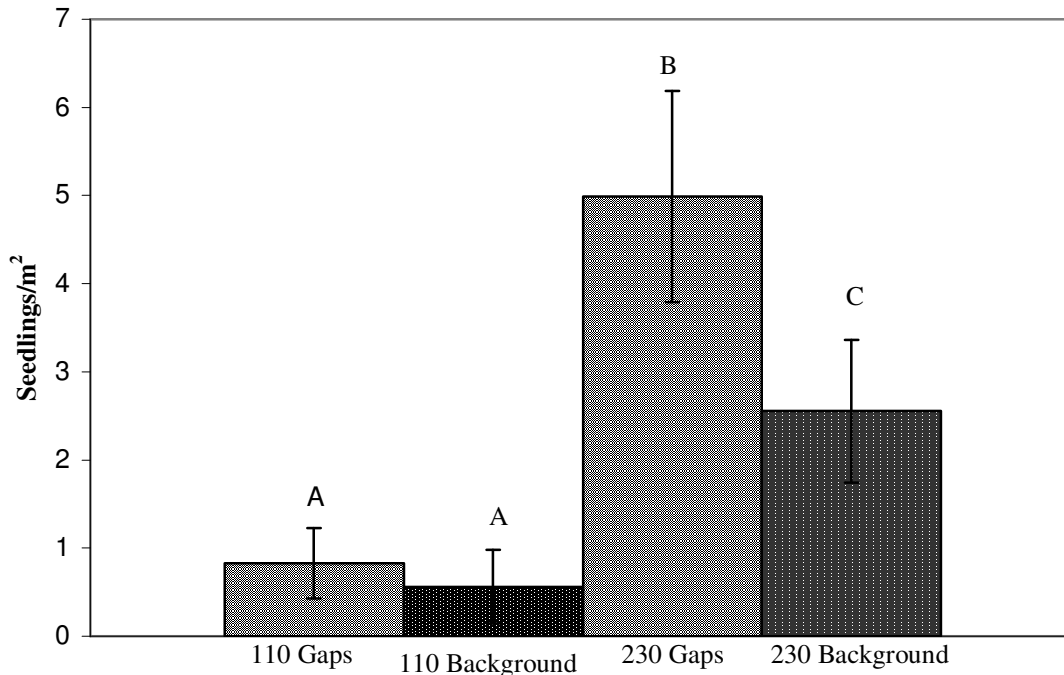

Figure 1 Density of first year seedlings in C110 by species and location within gaps or background plots. Using a t-test assuming unequal variance there was no significant (p < 0.05) differences between species densities within and without gaps. Different letters indicate significantly (p < 0.05) different densities between species for area type (gap or beyond gap) using a t-test assuming unequal variances (df_{gap}=38 and df_{background}=13).
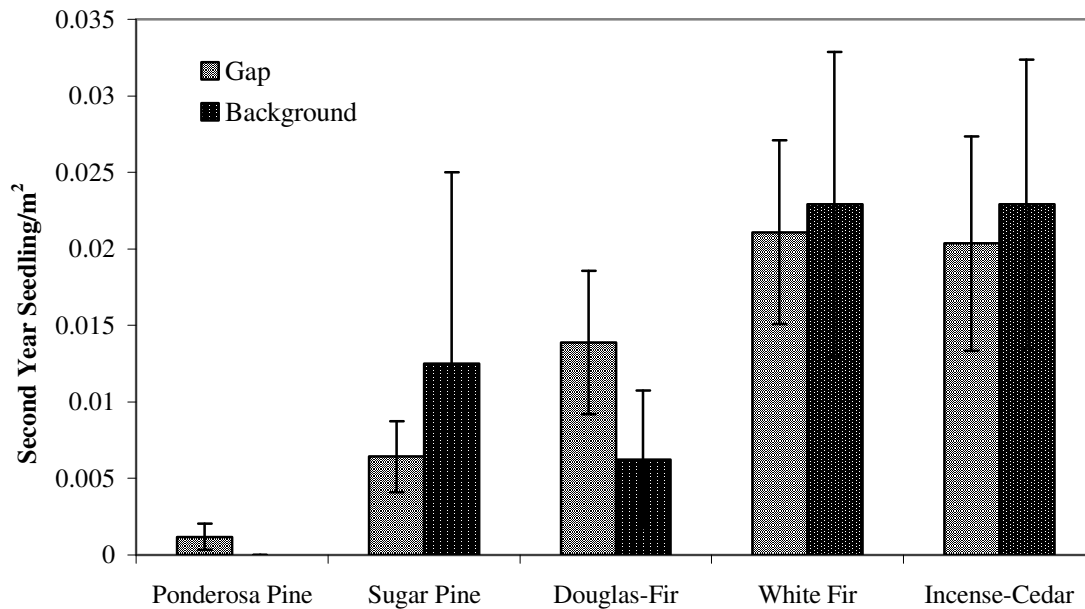
Figure 2 Second year seedling density in C230 by species within each plot type. Using a t-test assuming unequal variance there is no significant ($p < 0.05$) difference between the density of seedlings in the gap and background plots for any species (n_{gap}=34 and $n_{background}$=13).
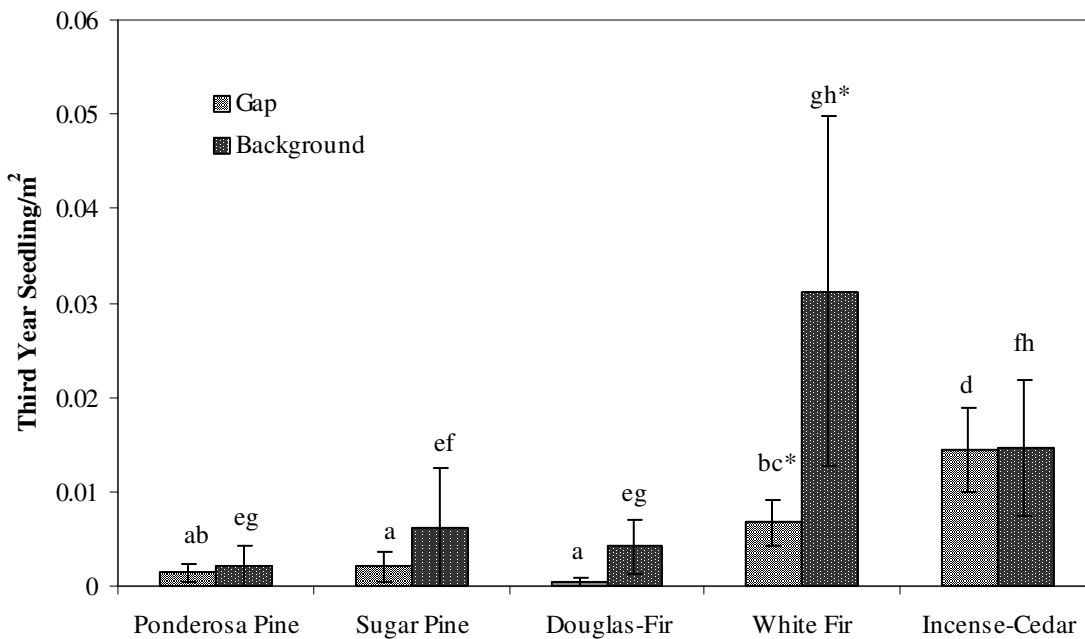
Figure 3 Third year seedling density in C230 by species within each plot type. Different letters indicate significantly ($p < 0.05$) different densities between species for area type (gap or background plot) using a t-test assuming unequal variance. An * indicates significant ($p < 0.05$) difference between the density in gaps and background plots for that species using a t-test assuming unequal variance. (n_{gap}=34 and $n_{background}$=13)

Figure 4 Density of first year seedling ($\pm$ 1 S.E) in gaps and background. The letters denote significant (p < 0.05) differences between seedling densities using t-tests assuming unequal variance. n= 39, 14, 34, and 13 respectively.

Seedling Density by Species   When the first year seedlings were analyzed by species in C110, fir density was higher in gaps than in the background plots (t = 1.577, df = 48.650 p = 0.0606) (Fig. 1). Neither pine (t = 0.947, df = 36.732, p = 0.1749) nor incense-cedar (t = 1.308, df = 16.895 p = 0.1043) first year seedling density differed between gaps and background plots (Fig. 1). Second and third year seedlings examined by species showed no significant (t < 1.4, p > 0.09) difference between the density of seedlings in gaps and in the stand background (Fig. 2 and Fig. 3 respectively).

Seedling Distribution   When first year seedling density in gaps was compared to first year seedling density beyond the gap; there was a significant positive linear relationship (r^2 = 0.3204) (Fig. 6).

The beyond gap area had a lower density of second year seedlings than the gap area when seedling species were pooled together before analysis (t = -1.8630, df = 25.3879, p = 0.0370). When the second year seedlings were separated out into species this relationship between gap and beyond gap seedling density was not apparent (Fig. 7) except for the white fir, which had a higher density in the beyond gap (t = 2.296, df = 32, p = 0.0142).   There was a significant linear

relationship between the gap and beyond gap second year seedling density when the species were pooled together (Fig. 8).
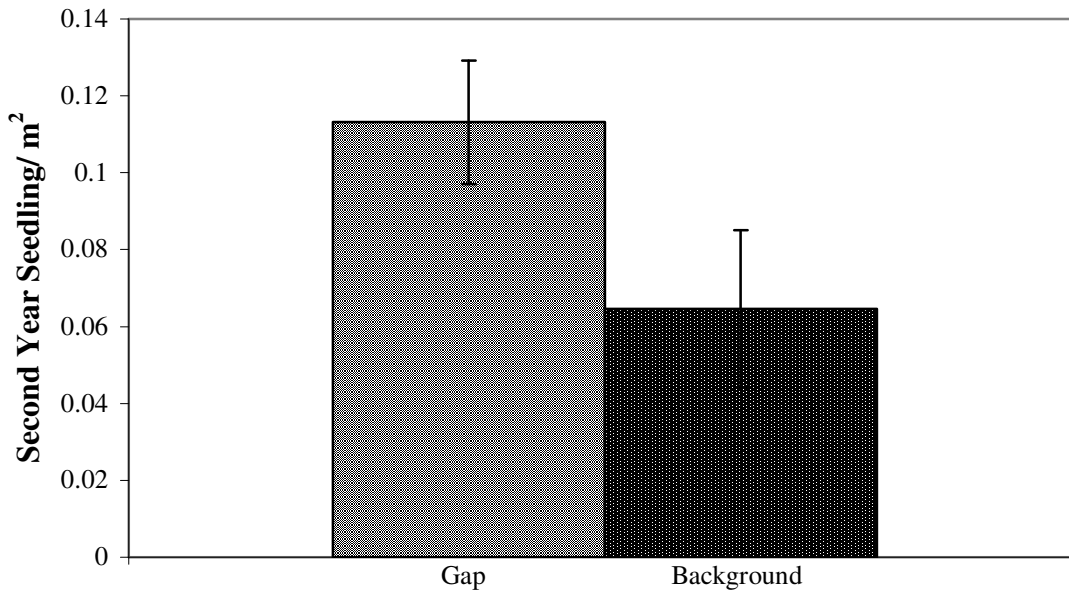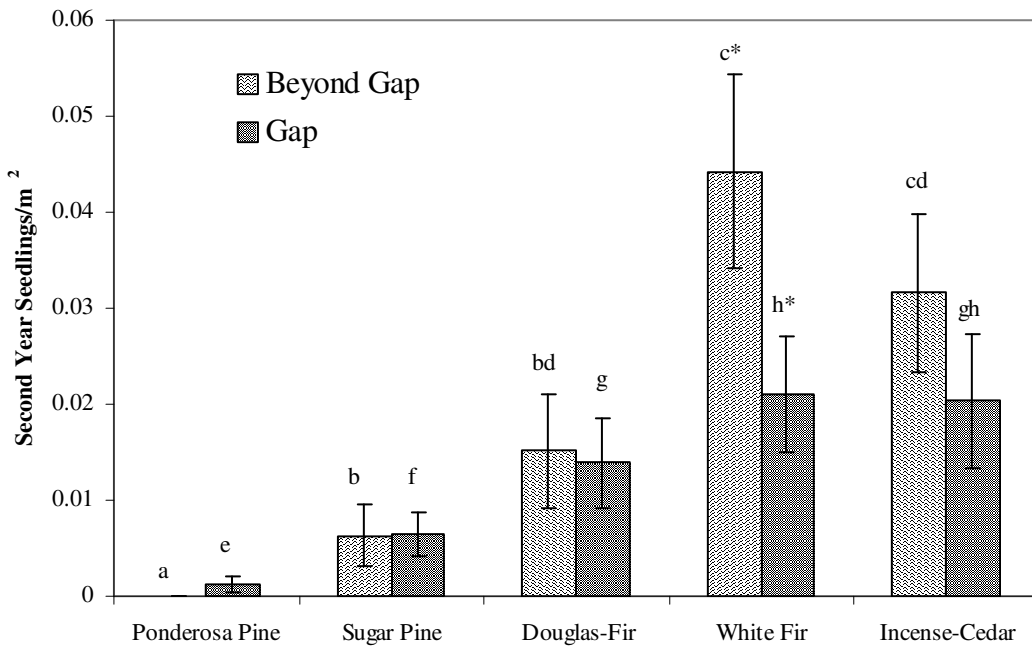

Figure 5 Second year seedlings density by plot type in C230 ($\pm$ S.E.). Using a t-test assuming unequal variance there was a significantly ($p < 0.05$) higher density of seedlings in gap plots than in background plots (n_{gap}=34 and $n_{background}$=13).

There was no difference between the density of third year seedlings in the gap and the beyond gap areas ($t = 0.9465$, $df = 11.753$, $p = 0.1815$). When third year seedlings were analyzed by species the white fir (the only species that had a significant difference between the gap and beyond gap density) was in higher density in the beyond gap than in the gap (Fig. 9). There was a weak but significant ($R= 0.3481$, $p < 0.05$) linear relationship between the gap and beyond gap density when the third year seedlings of all species were pooled together (Fig. 10).
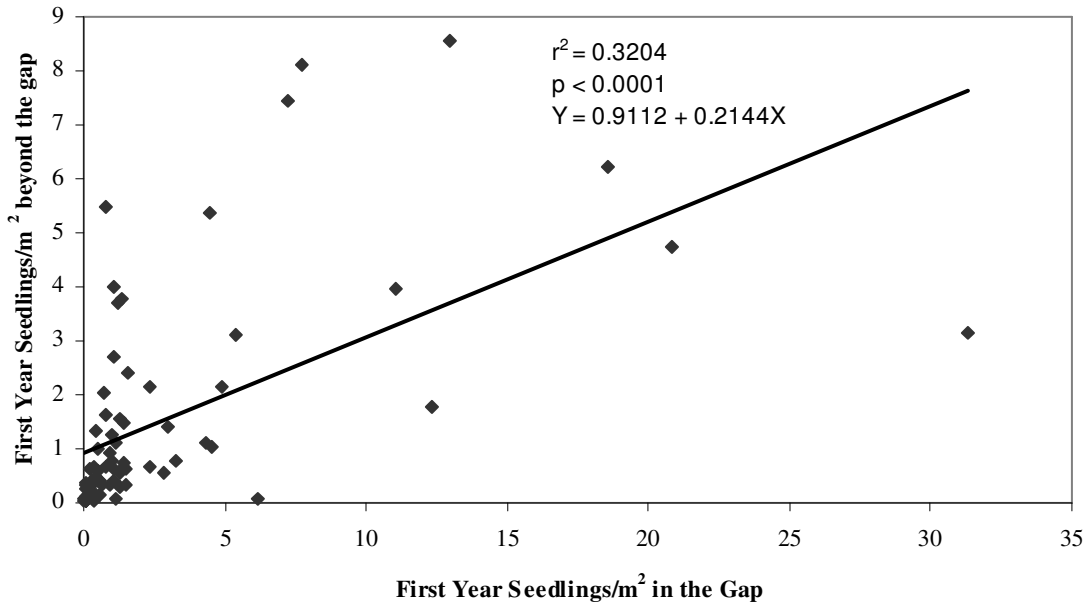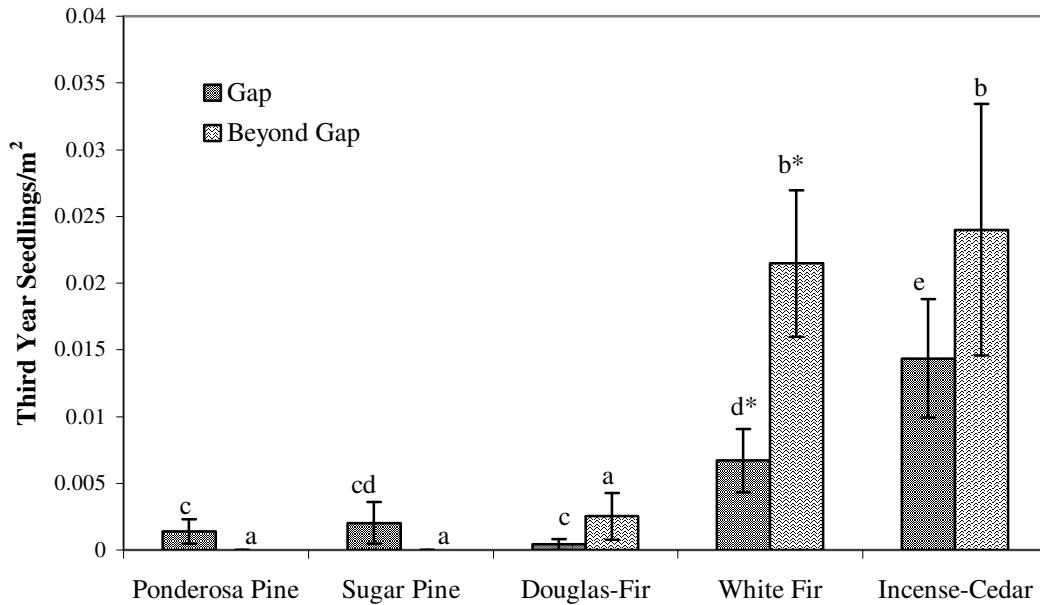
Figure 6 First year seedling density beyond gaps plotted against first year seedling density in gaps in C110 and C230. The trend line indicates a significant (p < 0.0001) positive correlation between the density of seedlings in gaps and beyond gaps.

Figure 7 Second year seedling density in C230 by species within each plot type. Different letters indicate significantly (p < 0.05) different densities between species for area type (gap or beyond gap) using a t-test assuming unequal variances (n = 34). An * indicates significant (p < 0.05) difference between density in gap and beyond gap for species using a t-test assuming unequal variances (n = 34).
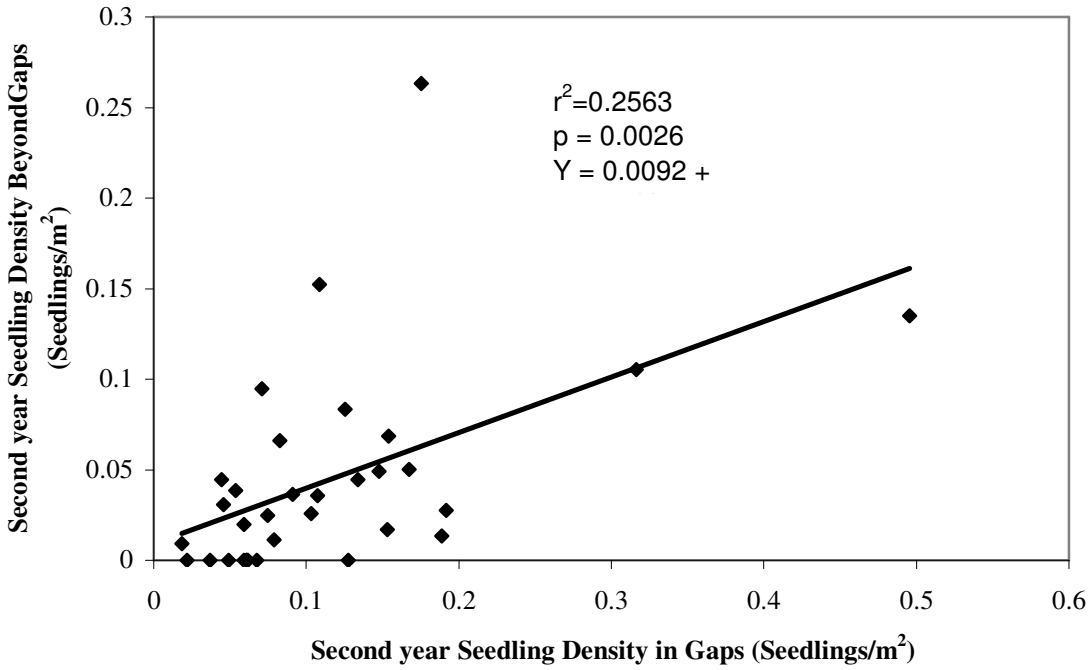
Figure 8 Second year seedling density in post gaps plotted against second year seedling density in gaps in C230. The trend line indicates a significant (p = 0.0023) positive correlation between the density of seedlings in gaps and beyond gaps.
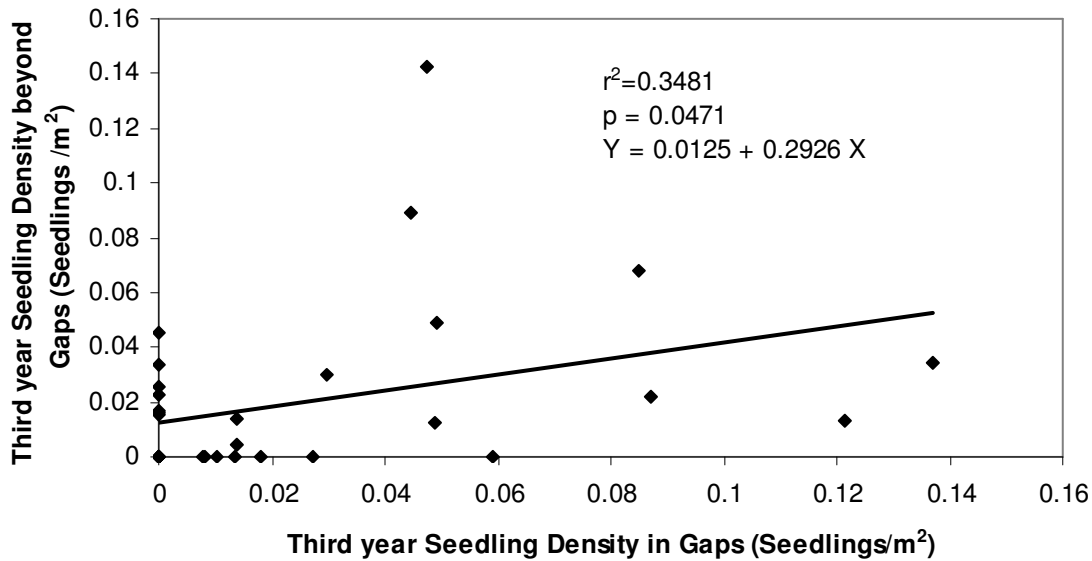

Figure 9 Third year seedling density in C230 by species within each plot type. Different letters indicate significantly (p < 0.05) different densities between species for area type (gap or post gap) using a t-test assuming unequal variances (n = 34). An * indicates significant (p < 0.05) difference between density in gap and post gap for species using a t-test assuming unequal variance (n = 34).

Figure 10 Third year seedling density in post gaps plotted against second year seedling density in gaps in C230. The trend line indicates a significant (p = 0.0471) positive correlation between the density of seedlings in gaps and beyond gaps.

Gap Size There was a significant positive correlation between gap size and first year seedling density among but not within locations (Table 2). No correlation was evident between first, second, or third year seedlings density by species and gap size (Table 3). There was a negative correlation between gap size and second year seedling density when all species were pooled together (ρ = -0.4586, p = 0.0073). There was no correlation between gap size and third year seedling densities when all species were pooled together (ρ = 0.0116, p = 0.9490).

Table 2 Correlation between gap size and first year seedling density. Only when the two stands are analyzed together was there a significant (p < 0.05) correlation between size and density of first year seedlings.

	Spearman's ρ	p
Compartment 230 and Compartment 110	0.2820	0.0156
Compartment 110	0.0546	0.7415
Compartment 230	-0.0527	0.7672

Substrate type   Seedling density in C110 was positively correlated with percent bare mineral substrate (Table 4) and negatively correlated with percent litter substrate (Table 4). These correlations were not evident in C230 (Table 4). Individual species varied in their response to ground cover, the fir showed a negative correlation with percent litter substrate and a

positive correlation with percent bare mineral and charred substrate (Table 5). Neither pine nor

incense-cedar showed any significant correlation with percent substrate type (Table 5).

Table 3 Correlation between seedlings of different species and gap size in C110 for first year seedlings and C230 for second and third year seedlings. There is no significant ($p < 0.05$) correlation between gap size and seedling density for any species or age group.

Species	Seedling age (Years)	Spearman's ρ	p
"Pine" (Ponderosa and Sugar Pine)	1	0.2148	0.1892
"Fir" (White Fir and Douglas Fir)	1	0.0235	0.8871
Incense-Cedar	1	0.1126	0.4949
Ponderosa Pine	2	-0.1147	0.5249
Sugar Pine	2	0.1724	0.3372
Douglas-Fir	2	-0.0404	0.8235
White Fir	2	0.2160	0.2274
Incense-Cedar	2	-0.0214	0.9058
Ponderosa Pine	3	-0.0298	0.8692
Sugar Pine	3	-0.2545	0.1529
Douglas-Fir	3	0.0928	0.6074
White Fir	3	0.1504	0.4036
Incense-Cedar	3	0.0197	0.9133

Table 4 Correlation between percent substrate and first year seedling density by compartment. There was no correlation between percent substrate in C230 though there was significant ($p < 0.01$) negative correlation between percent area with litter substrate and the seedling density in C110.

Substrate (%)	Compartment	Spearman's ρ	p
Bare Mineral Soil	110	0.2537	0.0668
Charred Soil	110	0.1260	0.1942
Litter	110	-0.3542	**0.0093**
Bare Mineral Soil	230	-0.0032	0.9834
Charred Soil	230	0.1602	0.2821
Litter	230	0.0307	0.8375

Table 5 Correlation between percent substrate and first year seedling density by species in C110. There was significant (p < 0.01) positive correlation between the percent area in bare mineral soil and fir density and significant (p < 0.001) negative correlation between the percent area in litter substrate and the fir density.

Substrate	Species	Spearman's ρ	p
% Area Bare Mineral Soil	Fir	0.3520	**0.0097**
% Area Charred Soil	Fir	0.2382	0.0859
% Area Litter	Fir	-0.4714	**0.0004**
% Area Bare Mineral Soil	Pine	0.2252	0.1049
% Area Charred Soil	Pine	0.0610	0.6645
% Area Litter	Pine	-0.1430	0.3070
% Area Bare Mineral Soil	Incense-Cedar	-0.0267	0.8494
% Area Charred Soil	Incense-Cedar	-0.1587	0.2564
% Area Litter	Incense-Cedar	0.0514	0.7146

Discussion

Species Composition   The shade tolerant species dominate both the gap and non-gap portions of the stands. This could be an effect of the low light levels throughout the stand or be due to a higher level of seed source. Since there is no data available on the seed source no conclusions can be drawn from this data.

Seedling Densities The gaps appear to have no consistent effect on the seedling density of timber species (Fig. 1-5). The higher density of seedlings in gaps for first and second year seedlings in C230 and the lack of difference between gaps and background plots in the first year seedlings in C110 and the third year seedlings in C230 is similar to the inconsistencies in the literature where some studies show more regeneration of softwood and hardwood trees in gaps (e.g. Bobiec 2007, Gray and Thomas 1996) while others have found lower regeneration density in gaps (Arevalo and Fernandez-Palacios 2007). It is possible that the logging and site preparation is making the gaps less favourable for seedling establishment the year after the harvest. This drop in favorability could be leading to the similar densities between gap and background densities in the seedlings germinating the year after the harvest.

Species Densities No species shows higher seedling density within gaps when compared to the background of the stand. Since it has been shown that gaps with adequate characteristics (light, soil moisture content, nutrients, and seed source) will increase regeneration of shade intolerant species (Pecot *et al.* 2007), it appears that there is some factor or factors, possibly size, which was not adequate for increased regeneration of either shade intolerant or tolerant species in these single-tree selection gaps. The lack of species density difference between gaps and

background plots could be partially due to the very low average density and high variation making this sample size inadequate to measure the difference between gap and background seedling density.

There is no single factor with which all species density correlate. Though not specifically addressed in the studies questions their densities do correlate strongly with each other (Table 6). This correlation between species density suggests that there is some unmeasured factor that is influencing seedling density.

Table 6 Correlation between gap size and first year seedling density by species in C110. There is no significant ($p \leq$ 0.05) correlation between the density of any species group and gap size.

Species	Spearman's ρ	p
Fir	0.0235	0.8871
Pine	0.2148	0.1892
Incense-Cedar	0.1126	0.4949

Seedling Distribution Though not always significant, the higher density of shade tolerant species in the beyond gap area than the gap area suggests that there is some special selection of species based on their shade tolerance. Though there may be some sort of gradient operating which is selecting for more shade tolerant species, the correlation between seedling density in gap and beyond gap areas across age classes suggests that the effect of the gap extends beyond the dripline as has been found in other studies (Runkle 1982, Canham *et al.* 1990).

Gap Size Gap size does not show a clear relationship with seedling density as has been found in studies of other ecosystems where both positive and negative relationships between gap size and seedling density have been found (Fajardo and de Graaf 2004, Gagnon *et al.* 2004, Diaci *et al.* 2005). However, the corresponding differences between average seedling density and the average gap size between the two compartments, suggests that size may be playing a role in seedling density but this data is insufficient to declare this absolutely.

Substrate Type The differences in the correlations between ground cover and seedling density between the two stands could be due to the exposure time of the bare mineral and charred substrates. Valkonen and Maguire (2005) showed that conifer seedlings have preferences between different substrates. Part of this preference could be due to changes in soil organisms in disturbed soils (Parsons *et al.* 1994). It is possible that the time since the disturbance has been long enough three years after harvest that pathogens and symbionts have been reintroduced to the disturbed soil (Korb *et al.* 2004) changing its suitability for seedlings. The positive correlation

between the density of fir seedlings and the percent charred and bare mineral substrates and the negative correlation between fir and litter substrate in C110 corresponds with other studies that have found that conifers prefer bare mineral substrates to substrates with lots of organic matter (Lorenzetti *et al.* 2008 and Valkonen and Maguire 2005).

Conclusions These gaps are producing, on average, the minimum stocking levels (0.074 seedlings/m^2) required by the State of California Forest Practice Rules (California Department of Forestry and Fire Protection 2008) when second and third year seedlings are considered together. However the majority of these seedlings are shade tolerant species and the point of gap silviculture is to promote the regeneration of shade intolerant species. Though gaps have the potential to increase regeneration of conifer species with some selection for shade intolerant species; however, it would be necessary to run a larger multi-year study to say conclusively how gaps are effecting regeneration in the Sierra Nevada mixed conifer forest. Small-scale disturbances such as single-tree selection harvests do create different environmental conditions (Coates and Burton 1997), but this study does not find that these gap conditions lead to consistent significant changes in the density and composition of seedlings in this environment.

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