Chapter 1

Regeneration of giant sequoia (*Sequoiadendron giganteum*) in experimental gaps: Implications for restoration of a long-lived pioneer species

Abstract

To inform giant sequoia restoration treatment options, I assessed the responses of different phases of giant sequoia regeneration (germination, survival, and growth) to experimental gaps within a native giant sequoia grove. Twenty gaps were created, ranging in size from 0.04 to 0.5 ha. Following gap creation, I sowed seeds and planted seedlings along north-south transects across gaps. Transects were planted on paired ash and bare soil substrates to find the effect of an ash substrate on regeneration. The relationship between gap size and 2nd year seedling growth was best modeled with an asymptotic curve for both ash and soil substrate seedlings. Seedling growth increased with gap size until about 0.2 ha, where increases in growth diminished sharply. Within gaps, an ash substrate and placement near central positions encouraged increased seedling growth. Reliance on natural germination of sewed seeds for seedling establishment proved difficult. Once established, planted seedlings survived at similar levels in all gap sizes with only slightly elevated levels of mortality near north edges of gaps. Long-lived pioneer species such as giant sequoia require restoration treatments that involve relatively intense disturbances to facilitate cohort establishment and recruitment.

Introduction

Recovery from the greatly altered conditions of fire-dependent ecosystems will depend on near-term management decisions that seek to actively restore desired conditions (Covington 2000). Such restorative treatments proposed within native giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz) groves are often aimed at promoting the initiation of a new cohort of giant sequoia that will eventually recruit into the canopy. When contrasted against the frequency of cohort initiation events during the past two millennia, it is clear that the modern era of fire suppression has resulted in a "missing cohort" that would have otherwise become established during the past century (Stephenson 1994). Given its extreme longevity, the current giant sequoia population can easily absorb a century of missing regeneration without long term impacts but the consequences of continued regeneration failures will increase dramatically with time. The demographic evidence that suggests the need for restoration treatments is boosted by support generated from the great social values placed on this species' exceptional cultural significance and monumental stature. Cohort initiation thus appears to be a justifiable objective both ecologically and socially. In practice, however, treating a forest in order to promote the establishment of a long-lived pioneer species such as giant sequoia presents a unique challenge to comparably short-lived scientists and managers. A significantly intense disturbance that may be perceived as destructive must be part of the treatment, the ultimate success of which will not be assessed for centuries.

Restoration efforts in giant sequoia groves are further challenged by the fact that a variety of stakeholder interests seek to influence agency decisions about management

(Rigg 2001). In addition, as with natural resource management regimes in general, treatments must meet objectives with efficient use of limited resources and with minimal conflict to competing objectives. The challenges inherent to proactive restoration projects should not preclude their implementation, however, for the ecological risks of no action far outweigh the risks of acting with uncertainty (Covington 2000). Long-term uncertainty, which will always be present to some degree, can be reduced over time with an active adaptive management approach (*sensu* Walters and Holling 1990) that gradually improves treatment efficacy. In the short-term, high-intensity treatments that are necessary to begin the restoration process can presently benefit from experiments that target areas of ecological uncertainty and that are specifically designed to assess treatment options. It is within this framework of reliance on both rigorous research projects as well as practical, long-term management experiments that species restoration treatments should move forward with calculated haste.

A logical first step in species restoration is understanding the life-history of the species being restored and the ecological obstacle to it perpetuating itself. Long-lived pioneer species such as giant sequoia are unique in that they seem to avoid the tradeoff between rapid growth and longevity that is typically observed in coexisting tree species (Huston and Smith 1987). Among its associated conifer species, it is both the longest lived (Stephenson 2000) and the fastest growing as a juvenile under high-resource conditions (York et al. 2003). Even under low resource conditions, it has a marked capacity to survive (This dissertation, Chapter 3). Examples of long-lived pioneer species such as giant sequoia can be found the world over (Table 1). By growing fast and living long, these species' life-histories would seem to confer a striking competitive advantage.

However, they invariably have an Achilles heel that limits their range and density. In the case of giant sequoia, it is constrained by the limited conditions under which successful regeneration can occur (Rundel 1972, Harvey and Shellhammer 1991). It is somewhere within the regeneration process- from seed to physiologically self-sufficient seedling- where giant sequoia populations become bottlenecked. Successful restoration treatments will therefore be those that focus on creating conditions that promote the successful establishment of seedlings that are capable of recruitment into the canopy.

As with most tree species, giant sequoia is disturbance dependent- requiring the creation of canopy gaps to emerge into the canopy. Given that discrete canopy gaps are needed for giant sequoia regeneration, the most important area of current uncertainty is in the specific relationship between gap size and regeneration. Understanding within-gap patterns of regeneration is also important since they drive gap-level patterns and within-gap treatments can influence these outcomes. This information is needed, regardless of whether restoration treatments are implemented with fire or mechanical means. In creating canopy gaps with a restoration treatment, a number of potential factors that influence giant sequoia regeneration can be controlled both between and within gaps. The size of the gap (York 2004), the substrate quality (Harvey and Shellhammer 1991), and within-gap position of regenerating seedlings (Demetry 1995) are all influences that can be altered by the choice or priority of treatment options. Partitioning out their relative importance in terms of influencing germination, survival, and early growth is the main intent of this study.

This research was designed as an experimental gap study, relying on control of field conditions to reduce the high variability often found within and between naturally occurring gaps (e.g. Lawton and Putz 1988). I necessarily use artificial creation of gaps to control gap size, and artificial regeneration techniques of direct seeding and seedling planting in order to control the spatial arrangement of regeneration. My aim was to primarily describe functional relationships between gap size and giant sequoia germination, survival, and early growth. Secondarily, I describe within-gap influences of substrate and position on those same components of regeneration. To best inform restoration efforts, I rely on information-theoretic model selection procedures to analyze the data and to rank the different factors of giant sequoia regeneration based on strength of evidence. The study is designed to give specific insight into giant sequoia restoration, and to discuss a general approach to understanding and conserving long-lived pioneer species.

Methods

Study area

The study was conducted at Whitaker's Forest Research Station (WFRS) in the southern Sierra Nevada Mountain range of California. WFRS is within the Redwood Mountain giant sequoia grove, about 5 km to the south of the Grant Grove visitors center in Kings Canyon National Park. Gaps were installed across a 100 ha area between elevations of 1615 and 1830m. Aspects in the study area are mainly west-facing, on moderate slopes of 15-30%. Soils are of granitic origin, generally deep (>2m) but with some rock outcrops. Precipitation in the area is variable from year to year, averaging 107 cm per year and ranging from 40 to 160cm during the last 30 years at Grant Grove, 6.4

kilometers to the north of WFRS (NOAA 2005). Much of the precipitation (>80%) comes from winter snows and spring rains, while summers are relatively dry.

The first timber harvesting activity in the area took place during the 1870’s. This harvest removed many of the larger sugar pines (*Pinus lambertiana* Dougl), and some of the emergent giant sequoias (Metcalf 1940)**.** The giant sequoia individuals currently in the mature canopy layer (excluding the emerging ancient trees) belong to a single cohort. Age-reconstructions of numerous individuals in the field suggests that this cohort established after the 1870’s logging event.

A second harvest in 1946 removed about 42% of the standing volume from trees that were greater than about 90cm diameter at breast height (Metcalf 1951). As was typical of the time, the harvest targeted the larger trees and was distributed extensively throughout the area. Despite the amount of volume removed, the disturbance did not result in the initiation of a cohort of giant sequoia. Even the smallest giant sequoia individuals found in a reconnaissance of the study area before treatments were installed were reconstructed to originate from the first logging activity in the 1870’s. The failure for a cohort to initiate after this second disturbance is likely a result of the diffuse nature of the tree removal and the lack of any post-harvest treatments that created a mineral soil substrate. As is common throughout grove areas, no giant sequoias less than 100 years old could be found in the study area prior to the treatment.

Vegetation at WFRS is dominated by a Sierran mixed conifer forest type (Laacke and Fiske 1983) with the addition of giant sequoia. The canopy structure is distinctly two-tiered, with an emergent upper tier of approximately 1.5 large giant sequoia trees per hectare that are estimated to be over 1000 years old. The second tier forms the main canopy of mature individuals, most of which originated from the 1870’s harvest. Tree species in the second tier of the canopy include (in order of basal area dominance) giant sequoia, incense cedar (*Calocedrus decurrens* (Torr.) Florin), white fir (*Abies concolor* (Gord. & Glend.) Lindl.), sugar pine, and ponderosa pine (*Pinus ponderosa* (Dougl. ex Laws.). Basal area density of the main canopy, estimated from 87 permanent plots throughout the study area, averages 65 m^2/ha (WFRS on-line data, 2005). Trees in the main canopy receiving full light from above (i.e. codominant) have grown in stature to 27-34m in 50 years. As is typical in areas of this forest type not disturbed by fire or intense anthropogenic disturbances, regenerating trees in subcanopy size classes are dominated by white fir and incense-cedar.

Experimental treatments and data collection

Treatments were designed to test the possible influences that restoration treatments can have on the process of giant sequoia regeneration. Gap size, within-gap position, and substrate treatments were installed during summers of 2001 and 2002. Twenty circular gaps ranging in size from 0.04 to 0.4 ha were created. Expressed relative to canopy height, the ratio of gap diameter to canopy height for this range is 0.75 for the smallest gap and 2.11 for the largest gaps. Prior to gap creation, the gaps were measured on the ground to provide 5 replicates of 4 size classes (0.05, 0.1, 0.2, and 0.4 ha). Circular boundaries for the gaps were identified by locating a center point and measuring the appropriate horizontal radial distance to gap edge in each cardinal direction with a tape. Larger gaps (0.2 and 0.4 ha) required measurements to inter-cardinal directions as well. The identified gap edges were then connected with flagging to form a circle. All trees within the flagged areas were felled towards gap centers to avoid damage to surrounding trees. As expected, the post treatment gap sizes were slightly different than the measured pretreatment sizes because the canopy drip-lines forming gap edges are often variable (i.e. the geometries of gap drip-lines are different than the bole-lines). Gap sizes used for analysis were estimated from measurements of diameters between canopy driplines along south-north transects of each gap and assuming circularity. Post treatment gap sizes deviated from target gap sizes by as much as 50%, with no obvious bias for gaps becoming larger or smaller than the target size (10 were bigger and 10 were smaller than the target size). The size range was chosen in order to replicate the speculated range of gap sizes that typically occurred under a pre-fire suppression era disturbance regime. I inferred this size range from reconstruction studies and descriptions of modern prescribed fire effects on gap size (Bonnicksen and Stone 1981, Bonnicksen and Stone 1982, Stephenson 1994, Demetry 1995). Some fire-created gaps created before the modern era of fire suppression were undoubtedly larger than the 0.4 ha maximum used in this study (e.g. Swetnam 1993), but the available reconstruction studies suggest that most gaps were less than 0.4 ha in size.

Trees within gap boundaries were cut with chainsaws and skidded out with tractors. Post-harvest debris was piled into windrows 5 meters wide and extending along the south-to-north equators of gaps. During the fall after the harvest, the windrows were burned during conditions that facilitated near-complete consumption of debris. The substrate treatment was placed along the south to north transects in order to overlap with the steepest gradients in above and below ground resources. Giant sequoia seeds were sewn at spots every 3 meters along the transects and extending 12 meters into the matrix on the south and north edges. One transect was placed on the ash substrate treatment, while a paired transect was sewn on the adjacent bare mineral soil substrate. Ash-soil pairings only occur beneath the gap between drip-lines since no debris was burned beneath the canopy matrix. Seeds were collected from emergent ancient trees throughout the study area. They were screened to increase viability, which averaged 74% (determined by x-ray of a sample). At each seed spot, 5 seeds were sewn thus ensuring the probability of at least one viable seed per spot at greater than 99%. Seeds were soaked in running water for 48 hours and then sewn at each spot in early spring of 2004. Sewing was repeated at every other spot in the fall for germination in spring of 2005.

Seedlings of giant sequoia were raised from the same source of seeds used for the seed sewing treatment. They were raised in containers for 1 year in a nursery before planting. Similarly to the seed-sewing treatment, seedlings were planted every 3m along north-south transects in a paired ash and soil substrate design. Transects extended 12 meters into the matrix on both sides of the gap, where only soil substrates were planted. Seedlings were double-planted at each planting spot. One year after planting, spots where both trees had died were replanted with another seedling. This pulse-style planting treatment was done in order to increase the probability of at least one seedling eventually becoming established and to provide a mortality index, where from 0 to 3 seedlings died at each spot over two years.

The regeneration process was divided into three logical stages that could be measured in terms of their response to gap size and within-gap treatments. Seed germination was monitored in early summer of 2004 and again in 2005 to measure spring germination frequency following the two sewing treatments. Each seed spot was visited and tallied by presence or absence of at least one germinant. Planted seedling mortality was assessed at the end of each of the first two growing seasons after planting. Seedlings were presumed to be dead when no green foliage was present. Early seedling growth was assessed by direct measurement of all seedlings' basal diameter and height after the first and second growing seasons.

Data Analysis

Analytical Approach. I relied on an information-theoretic approach to analyze the data. Restoration efforts that install treatments based on expectations built by predictable but variable ecological relationships are by nature well-suited to be informed by analyses that test multiple hypotheses (models) of simple functional relationships. In the case of giant sequoia restoration, understanding the general relationship between gap size and regeneration can help predict how restoration treatments that create different gap sizes might influence regeneration. Rather than testing whether or not *any* relationship exists, a model selection procedure that ranks candidate models and gives relative strengths of evidence provides an instructive assessment of what kind of relationship might be superior given the data. Further, penalizing for model complexity increases the probability that the relationship will hold true given widespread restoration implementation outside of the study area's domain. Model selection can also be used to rank the relative importance that individual predictor variables have in influencing the response variables. Restoration efforts can then be designed to prioritize treatments in order to most efficiently achieve objectives with available resources. Analysis was performed at two levels, corresponding with the experimental design. First, I considered between-gap effects on the responses of seed germination, seedling mortality, and seedling growth to gap size and substrate. Second, I focused on within-gap patterns of regeneration, quantifying the relative influences of position, substrate, and their interactions. For the analysis, I used only the seeds and seedling measurements that were located beneath the gaps (between drip-lines). The matrix spots were excluded for this analysis since they did not have ash substrate treatments and therefore created an unbalanced design (and because restoration treatments are unlikely to be applied outside of gaps).

Gap size influence. The predictor variable is gap size. I used only those gaps that had complete ash substrate treatments (n=18), so that I could do separate model fitting for paired ash and soil substrates. The response variables are gap-level means for germination, mortality, and relative seedling growth in height and diameter. Germination is expressed as the percent of seed spots in the gap that had at least one germinant present following either of the two sewing treatments. Relative growth for each seedling surviving through the second year was calculated by dividing the second year growth increment in height or diameter by the measurement taken after the first year. Relative second year growth is used in this case in order to remove the variability due to initial size differences and nursery effects and to reduce variability in the gap size-seedling growth relationship caused by non-gap size influences.

Mortality is expressed by deriving a mortality index for each planting spot, and then averaging index values across all planting spots per gap. Where both seedlings were dead after the first year, another seedling was planted. After the second growing season, each seedling was given a 0 value if still alive and a 1 value if dead.. The possible mortality index values per spot were 0 out of 2 seedlings dead (0), 1 out of 3 dead (0.33), 1 out of 2 dead (0.50), 2 out of 3 dead (0.67), or 3 out of 3 dead (1.00). Gap level averages are therefore a measure of mortality incidence for the whole gap over two years.

The intent of the analysis is to describe functional relationships between gap size and indicators of regeneration, plus any alteration of that relationship as a function of ash substrate. I identified a set of a priori candidate models describing potential relationships, then used model selection to rank the models and quantify the strengths of evidence. The models were used to fit each regeneration variable (germination, mortality, and growth) to gap size for ash and soil substrate treatments separately. Only treatments that had paired ash and soil substrates were used to calculate averages. The candidate set was made up of three simple models- linear, quadratic, and asymptotic. Each model represents a different functional relationship and implies a distinct relevance for restoration. A sloping linear relationship between gap size and the regeneration variable would imply a monotonic relationship, and that either the smallest or the largest gap size (depending on whether the slope was positive or negative) could most influence the given regeneration variable in a restoration setting. A quadratic equation would imply a certain maxima within the size range considered, where beyond a gap size threshold the effect declines. An asymptotic fit would imply that the response variable increases with gap size, but then returns diminish and the effect levels off. An asymptotic relationship was described with a simple 2-parameter Michaelis-Menton equation, with one parameter equal to the asymptote and the other controlling the slope of the lower portion of the curve before the asymptote is reached.

To rank the models according to goodness of fit while penalizing for model complexity I used a modified Akaike's information criterion (AIC) derived by Sugiura (1978):

$$AIC_i = n\log(\frac{RSS}{n}) + 2K + \frac{2K(K+1)}{n-K-1},$$

where AIC is the bias-corrected criterion for model alternative i, RSS is the residual sum of squares of the model's regression, n is the sample size, and K is the number of parameters. The modified AIC incorporates a bias-correction term to account for small sample:parameter ratios among the alternatives. The model alternatives have ratios of 18:2 for the asymptotic and linear functions, and 18:3 for the quadratic and sigmoidal functions. To evaluate candidate models in relation to the highest ranked model, the AIC values are transformed to Akaike weights and normalized to sum to one. The weights are interpreted as the likelihood that within the limits of the data and the set of alternatives, the given model is the most appropriate choice. The application of AIC for statistical inference in ecological studies is described in detail by Anderson et al. (2000) and Johnson and Omland (2004).

Post model selection analysis depended on which of the three possible outcomes occurred:

Outcome #1: For both ash and soil seedlings, the same model is selected and parameters are significant (slope parameter 95% confidence intervals do not include zero).

Post selection analysis: Compare the parameters of the selected model between the two groups. If confidence intervals overlap, then functionally they are the same (given this data set). Redo the analysis with the two treatments grouped together to increase precision in the final gap size–regeneration relationship.

Outcome #2: A different model is selected for the two treatment groups and parameters are significant (Confidence intervals of slope parameter do not include zero).

Post selection analysis: None. The ash substrate changed the functional relationship. The model selection ranks and evidence ratios are the result.

Outcome #3: Model ambivalence. It is difficult to distinguish performance between models.

Post selection analysis: Explore the reason for the ambivalence. The reason could be either a general lack of *any* relationship between gap size and the response variable, or a failure to distinguish between models because of data variability and small sample size. If no difference between ash and soil patterns exists, group them together to increase precision of the response variable and hence increase the power of model selection to distinguish between models.

Within-gap influences. Within gaps, patterns of regeneration variables were assessed as influenced by treatment factors of substrate, orientation (south v. north half), and proximity to matrix (i.e. gap edge). These factors represent all possible positions along the resource gradients that developed as a result of gap creation. It was necessary to separate out orientation and proximity to matrix as variables (as opposed to a single measurement of distance across gap from edge to edge), since stark differences in resource availability can occur on the south versus north sides (Canham et al. 1990, York et al. 2003). In other words, I do not expect a linear gradient in resource availability across gaps from edge to edge.

In this case, the experimental unit is reduced to each planting or sewing spot. For germination, the response variable is presence or absence of a germinant during either of the two years following sewing treatments. Germination frequency was too low to perform separate analyses by year. Mortality is expressed as an ordinal-ranked variable, depending on how many seedlings died at each spot. The index values for each spot rank degree of mortality incidence, but are not scaled continuously because some spots had a third seedling planted during the second year, while others had two seedlings planted only the first year. Instead of relative growth, I used absolute seedling size as a response variable since this part of the analysis is designed to find specific effects of treatments on the magnitude of seedling size (as opposed to non-linear functional relationships with the gap level analysis). Where both seedlings were present after two years, they were averaged. Seedling size was estimated by multiplying basal diameter by height (cm^3). I used only seeds and seedlings planted within gap drip-lines, and that had paired ash and soil substrate treatments (n=365 seedling spots and 442 seed spots). Variances in the response variables are partitioned among the treatment parameters with models that are appropriate given the type of data. I used a logistic regression for germination, an ordinal regression for mortality, and a generalized linear model for seedling size. Seedling size was natural log transformed, and mortality was arcsine-square root transformed. Means and confidence intervals are back-transformed when reported.

The overall influence of each treatment was assessed by evaluating the uncertainties that resulted from building the models with a set of candidate models. The candidate models were made up of different combinations of parameters that could potentially explain regeneration with the treatments (Table 2). Inference is based primarily on the relative importance value for each parameter. Importance value is calculated as the sum of all Akaike weights for the models in which the given variable appears (Burnham and Anderson 2002). Because of the particular reliance on importance values for making inferences in this case, it is necessary to have each parameter represented equally across the candidate set. I therefore confined the candidate set to include the individual variables of substrate, proximity, and orientation (north v. south half) plus the three possible 2-way interactions between these variables. Global models for all three individual variables and interactions are also included. This gives each individual and interaction parameter representation in two of the candidate models. More combinations are possible (for example a three-way interaction), but this would result in model imbalance. Including all possible models would give parameter balance but would dilute the power of model selection by having too many models (Burnham and Anderson 2002). With the given set of candidate models, a variety of complexity and restoration implications are represented (Table 2). Calculation of AIC values from the residual sum of squares of the generalized linear model was performed similarly to the equation above, except without the small sample correction. For the germination and mortality regressions, AIC is derived from the uncertainty indicated by the log-likelihood of the whole model, which replaces the RSS in the above equation (Anderson et al. 2000)

Results

Gap size influence

Seedling growth. The asymptotic relationship was ranked highest for both soil and ash substrate seedlings with moderate support (Table 3). Seedlings in the ash bed grew at a faster rate than seedlings in the soil substrate, but the ash substrate did not change the relationship between gap size and growth as interpreted by the overlapping confidence intervals for the models' parameters. When all seedlings within gaps are combined to increase the per gap precision (and increase the sample size by two gaps), the asymptotic fit is the best model with strong support (asymptotic AIC weight = 0.81, quadratic AIC = 0.18, linear AIC <0.01). Height growth increased sharply with the smaller gap sizes and approaches saturation around 0.2 ha (Fig. 1A). This gap size corresponds to a gap diameter to canopy height ratio of 1.5.

As with height growth, the asymptotic relationship between gap size and basal diameter growth was ranked highest for both substrates, with relatively strong support (Table 3). The ash bed did not change the relationship between gap size and diameter growth as interpreted by the overlapping confidence intervals for the models' parameters. When all seedlings within gaps are combined to increase precision, the asymptotic fit is again the best model with strong support (asymptotic AIC weight = 0.76, quadratic = 0.18, linear = 0.07). As with height growth, the effect of gap size saturated by around 0.2 ha (Fig. 1B)

Seed germination. For both ash and soil substrates, a linear relationship between gap size and % germination rate was the selected model (Table 3). There was, however, ambivalence between the linear and asymptotic models. Ambivalence is a result of the weak overall effect of any relationship between gap size and germination. This is indicated by the fact that the confidence intervals for the linear fit slopes include zero (they therefore overlap with each other as well). When ash and soil substrates are combined together to improve the precision and power of detecting a gap size effect, there is still ambivalence between the linear and asymptotic models. The linear fit does reveal a weak but consistent negative effect of gap size on germination (95% CI of slope = -0.88 to -0.12 % per gap). The larger gaps therefore tended to have slightly lower germination rates.

Seedling mortality. As with the germination results, the model selection did not distinguish between linear and asymptotic fits, and the selected models' slope parameters had confidence intervals that included zero (ash and soil model slope parameter confidence intervals therefore overlap). When seedlings from the ash and soil substrates are combined together, the ambivalence remains and no effect of gap size on seedling mortality index can be detected (slope CI = -0.29 to 0.72 per gap).

Within-gap influences

Seedling size. The highest ranked model included all variables influencing seedling growth without interactions, although the second ranked model with all possible interactions also had considerable support (Table 4). Most of the cumulative support (85%) is encompassed by these two models. The importance values, which measure the relative importance of each variable by summing the AIC weights across the models in which each variable appears, are 0.56 for all three single variables of substrate, matrix proximity, and orientation (essentially the AIC weight of the highest ranked model). Increasing distance from matrix, presence of an ash substrate, and placement on the south half had positive effects on seedling size (Fig. 2). The interactions had lower importance values than the individual variables. The substrate*proximity variable had the highest value of 0.44, while the substrate*orientation and proximity*orientation interactions each had the lowest importance values of 0.29.

Seed germination. Despite the use of screened seeds and applying the sewing treatment over two years, very few of the sewed seeds germinated. Only 50 of the 442 seed spots that had paired ash and soil substrate treatments had at least one germinant. The lack of germination contributed to a lack of resolution of a superior model among the candidates. The logistic regression was best fit with a simple 1 parameter regression with proximity as a predictor of germination (Table 4). Proximity also had the greatest importance value among the variables. The other single-parameter models and the simple additive models also had support. Because of the overall low germination frequency, the actual effect of within gap treatments was only slight. Germination tended to occur at distances farther away from the matrix. Spots with germinants present had a mean relative distance from the matrix of 0.54 ($CI_{95\%}$= 0.46-0.62), while spots without germinants had a relative distance of 0.45 ($CI_{95\%}$= 0.42-0.48). The ash bed substrate had a slightly higher germination frequency (14.0%) compared to the soil substrate (8.6%). Similarly, north v. south placement had only a slight effect. Germination occurred at 13.5% of the south half seed spots and 9.4% of the north half seed spots.

Seedling mortality. The proximity by orientation interaction was the highest ranked model, with strong support (Table 4). The proximity by orientation interaction was especially important as indicated by the importance value and the fact that it was in the two highest ranked models that together accounted for >96% of the cumulative AIC weights. Mortality is constant along the southern halves of the gaps, and increases with proximity to matrix along the north halves (Fig. 3). On average (back-transformed), mortality at each planting spot was 46% (CI= 42-49) for north row seedlings and 36% (CI=33-40) for south row seedlings. These are considered index values of mortality because of the method of replanting over two years.

Discussion

Factors of gap size, substrate, and position within gap all influenced the process of giant sequoia regeneration. The relative influences that each of the factors have on germination, survival, and growth can help prioritize restoration treatments in order to increase the chance of successfully meeting restoration goals.

Gap size effects

After two years, gap size had a profound influence on seedling growth, resulting in faster growing seedlings with increasing gap size. However, the influence diminished markedly above about 0.2 ha (Fig. 1). The effect of gap size on germination and mortality was comparatively weak. If germination frequency indeed tends to decline slightly with larger gaps as it did in this study (possibly because of increased seed desiccation), the benefit of larger gaps from increased growth would likely far outweigh the negative effect of reduced germination. Mortality of planted seedlings was relatively low for all gap sizes, even the smallest gaps. The contrast between mortality and growth results emphasizes the importance of distinguishing between the different traits that make up a species' shade tolerance. In agreement with other work (This dissertation, Chapter 3), giant sequoia individuals were relatively insensitive to resource availability in terms of survival. Yet they responded markedly in terms of growth. If establishment of a surviving cohort without regard to the cohort's growth is the restoration objective, then gap size appears to have little impact. Gap presence, however, did influence survival. In a companion study, seedlings were planted beneath the matrix forest next to these gaps. Seedlings beneath the canopy had 52% mortality, while seedlings planted beneath gaps had 25% mortality. Mortality would likely be even higher if the beneath-canopy seedlings were not planted directly adjacent to canopy gaps.

The asympototic gap size-growth relationship with giant sequoia seedlings was also found in a study done outside of grove boundaries (York et al. 2004, This dissertation, Chapter 2). The asymptotic functional relationship appears to be common in temperate studies that have defined gap size-growth relationships for other species (e.g. Minkler and Woerhide 1965, Coates 2000, Webster and Lorimer 2002). Studies that have described monotonic relationships (e.g. McDonald and Abbot 1994, Gray and Spies 1996) either did not consider an asymptotic relationship as a possibility, or simply considered a gap size range below the given threshold point where the gap size effect diminishes. Because of canopy heterogeneity and density variability between study areas, it is difficult to generalize about an average diameter:canopy height ratio where the asymptote occurs. The range that can best be inferred from the studies cited above is between 0.2 and 2. Additional studies are needed to define a more precise range and to detect any differences in the asymptote due to differences in resource gradient patterns between forest types. Defining gap size as a continuous variable, rather than categorizing gaps by “big” or “small,” will also aid in comparisons between studies and forest types.

Ash substrate effects

Prescribed fires have been a cornerstone treatment for restoration efforts in native grove areas managed by the National Park Service since 1969, and will likely continue into the future (Manley et al. 2001). In order to preserve the experimental control of gap size and shape that was necessary for this study, machines- not fires- were used to create the gaps. Whether or not agencies should use mechanical treatments in addition to prescribed fire has been thoroughly debated (Stephenson 1999). As the debate continues, disturbances of various sources and phenomena continue to impact giant sequoia groves. A number of gap-causing agents can result in either ash or soil substrates, at least one of which is necessary for giant sequoia germination (Stark 1968). Large windthrows, surface water movement that transports litter, and mechanical treatments such as logging or scarification by hand can all result in mineral soil substrates. An attempt to retain this study's relevance to gaps created by fire or other means was made by creating the ash substrates as a direct comparison to the adjacent mineral soil substrates.

As with the only other experimental assessment of giant sequoia regeneration within artificial gaps (Stephens et al. 1999), seed germination in this study was low. In their study, Stephens et al.'s (1999) attempts at promoting regeneration using site preparation methods produced very little seedlings even after methodically burning debris piles beneath target trees with the intention of heating crowns to release seed. The lack of germination in that case was attributed to the particularly dry year, although no estimate of seed supply was done to verify that there was seed release. In this study, the first season that seeds and seedlings were planted was a relatively dry year (76.6cm, 28% below average; NOAA 2005), and the second season when planting and sewing was repeated was a relatively wet year (164.5cm, 54% above average; NOAA 2005). My concerted effort to use direct seeding as a method of regeneration did not prove to be practical as a restoration treatment. Even after sewing stratified seeds over multiple years encompassing two different levels of moisture and on two different substrates, it is not likely that the treatment resulted in a population of germinants dense enough to lead to successful establishment of a mature cohort within this gap regime. Systematic surveys for natural regeneration within these gaps (York, *unpublished data)* have so far not detected any natural regeneration, supporting the possibility that the solitary act of creating gaps mechanically without any subsequent artificial regeneration treatment may not be sufficient for initiating a cohort of giant sequoia.

The density of seeds sewed in this study is far less than would be expected following an intense prescribed fire, where concentrations as high as 7500/m2 have been reported (Hartesveldt and Harvey 1967). The sheer quantity of seeds released during and after an intense fire is difficult to simulate with an artificial sewing treatment. Although the cost of sewing is much less than the cost of planting seedlings, the former appears to be much less reliable for cohort restoration when not using a fire to create the canopy gap. Giant sequoia seedlings have been planted at large scales beyond grove boundaries with high success, including within gap-based silvicultural regimes where giant sequoia survival in one case was higher than for five other native Sierran species (This dissertation, Chapter 2). Based on similar premises, the benefits of planting seedlings were also noted by Stephens et al. (1999), who planted seedlings within the Mt. Home grove but had much higher mortality than so far observed in this study (personal observation).

While the ash substrate did not influence the functional relationship between gap size and seedling growth, survival, or germination at the gap level, it did influence individual seedling size within gaps considerably (Fig. 2). The main effect of the ash treatment was to increase seedling growth in all positions, with a pronounced effect in gap centers. The possibility that the ash substrate (and associated increases in nutrient availability or increased wettability) might change the tolerance of giant sequoia seedlings to low-resource environments by increasing the capacity for growth or survival was in general not supported. Support would have come from a large effect of ash substrate on seedling growth or survival at gap edges (low resource availability) compared to at gap centers (high resource availability). Instead, the ash substrate increased growth at all positions along the resource gradient and was relatively ineffective in influencing germination and survival.

While restoration treatments do not *require* ash substrates for survival and growth of seedlings, rapid growth appears to be facilitated in all gap environments and sizes by an ash substrate. Whether this early surge in growth will result in actual "catching up" by this cohort to the missing cohort that would have established without fire suppression can only be verified by tracking these individuals over time. Subtle differences in juvenile performance often determine a tree's success in completing its life cycle (Knapp and Canham 2000, Landis and Peart 2005), and I have observed positive effects of ash substrate on giant sequoia size 16 years after planting (*unpublished data*). It is therefore possible that the ash substrate will at least reduce the amount of time that will pass before mature, seed-bearing trees develop, potentially offering a competitive advantage for later emergence into the canopy.

The question of whether rapid seedling growth should be an objective of restoration in the case of giant sequoia is an important consideration that could profoundly influence the design of restoration treatments. For example, rapid growth compared to associated species following the 1870’s disturbance led to the present structural and compositional dominance by giant sequoia in the upper canopy of the study area. Because of giant sequoias’ dominance, there is no shortage of nearby replacement trees for the ancient trees that now exist. Hence rapid growth was at least a contributor to the current positioning of probable replacement trees. There are, however, numerous giant sequoia individuals in the mid-story that did not outgrow neighbor trees. They persist as a suppressed bank of potential trees that could possibly recruit into the upper canopy following a disturbance. Given the capacity for giant sequoia saplings to release following suppression (Chapter 3), the long-term dynamics of giant sequoia in terms of recruitment probability from these mid-story positions needs further study. As one of the fastest and largest growing species (Stephenson 2000) in the mixed conifer forest (if not the world), growth might also be a relevant consideration for projects seeking long-term storage of atmospheric carbon.

Gap position effect

As expected, growth was in general greater near the resource-rich gap centers. The slight skew of higher seedling growth towards the south sides of gaps was surprising, given a similar study north of grove boundaries that found growth after 3 years to be heavily skewed towards north sides (York et al. 2003). Light penetration into the south edges of the gaps may have been greater in this study because of a patchier canopy caused by the emergent giant sequoia individuals. Alternatively, high levels of evaporative stress near northern edges in this study may have been more influential because of climatic differences between study periods or because of this study location’s slightly lower latitude (2 degrees difference). As resource gradients in these gaps are measured in the future, insights into the causes of these edge effects will help explain observed growth patterns.

The origin of the mature giant sequoia trees dominating the primary canopy layer in this study area can all be traced to a single cohort establishing immediately following the logging/burning event during the 1870’s. Patches of ancient trees elsewhere can similarly be reconstructed to originate from intense fires that created canopy gaps >0.03 ha (Stephenson 1994). In this study, I attempted to apply treatments that were similar to those past cohort-initiating events in terms of gap size and tree mortality intensity. Because of the role of fire in releasing and promoting germination, and because of some research suggesting a beneficial effect of burn piles on regeneration (Harvey and Shellhammer 1991), I expected germination to be more abundant on ash bed substrates near the central portions of gaps. While germination was indeed higher in these areas, the effect was only slight.

Relying on natural seed germination likely requires a much larger intensity of seed input, both in terms of density and frequency. Because seeds have to be sewn in the fall season, it is impossible to predict the germination conditions during the following spring. It may be necessary to either accept high variability in germination success following restoration treatments from year to year (including complete failures), or apply sewing treatments across multiple years. Although I observed some seeds that germinated two years after sewing, overwintering is not common enough to rely on for opportunistic establishment during adequate conditions (Harvey et al. 1980).

Most mortality of seedlings occurred on the north sides of gaps, increasing with proximity to the north edge. As observed in other studies (Rundel 1972, Harvey et al.

1980), the dominant cause of mortality was undoubtedly desiccation, as no signs of other damaging agents were noted. The desiccation was likely a result of greater levels of evaporative stress from peaks in radiation intensity occurring north of gap center (York et al. 2003). The blackened ash substrate likely resulted in increased surface temperatures and vapor pressure deficits, but did not result in greater mortality. The benefit of the ash substrate in terms of growth (Fig. 2) may be off-setting any negative influence of above-ground heating on survival.

In this gap regime, a cohort of surviving seedlings was best established by planting seedlings within gaps at slightly higher densities near north edges to offset higher levels of mortality. A subset of rapidly growing seedlings was promoted by preparing an ash substrate and by planting seedlings near gap centers. Depending on objectives (establishment, survival, and/or growth), restoration treatments can be designed using these results to increase the probability of success. Because of variability between sites and seasons, these results are not likely to hold true in every instance. Restoration programs should identify areas of uncertainty in the degree to which this research might be locally applicable, and then test uncertainties through an adaptive management approach as presented by Walters and Holling (1990).

Long-lived pioneer species restoration

The long-lived pioneer concept has been used in various forest types to classify a type of species- those that colonize rapidly following large disturbances and then persist- into a unique successional category (e.g. Lusk 1999, Finegan and Delgado 2000, Ogden et al. 2005). Although susceptible to the pitfalls of any categorization, long-lived pioneer might indeed be a useful integrative concept since it provides an exception to the colonizer-competitor tradeoff typically observed between fast-growing and long-lived species (Loehle 1988, Tilman 1994). As demonstrated by Ford and Ishii (2001), however, to become integrative the concept first needs to be strengthened by progressively assessing similarities between potential long-lived species from different systems, and by exploring biological causalities for why they exist.

Emergence to a dominant canopy position following disturbance is a common and necessary trait of long-lived pioneers that allows for long-term persistence. Because the probability of establishing an emergent position is typically correlated with rapid early growth (Wright et al. 2000, Landis and Peart 2005), it follows that long-lived pioneers share rapid growth under high-resource environments as a common attribute (but see Lusk 1999 for a possible exception). While a generally positive relationship between growth and gap size applies for most tree species, the specific details of the relationship might reveal a distinguishing characteristic of long-lived pioneer species. The two more-commonly studied species referred to as long-lived pioneers (*Sequoiadendron giaganteum*: Ishii and Ford 2002, *Pseudotsuga menziesii* in the Pacifc Northwest: Ogden et al. 2005) are both relatively sensitive to gap size and have asymptotic relationships that saturate at distinctly large gap sizes (Fig 1, Gray and Spies 1996). This attribute is consistent with the "dependence" of these long-lived pioneers on moderate or intense disturbances that create large canopy gaps (Spies et al. 1990, Stephenson 1994). Certainly, whether this is an additional similarity between long-lived pioneers that will boost its usefulness as an integrative concept needs to be explored with other species. Potentially, the quantification of a species' particular saturation point at which gap size no longer results in additional growth may provide a useful descriptive metric of species life-histories that also has obvious management application. This saturation point may be considered the population analog to the saturation point or light compensation point for photosynthesis in individuals.

The question of why the long-lived pioneer life history exists for giant sequoia is related to the particular disturbance regime that it is associated with. Large, infrequent disturbances (i.e. catastrophic) are usually assumed to be non-adaptive since they occur less frequently than the longevity of most organisms. For the longest-lived organisms that either have a life-span that is similar or slightly shorter than the return interval of the disturbance, however, large disturbances may be an adaptive force that selects for longevity (Pollmann 2004). For giant sequoia, adaptations for persisting through numerous low- and moderate-intensity disturbances (e.g. rapid growth, serotiny, thick bark) facilitate survival until a disturbance with enough intensity creates a canopy gap big enough for regeneration and recruitment. Hence, while giant sequoia is adapted to a low-intensity, high-frequency surface fire regime (Kilgore and Taylor 1971), it is also adapted to the very infrequent high-intensity fires that have occurred in its range (Swetnam 1993). Intense fires occurred more frequently than the 2000+ year lifespan of giant sequoia (Stephenson and Demetry 1995). For long-lived pioneer species, intense disturbances are likely to be a key component in their persistence.

Treatments that restore or mimic the intensity of disturbances that facilitate regeneration of long-lived pioneers can be expected to meet great public scrutiny. Intense fires in giant sequoia groves, for example, are a visually destructive process that often conflicts with local air quality standards. Despite these social and logistical challenges of restoring intense disturbances, they may be particularly effective at meeting restoration goals (Fule et al. 2004). Relict conifer species such as giant sequoia (e.g. *Sequoia sempervirens* and *Wollemia nobilis*) are at a practical advantage because public support is easily garnered for such unique and attractive species (Briggs 2000). Justifications for careful treatment installations can also benefit from experiments that quantify responses of ecological variables to ranges of environmental conditions and specifically test a range of treatment options.

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Tables

Table 1. Species classified as long-lived pioneers

Species	Forest type	Longevity	Traits noted in literature	Reference
Sequoiadendron giganteum	Temperate conifer	3000+ years	Massive, fast growing, disturbance colonizer	Stephenson 1994
Sequoia sempervirens	Temperate conifer	2200+ years	Rapid growth after disturbance, huge size, long-lived	Huston and Smith 1987
Pseudotsuga menziesii	Temperate conifer	1000+ years	High LAI, epicormic branching when old	Ishii and Ford 2002
Weinmannia trichosperma	Temperate rainforest	730+ years	Mid-tolerant, needs large gaps to establish	Lusk 1999
Nothofagus alpine	Temperate deciduous evergreen	700+ years	Fast growing, “mid-tolerant”; outgrows congenitors in gaps	Pollman 2004
Pinus strobes	Temperate	450 years	Long-lived, light-demanding, rapid growth (but delayed)	Huston and Smith 1987
Liriodendron tulipifera	Temperate hardwood	300+	Gap dependent, establishes after gaps and outgrows adv. regen; long-lived, very large; often grows in pure stands	Huston and Smith 1987
Agathis australis	Temperate conifer (New Zealand)	*Not available*	Light-demanding, rapid regen. after coarse disturbance, canopy emergent	Ogden & Stewart 1995
Anacardium excelsum	Tropical	*Not available*	Orthotropic, high LAI, long-lived, efficient leaves	Kitajima et al. 2005
Lueha seemannii	Tropical	*Not available*	Plagiotropic, high LAI; dense layer of outermost leaves, long-lived, efficient leaves	Kitajima et al. 2005

Table 2. Candidate models for evaluating within-gap influences on regeneration and their implications for restoration

Model*	Restoration implication
S (Substrate)	Treatments that alter the substrate will have the most influence regeneration
P (Proximity to matrix)	Treatments that alter the proximity of regeneration to the matrix forest will be most influential
O (Orientation)	Treatments that alter the placement of regeneration either on the south or north half of gaps will be most influential
P+O+S	All three variables vary independently and are important influences on regeneration;
P+S+P*S	The combination of substrate and proximity is of primary importance
O+S+S*O	The combination of substrate and orientation is of primary importance
P+O+P*O	The combination of proximity and orientation is of primary importance
P+O+S+S*O+P*S+P*O	All possible combinations of substrate, proximity, and orientation are important

*Note that all additive combinations are not considered.

Table 3. Model selection results for the relationship between gap size and regeneration indicators.

Model ranks	Ki	AICi	Wi	Evidence ratios	95% likelihood confidence interval of slope parameter
Height Growth					
Soil					
1. Asymptotic	2	-43.07	0.63		0.02-0.19
2. Quadratic	3	-41.58	0.30	2.10	
3. Linear	2	-38.65	0.07	9.13	
Ash					
1. Asymptotic	2	-48.93	0.78		0.03-0.15
2. Quadratic	3	-45.93	0.17	4.50	
3. Linear	2	-43.26	0.05	17.06	
Diameter Growth					
Soil					
1. Asymptotic	2	-42.77	0.67		0.03-0.32
2. Quadratic	3	-40.41	0.21	3.26	
3. Linear	2	-39.34	0.12	5.58	
Ash					
1. Asymptotic	2	-44.55	0.76		0.02-0.15
2. Quadratic	3	-40.76	0.11	6.65	
3. Linear	2	-40.98	0.13	5.95	
Seed Germination					
Soil					
1. Linear	2	-77.21	0.57		-0.77- 0.08
2. Asymptotic	2	-75.90	0.29	1.93	
3. Quadratic	3	-74.41	0.14	4.07	
Ash					
1. Linear	2	-74.81	0.44		-0.90- 0.01
2. Asymptotic	2	-74.74	0.43	1.04	
3. Quadratic	3	-72.28	0.13	3.54	
Seedling Mortality					
Soil					
1. Linear	2	-59.00	0.45		-0.77 - 0.08
2. Asymptotic	2	-58.70	0.39	1.16	
3. Quadratic	3	-56.84	0.15	2.95	
Ash					
1. Asymptotic	2	-64.71	0.43		-0.03 - 0.28
2. Linear	2	-64.36	0.36	1.19	
3. Quadratic	3	-63.33	0.21	1.99	

Table 4. Model ranks and importance values of within-gap influences on regeneration indicators. The highest ranked models that sum to >95% of the normalized AIC weights are reported. S = substrate (ash or soil), P = proximity to edge, O = orientation from gap center (south or north)

Model	AICw	Evidence ratio	Cumulative weight	Importance value of variables
Seedling size				**S=0.56, P=0.56, O=0.56, S*P=0.44, S*O=0.29, P*O=0.29**
1. S+P+O	0.56		0.56	
2. S+P+O+S*P+S*O+P*O	0.29	1.95	0.85	
3. S+P+S*P	0.15	3.84	>0.99	
Seed germination				**P=0.45, S=0.35, O=0.29, P*S=0.11, P*O=0.07, O*S=0.5**
1. P	0.30		0.30	
2. S	0.19	1.55	0.50	
3. S+P+O	0.15	2.00	0.65	
4. O	0.13	2.25	0.78	
5. S+P+S*P	0.10	3.05	0.88	
6. P+O+P*O	0.07	4.59	0.95	
Seedling mortality				**P*O=0.97, O*S=0.22, P*S=0.22, O=0.03, P=0.02, S=0.02**
1. P+O+P*O	0.75		0.75	
2. S+P+O+S*P+S*O+P*O	0.22	3.44	0.97	

Figures

Figure 1. Effect of gap size on relative growth of seedligns during the second year after planting. The model-selected asymptotic fit is used to describe the relationship. A. relative height growth. B. relative basal diameter growth. Seedlings were planted along south-north transects at Whitaker's Forest Research Station, CA within the Redwood Mountain Grove.

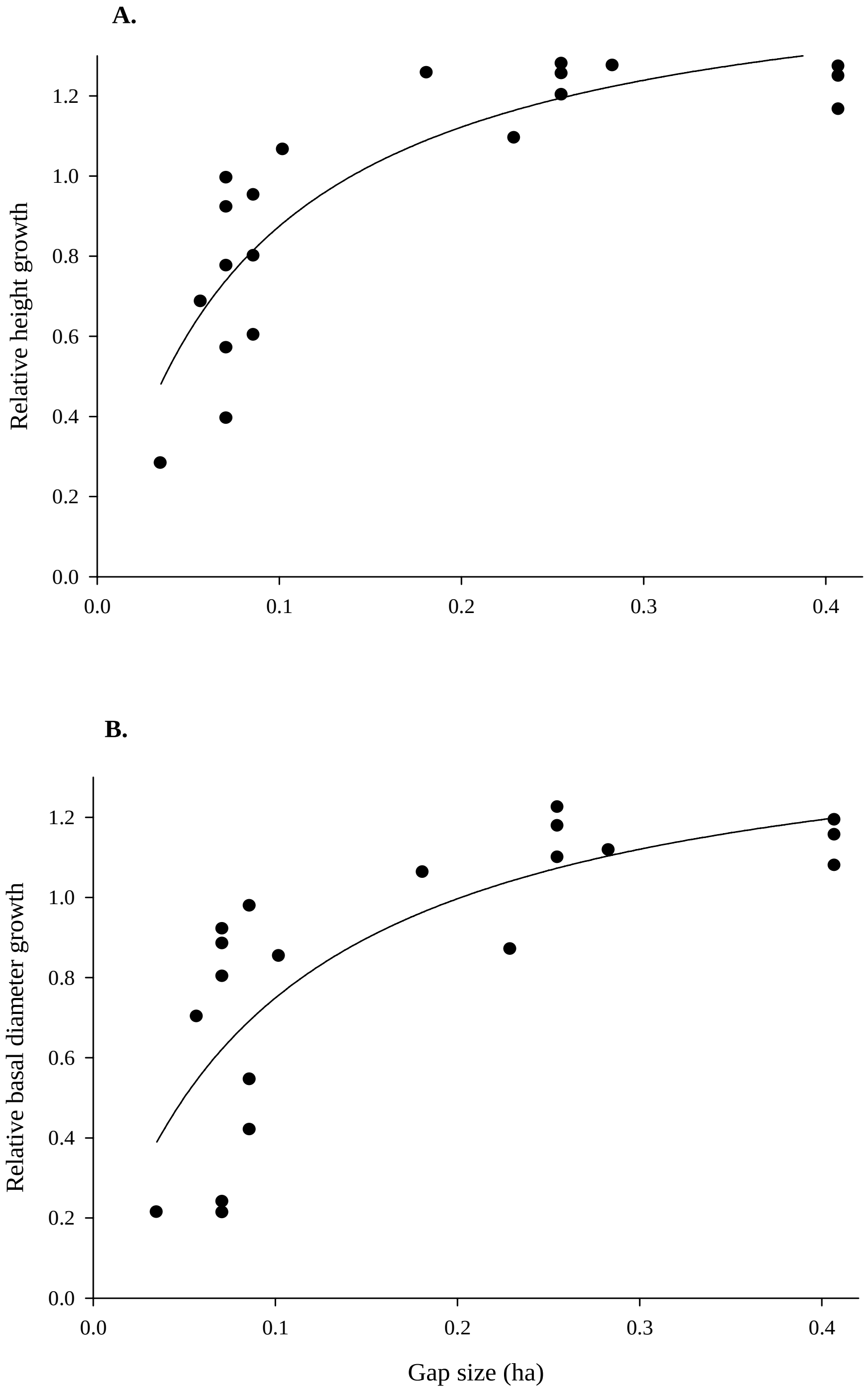

Figure 2. Influence of proximity to matrix, orientation, and substrate for 2 year old planted seedlings in gaps ranging in size from 0.04 to 0.4 ha at Whitaker's Forest Research Station, CA in the Redwood Mountain grove. The dashed vertical line represents gap center. The lines are quadratic fits of seedling size, displaying the average profile of seedling size across 20 gaps from north to south drip-line edges.

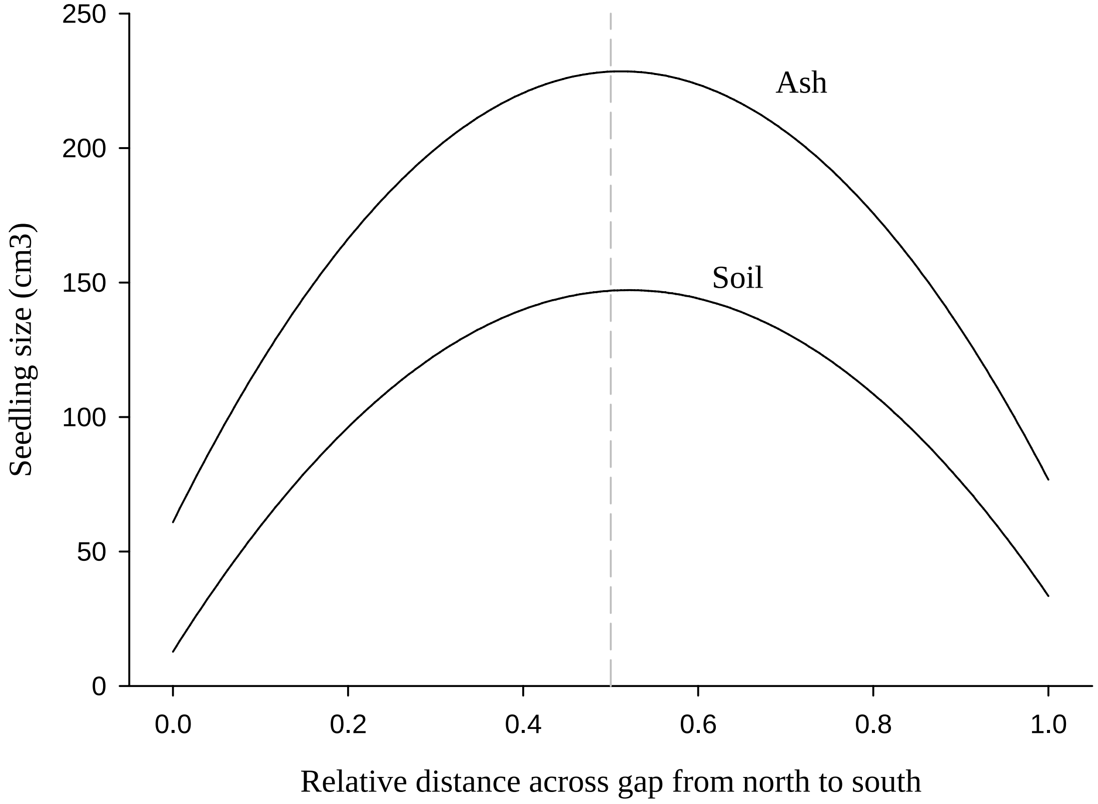

Figure 3. Influence of gap position and matrix proximity on mortality within experimental gaps at Whitaker's Forest Research Station, CA. The Y-axis is the average fraction of seedlings dead from two planting spots at paired distances from gap edge. Each planting spot had from 2 to 3 seedlings planted over two years..