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RESEARCH ARTICLE

Giant Sequoia (*Sequoiadendron giganteum*) Regeneration in Experimental Canopy Gaps

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Abstract

Restoration of giant sequoia populations is a high priority for managers, but few experimental studies have examined the efficacy of restoration treatments. To inform giant sequoia restoration treatment options, we assessed the response of giant sequoia regeneration (germination, mortality, and growth) to experimental gaps within a native giant sequoia grove. We created experimental gaps, ranging in size from 0.05 to 0.4 ha. Following gap creation, we sowed seeds and planted seedlings along north-south transects across gaps. Transects were planted on paired burned and unburned substrates. The seed-sowing treatment did not result in a cohort of established seedlings, although the amount of seeds sowed was far short of the potential amount released during intense fires. Mortality of planted seedlings did not vary with gap size (average 25% mortality). However, there was a distinct relationship between gap size and second year seedling growth. The relationship was best modeled with an asymptotic curve for both burned and unburned substrates. Relative seedling growth more than doubled as gap size increased from 0.05 to 0.2 ha, then increases in growth diminished. Growth rates of giant sequoia seedlings saturated above 70% light availability while increasing linearly with belowground resource availability. Long-lived pioneer species such as giant sequoia require restoration treatments that involve relatively severe disturbances to facilitate cohort establishment and recruitment.

Key words: **experimental gaps, long-lived pioneer, model selection, severe disturbance.**

Introduction

Recovery of fire-dependent forests will require active management to restore desired structures and processes (Covington 2000). Such restorative treatments proposed within native giant sequoia (*Sequoiadendron giganteum*) groves are often aimed at initiating new cohorts of giant sequoia that will eventually recruit into the canopy. When contrasted against the frequency of cohort initiation events reconstructed 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 the extreme longevity of individual trees (3,000+ year potential lifespan), the current giant sequoia population can endure a century of missing regeneration but the consequences of continued regeneration failures will increase dramatically with time. In practice, however, the use of restoration treatments to address regeneration failures of long-lived pioneer species, such as giant sequoia, presents a unique management challenge: a significantly severe disturbance must be part of the treatment and the success of efforts will not be judged for centuries.

Restoration efforts in giant sequoia groves share challenges common to the management of "charismatic" natural resources. Any plan must address the concerns of numerous and diverse stakeholders (Rigg 2001) while meeting essential operational objectives (e.g., efficient use of limited resources; minimal conflicts with competing objectives). Uncertainty in the efficacy of treatments can lead to delays or avoidance of treatments altogether (Maser et al. 1994). However, the dilemmas inherent in proactive restoration projects should not preclude their implementation. Often the ecological risks of no action far outweigh the risks of acting with uncertainty (Covington 2000).

The native population of giant sequoia is restricted to approximately 67 groves (total area ∼15,000 ha) along the western slopes of California's Sierra Nevada range (Willard 2000). Fire suppression policies starting in the early 1900s have altered forests (Stephens & Ruth 2005), and recent changes in fire severity have had broad ecological impacts (Miller et al. 2009). Giant sequoia is constrained by the limited conditions under which successful regeneration can occur (Rundel 1972; Harvey & Shellhammer 1991). Restoration treatments should therefore focus on creating conditions that promote the successful establishment of seedlings. Establishment is conspicuously linked with disturbance—the creation

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of canopy gaps is necessary for regeneration and emergence into the canopy (Harvey et al. 1980). However, the functional relationship between regeneration and specific gap characteristics is poorly understood. When canopy gaps are created, gap size (York et al. 2004), substrate quality (Harvey & Shellhammer 1991), and resource gradients within gaps (York et al. 2003) are all influences on regeneration that can be altered by the choice of treatments (e.g., fire vs. mechanical treatments).

Using artificial regeneration techniques (direct seeding and seedling planting), we experimentally assessed influences of gap size, burning, and resource availability on giant sequoia regeneration to help prioritize treatment activities. Such manipulative experiments are rare in giant sequoia groves, where a lack of disturbances ranging in severity has increased vegetation homogeneity (Miller & Urban 2000). Our goals were to (1) describe the relationship between gap size and giant sequoia germination, mortality, and growth; (2) determine the influence of burned substrates on regeneration; and (3) examine gradients in light and water within gaps and their influence on growth.

Methods

Study Area

The study was conducted at Whitaker's Forest Research Station (WFRS) in the southern Sierra Nevada range of California. WFRS (36°42′N; 118°56′W) is within the Redwood Mountain grove, which lies mainly within Kings Canyon National Park. Gaps were installed across a 100 ha area between elevations of 1615 and 1830 m. Aspects in the study area are west-facing, on slopes of 15–30%. Soils are of granitic origin, generally deep (>2 m). Annual precipitation averages 107 cm/year, ranging from 40 to 160 cm during the last 30 years at nearby Grant Grove (NOAA 2005). Much of the precipitation (>80%) comes from winter snows and spring rains.

Vegetation at WFRS is dominated by a Sierra Nevada mixed conifer forest type (Fites-Kaufman et al. 2007) with the addition of giant sequoia. Fire suppression and grazing activity beginning in the 1800 s have influenced current forest structures within most groves (Stephens & Elliott-Fisk 1998; Abella et al. 2007). The canopy structure is relatively homogeneous and distinctly two tiered, with an emergent upper tier of approximately 1.5 very large (1,000+ years old) giant sequoia trees per hectare. The second tier forms the main canopy and includes (in order of decreasing basal area dominance) giant sequoia, incense cedar (*Calocedrus decurrens*), white fir (*Abies concolor*), sugar pine (*Pinus lambertiana*), and ponderosa pine (*Pinus ponderosa*). Basal area of this main canopy averages 65 m^2/ha. Most trees in the main canopy belong to a single cohort that established after logging in the 1870 s that removed virtually all the larger pine trees and approximately half of the emergent sequoias (Metcalf 1940). Harvesting activity took place in many of the native groves around the same time (Willard 2000). The subcanopy is conspicuously free of young giant sequoia and is composed largely of white fir and incense cedar, two shade tolerant species that typically dominate understories in the absence of recent fires or severe anthropogenic disturbances (Rundel 1971; Bonnicksen & Stone 1982).

Experimental Treatments and Data Collection

Twenty circular gaps ranging in size from 0.05 to 0.4 ha were created during the summers of 2001 and 2002. Some fire-created gaps occurring before the fire suppression era were undoubtedly larger than the 0.4 ha maximum used in this study (Swetnam 1993), but available studies (Bonnicksen & Stone 1981; Bonnicksen & Stone 1982; Stephenson 1994; Demetry 1995) suggest that most gaps were less than 0.4 ha in size. Our goal was to produce five replicates of four size classes (0.05, 0.1, 0.2, and 0.4 ha). The ratio of gap diameter to canopy height for this range is 0.75 for the smallest and 2.11 for the largest gaps. Gaps were located adjacent to, but not including, large giant sequoia trees. Size and location of gaps was largely dictated by the feasibility of fitting gaps in between giant sequoia trees. Gap locations cannot be randomized because of the population-wide requirement to protect large giant sequoia trees.

Trees within gap boundaries were cut with chainsaws and skidded out with tractors. An average stem volume of 233 m^3/ha was removed. Postharvest debris was piled into windrows 5-m wide and oriented along south–north transects

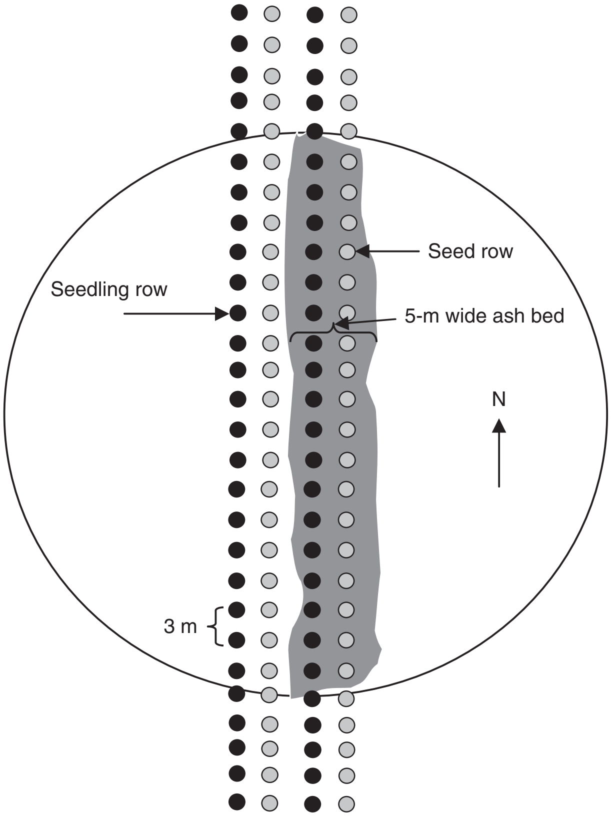

Figure 1. Overhead view of experimental layout in a canopy gap created at WFRS, California, U.S.A.

within gaps (Fig. 1). Two of the gaps were not accessible and did not have the piling treatment. During the fall after the harvests, windrows were burned during conditions that facilitated near-complete consumption. Burning lasted approximately 5 hours, whereas smoldering lasted approximately 48 hours, creating an ash layer estimated to be 5–8 cm deep. Giant sequoia seeds were collected from emergent trees throughout the study area and were sown every 3 m along two adjacent transects extending 12 m beyond south and north gap edges (Fig. 1). One transect had a burned substrate, whereas the other was unburned (i.e., bare mineral soil). Burned–unburned pairings only occur between drip-lines because no debris was burned beneath the surrounding canopy. Seeds were screened to increase viability. At each sowing location, five seeds were sown to increase the probability that at least one seed was viable at each location (>99% probability). Following poor germination in 2004, sowing was repeated at every other spot in the fall for germination in spring of 2005.

Planted seedlings of giant sequoia were grown from the same source of seeds used for the seed-sowing treatment. They were raised in containers for 1 year before planting in the spring of 2004. Seedlings were planted every 3 m in paired burned–unburned substrates, similar to the seed-sowing pattern (Fig. 1). Seedlings were double-planted at each planting spot. One year after planting, spots where both seedlings had died were replanted with another seedling. This repeated planting was carried out to increase the probability of at least one seedling eventually becoming established. It also provided a mortality index for each spot on the basis of the number of seedlings (zero to three) that died over 2 years.

We monitored all phases of regeneration: seed germination, seedling mortality, and seedling growth. Frequency of seed germination was monitored in early summer of 2004 and again in 2005. Each seed spot was visited and germination was tallied as presence or absence of at least one germinant. After the second growing season, each planted seedling was given a zero value if still alive and a one value if dead. The possible mortality index values per spot were 0 of 2 seedlings dead (0), 1 of 3 dead (0.33), 1 of 2 dead (0.50), 2 of 3 dead (0.67), or 3 of 3 dead (1.00). Early seedling growth was assessed by direct measurement of basal diameter and height of all seedlings after the first and second growing seasons.

Light availability was measured along north–south transects in every gap using hemispherical photography. Photos were taken along transects at 12-m intervals, spanning from 12 m north to 12 m south of gap edges. We took five photos in the smallest gap and twelve photos in the largest. Photos were taken with a Nikon 35-mm camera and a Nikkor fish eye lens (8 mm $f/2.8$) placed 1 m aboveground. Photos were taken near dawn or dusk to minimize direct lighting effects. Color slides were converted to digital images (900 dpi) that were analyzed with GLA software (Frazer et al. 2000) to compute the percent of total transmitted photosynthetically active radiation (%TTR). This index of irradiance calculated from film-based hemispherical photographs has proven to be one of the most reliable measures of light influence on seedling growth (Kobe & Hogarth 2007). We obtained a precision estimate of ±2% from remeasurement of a random subset (7%) of photos.

Water gradients were measured by sampling seedlings directly for stable isotope composition, an integrated measure of plant water status (Dawson et al. 2002). Carbon isotope ratios (^{13}C/^{12}C, hereafter referred to as δ^{13}C) measured from bulk leaf samples were analyzed to provide an index of water use efficiency (WUE) during the second year after planting. The carbon isotope fingerprint stored in plant material reflects WUE by recording the amount of photosynthetic activity per unit of stomatal conductance to water vapor (Farquhar & Richards 1984). Samples were collected from seedlings in the larger gaps that were more likely to have steeper water gradients. Following analysis of gap size (see below), gaps greater than 0.2 ha were judged to be sufficiently large for having high levels of resource availabilities at gap centers compared with gap edges. Within these gaps ($n = 7$), seedlings were sampled from centers and from within 6 m of the south and north edges. Five of the gaps had paired burned–unburned substrate treatments at each sample location. In these gaps, samples were collected from both transects. The other two gaps were not burned, and seedlings were collected from only unburned transects. Each seedling sampled ($n = 36$) therefore had a substrate treatment (burned or unburned) and a gap position treatment (north, south, or center). The leaf samples were ground to a fine powder, weighed, and analyzed for δ^{13}C using a mass spectrometer at The Center for Isotope Biogeochemistry at UC Berkeley.

Data Analysis

Gap Size Influence. We used only those gaps that had complete burned substrate treatments ($n = 18$), so that we could do separate model fitting for paired burned and unburned substrates. The predictor variable was gap size, and the response variables were germination, mortality, and relative seedling growth in height and diameter. Germination was expressed as the percent of seed spots in the gap that had at least one germinant present following either of the two sowing treatments. Mortality was expressed as the overall mortality incidence for the whole gap over 2 years, by averaging mortality index values across all planting spots per gap. To control for differences in initial seedling size, relative growth was calculated for each seedling by dividing the second year growth increment in height or diameter by the measurement taken after the first year. Mean relative growth per gap was then used for analysis.

To explore the functional relationship between gap size and regeneration, we combined likelihood-based methods with information theoretics (Buckland et al. 1997; Burnham & Anderson 2002). A set of candidate models were developed a priori and used to fit germination, mortality, and growth to gap size for burned and unburned treatments separately. The candidate set was made up of three informative models: linear, quadratic, and asymptotic. A quadratic equation implies that the response variable increases with gap size up to a maximum and then declines. An asymptotic fit implies a positive gap size effect, but then returns diminish and level off. This was described with a simple two-parameter Michaelis–Menton equation.

We solved for the parameter estimates that maximized the likelihood of the observed changes in regeneration measurements by entering the results from an iterative global optimization procedure, simulated annealing, into a local optimization procedure, Nelder–Mead (Nelder & Mead 1965). We validated the assumption of normally distributed errors by examining residuals. Statistical analyses and optimizations were conducted in S-Plus (7.0, Insightful Corp., Seattle, WA, U.S.A.).

Models were ranked according to goodness of fit while penalizing for model complexity using small-sample corrected Akaike's information criteria ($\mathrm{AIC_c}$; Burnham & Anderson 2002). Differences in $\mathrm{AIC_c}$ values ($\Delta\mathrm{AIC_c}$) between the best model (i.e., the selected model) and the other candidate models provide a measure of the relative difference between criterion outcomes. The $\Delta\mathrm{AIC_c}$ values were then used to calculate normalized Akaike weights (w_i), which were interpreted as the strength of evidence that a given model was the best model for the data among the candidate set. Evidence of the selected model's improvement over the other models was assessed by calculating evidence ratios (ratios between Akaike weights). We considered evidence ratios greater than two as strong support for model improvement (Burnham & Anderson 2002).

Within-Gap Regeneration Patterns and Resource Gradients. To characterize differences in regeneration response between basic categories of substrate (burned vs. unburned) and within-gap location (edge vs. center), we report magnitudes of differences between treatment means and t-based 95% confidence intervals (CI) of means (Zar 1999). Nonoverlapping intervals are considered evidence of a difference between treatments. All 20 gaps were included in this analysis.

To characterize gradients in light and water availability, gaps were grouped by size. Gaps less than 0.18 ha were functionally distinct from those that were greater in size (see Results, Fig. 2). Light was thus characterized separately for small (<0.18 ha) and large (>0.18 ha) gaps. Weibull fits were used to interpolate light patterns within gaps and also extending 12 m beyond their edges. The δ^{13} C measurements were analyzed with separate generalized linear models with gap location (south, north, or center) as the between-subject effect and substrate (burned or unburned) as a nested effect. Significance was judged with F-tests and $\alpha < 0.05$.

To assess the influence of resource availability on individual seedling growth, we again combined likelihood-based methods with information theoretics to compare alternative a priori models. Percent of total transmitted radiation was used to represent the light availability gradient, and distance to gap edge was used as an index of belowground resource availability. This index was used as an approximation of belowground resources because water and nitrogen availabilities do not necessarily co-vary with light availabilities within gaps. Models were fit to measurements of the relative increase in seedling size. Seedling size was estimated by multiplying basal area by height (cubic centimeter). Eight candidate models were developed to represent different hypotheses about the form of the seedling growth response curve as a function of light availability and the index of underground resource availability. We considered candidate models on the basis of two general functional forms: linear models (i.e., relative seedling growth directly proportional to light availability and soil resource index) and Chapman–Richards saturating models (i.e., relative seedling growth levels off at a threshold level of light availability and soil resource index, Bredenkamp and Gregoire 1988). For each functional form, we compared models in which light availability and distance to gap edge had an additive effect on seedling growth and models in which these parameters interacted (i.e., multiplicative effect). As described above, we used an iterative optimization procedure to solve for the maximum likelihood parameter estimates and compared models with corrected Akaike's information criteria.

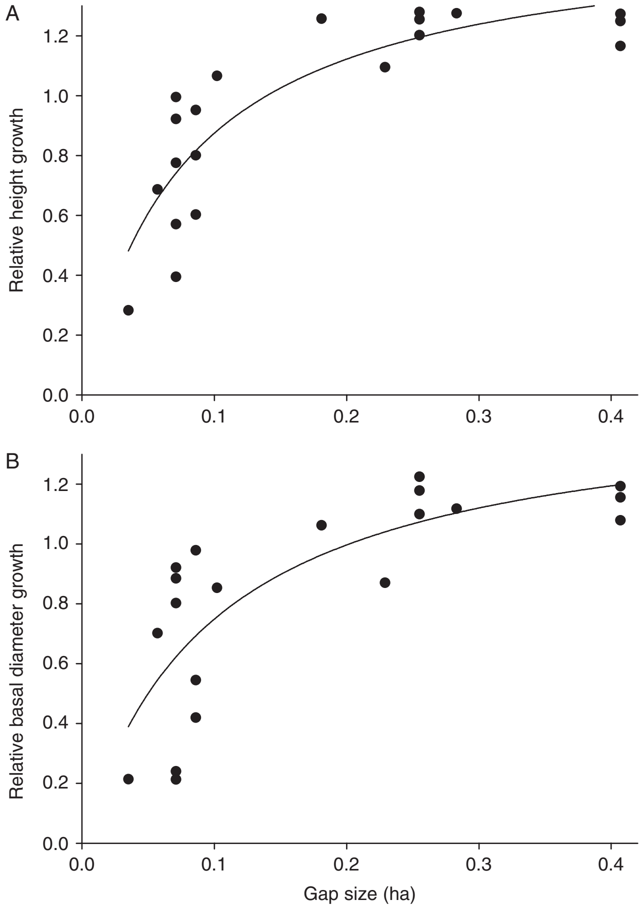

Figure 2. Effect of gap size on relative growth of seedlings during the second year after planting. The model-selected asymptotic fit is used to describe the relationship. (A) Relative height growth. (B) Relative basal diameter growth. Seedlings were planted along south–north transects at WFRS, California, U.S.A.

Results

Gap Size Influence

For both burned and unburned treatments, the strongest evidence was for a linear relationship between gap size and germination rate, although evidence was not much stronger than for an asymptotic relationship (evidence ratios < 2; Table 1). Model selection analysis for gap size effects on mortality also did not distinguish between linear and asymptotic fits (evidence ratios < 1.2). Overall, the effect of gap size on seed germination and seedling mortality was weak, with models accounting for less than 21% of observed variation (Table 1).

An asymptotic relationship between seedling growth and gap size was the highest ranked model with strong support (Table 1). For both height and basal diameter growth, there was little difference in the gap size–growth relationship between seedlings planted in the unburned compared with those planted in the burned treatments (Table 1). Given this similarity in functional form, we combined seedling measurements from burned and unburned treatments to model the seedling growth response to gap size with higher precision. Height and basal diameter growth increased sharply with gap size, then approached saturation around 0.2 ha (Fig. 2A & B). This gap size corresponded to a gap diameter to canopy height ratio of 1.5. The fraction of variation in growth explained by the top-ranked models ranged from 49 to 62% (Table 1).

Within-Gap Regeneration Patterns and Resource Gradients

Germination frequency was low, with 6 of the 36 transects not having any germinants at all and little difference in germination frequency by location or burn treatment (Table 2). Twenty-five percent of all seedlings planted in gaps died by the end of the second year, with mortality higher (although CI overlap slightly) along gap edges (30% mortality) compared with near-gap centers (17% mortality). Seedling growth was greater when seedlings were planted in ash substrates (27% increase in height and 34% increase in basal diameter), although CI again overlap slightly. Seedling growth was greater near-gap centers compared with near-gap edges (51% increase in height and 77% increase in basal diameter, Table 2).

The light patterns across gaps closely followed a Wiebull fit for both small ($r^2 = 0.82$) and large ($r^2 = 0.82$) gaps. Light availability was, in general, greatest in gap centers for both small and large gaps, with peaks occurring just north of centers in small gaps and just south of centers in large gaps (Fig. 3). Predicted light availability at gap centers was 51.9% for small gaps and 77.7% for large gaps. As expected, gradients were steeper in southern hemispheres of gaps compared with northern hemispheres.

The δ^{13} C values varied according to gap location ($F_{[2,25.24]} = 10.86$; $p < 0.001$), but no effect of substrate was detected ($F_{[3,1.70]} = 0.49$; $p = 0.69$). The δ^{13} C values were most positive (lower water stress) in gap centers ($\mathrm{CI}_{95\%} = -27.29$ to

Table 1. Model selection results for the relationship between gap size and regeneration.

Selected Model	*K**	*AIC Weight*	*Evidence Ratio to Next Best Model*	*r^2*	*95% Support Interval of Slope Parameter*
Seed germination					
Soil—linear	2	0.58	1.93	0.21	−0.72 to 0.024
Ash—linear	2	0.46	1.04	0.21	−0.84 to −0.045
Seedling mortality					
Soil—linear	2	0.47	1.16	0.21	−0.29 to 0.94
Ash—asymptotic	2	0.45	1.19	0.20	−0.038 to −0.006
Height growth					
Soil—asymptotic	2	0.67	2.63	0.49	0.013 to 0.14
Ash—asymptotic	2	0.81	5.6	0.62	0.03 to 0.12
Diameter growth					
Soil—asymptotic	2	0.70	4.08	0.51	0.01 to 0.20
Ash—asymptotic	2	0.78	5.95	0.51	0.02 to 0.12

**K* is the total number of parameters.

Table 2. Ninety-five percent confidence intervals ($\mathrm{CI}_{95\%}$) of means, organized by gap substrate and location.

	Substrate		*Location*	
Treatment	*Soil $\mathrm{CI}_{95\%}$*	*Ash $\mathrm{CI}_{95\%}$*	*Center $\mathrm{CI}_{95\%}$*	*Edge $\mathrm{CI}_{95\%}$*
Germination frequency (%)	5–16	10–23	4–21	16–30
Mortality index	0.07–0.24	0.12–0.28	0.08–0.28	0.23–0.38
Second year height (cm)	46.00–62.74	60.22–78.46	61.27–82.05	43.26–51.68
Second year basal diameter (mm)	10.65–15.86	14.73–20.80	15.16–21.64	8.92–11.89

Germination frequencies are from sowing locations where five seeds were sown and at least one germinant indicates a successful germination. Mortality and growth measurements refer to planted seedlings.

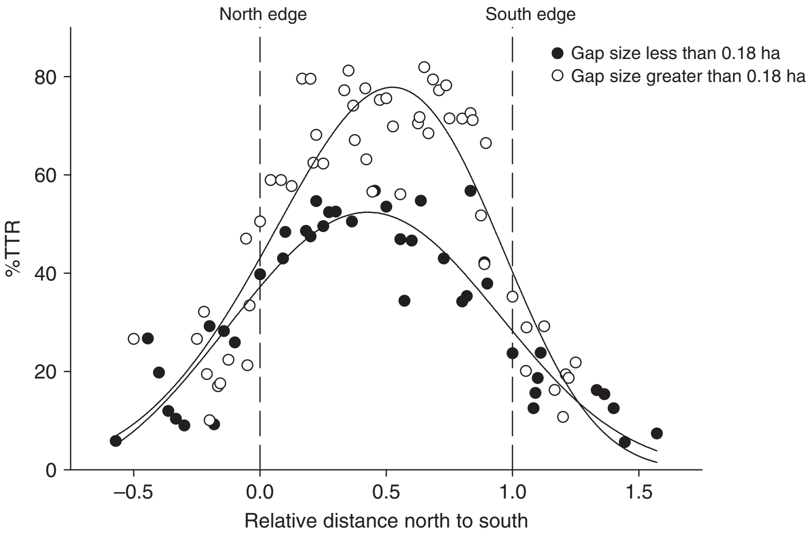

Figure 3. Light (%TTR) gradients extending along north–south transects in gaps ranging in size from 0.05 to 0.4 ha at WFRS, California, U.S.A. Data were fit with Weibull curves.

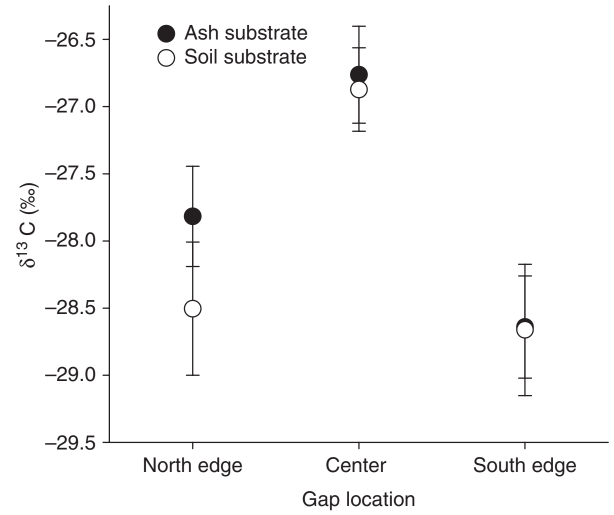

Figure 4. Intrinsic WUE estimated from carbon isotope ratios of seedling foliage samples across north–south transects in gaps at WFRS, California, U.S.A. Means and 95% CI are given for each within-gap location and substrate type (burned or unburned). More negative values on the *y*-axis indicate greater intrinsic WUE. North and south locations are within 6 m of gap drip-lines. Center locations are within 3 m of gap centers.

$-26.25\delta^{13}$C), whereas south and north locations were similar to each other (south $\mathrm{CI}_{95\%} = -29.22$ to $-28.08\delta^{13}$C; north $\mathrm{CI}_{95\%} = -27.73$ to $-27.59\delta^{13}$C; Fig. 4).

Table 3. Model rankings and goodness of fit for models of light availability and soil resource index on relative growth of giant sequoia seedlings.

Model	*K**	*AIC Weight*	r^2	*Evidence Ratios*
Saturating light + linear soil index	5	0.99	0.59	1
Saturating light and soil index	4	7.7E − 05	0.56	1.29E + 4
Saturating light × linear soil index	5	1.44E − 07	0.55	6.93E + 6
Saturating light	3	6.03E − 08	0.52	1.65E + 7
Linear light and soil index	3	8.15E − 14	0.52	1.23E + 13
Linear light	2	4.43E − 16	0.50	2.26E + 15
Saturating soil index	3	1.44E − 23	0.48	6.92E + 22
Linear soil index	2	1.22E − 30	0.44	8.23E + 29

**K* is the total number of parameters.

Model selection results did not differ between the unburned and burned substrates. All data were therefore combined for analysis. All models produced unbiased estimates of seedling growth and symmetrically distributed residuals. The best model was an additive relationship between a saturating function for light availability and a linear function for soil resource index (Table 3). This model explained 59% of the variation in growth. The strength of support for this model was overwhelming relative to all other models in the candidate set (evidence ratio > 10,000, Table 3). This model suggests that at the highest combined resource availability, planted giant sequoia seedlings could grow four to five times their initial size in 2 years (Fig. 5). Seedling growth was sensitive to gradients in both light and belowground resources. However, results from our growth analysis imply that the nature of this sensitivity varies depending on the index. Predicted growth rates increased with light availability until approximately 70% full sun. At higher light levels, there was no change in growth. In contrast, growth increased linearly with distance from edge even at maximum distances (Fig. 5), suggesting that for this range of gap sizes, belowground resources (i.e., water and/or nutrients) still constrain growth.

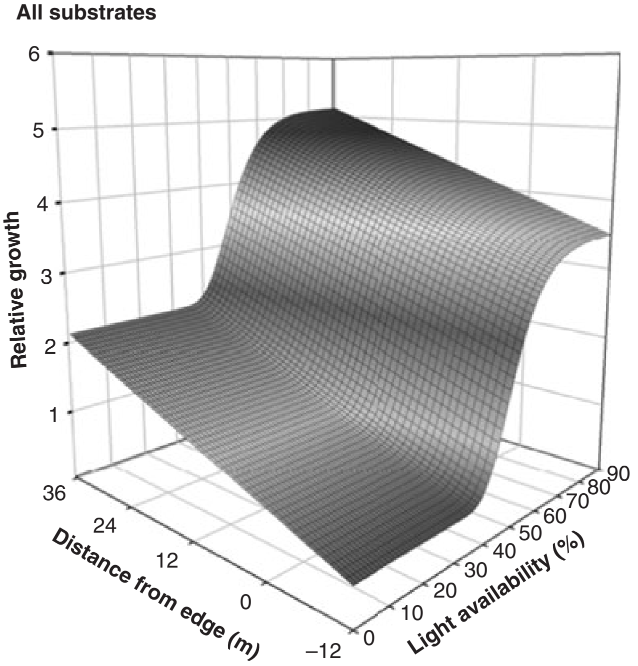

Figure 5. Predicted relative growth as a function of light availability and distance from gap edge (i.e., soil resource availability index) at WFRS, California, U.S.A. Predictions were generated from the top-ranked model shown in Table 3. Ash and soil substrate seedlings are combined. Note that some extrapolation beyond empirical data occurs where distance from edge is high yet light availability is low, and where distance from edge is low yet light availability is high.

Discussion

Gap size had a profound influence on seedling growth, which increased as gap size increased. The influence, however, diminished markedly above 0.2 ha. In contrast, the effect of gap size on seed germination and seedling mortality was weak. Clearly, the primary restoration benefit of larger gaps is increased growth.

Mortality of planted seedlings was low for all gap sizes, even in the smallest gaps where pioneer species such as giant sequoia might be expected to have high competition-related mortality. In a previous study carried out outside of native grove boundaries (York et al. 2006), giant sequoia survival was also relatively insensitive to competition, whereas growth was greatly affected. If establishment of a surviving cohort without regard to the cohort's growth is the restoration objective, then gap size appears to have little effect. Gap presence, however, was important. Seedlings planted adjacent to gaps had 52% mortality, whereas seedlings planted in gaps had 25% mortality. Mortality would likely be even higher if the beneath-canopy seedlings were not planted directly adjacent to canopy gaps.

An asymptotic relationship between gap size and seedling growth is common for temperate forest species (e.g., Minkler & Woerhide 1965; Coates 2000; Webster & Lorimer 2002; York et al. 2004). Studies that have described monotonic relationships (e.g., McDonald & Abbot 1994; Gray & Spies 1996) either did not consider an asymptotic relationship as a possibility, or considered a gap size range below the given threshold point where the gap size effect diminished. Because of canopy heterogeneity and site variability between study areas, the range in gap size where the asymptote occurs is wide. The range inferred from the studies cited above in terms of diameter:canopy height ratio is between 0.2 and 2.0. Additional studies that define gap size as a continuous variable are needed to define a more precise range and to partition differences in the asymptote to species versus site variation.

Prescribed fires have been a cornerstone treatment for restoration efforts within native groves managed by the National Park Service since 1969 (van Wagtendonk 2007). In this study, machines, not fires, were used to create the gaps. This was necessary to ensure the desired level of experimental control. Gap-based silviculture, where canopy gaps similar in size to those made in this study are created, could be a viable management option beyond national park boundaries (Stephens et al. 1999), where approximately 68% of grove areas exist. Although the burn treatment did not influence the functional relationship between gap size and seedling growth, mortality, or germination at the gap level, it did increase individual seedling size within gaps. The driver of this growth response was not explored in this study, but increased nitrogen availability is a likely contributor (Moghaddas & Stephens 2007). Other changes in soil properties following the burning could also have influenced seedling growth (Certini 2005).

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. In another study, a positive effect of burned substrates on giant sequoia growth persisted through the first 10 years (York et al. in press). Differences in juvenile performance can determine a tree's success in completing its life cycle (Knapp & Canham 2000; Landis & Peart 2005). Burning treatments may therefore reduce the amount of time needed for mature, seed-bearing trees to develop, potentially offering a competitive advantage for later emergence into the canopy.

Similarly to Stephens et al. (1999), we found low germination success of giant sequoia in artificial gaps. In that study, they tried to promote regeneration by burning debris piles beneath giant sequoia trees with the intention of heating crowns to release seed. They attributed the lack of germination to a particularly dry year, although seed supply was not measured to verify whether an adequate supply of seed was released. In this study, the first season that seeds and seedlings were planted was a relatively dry year (76.6 cm, 28% below average; NOAA 2005), and the second planting and sowing season was a relatively wet year (164.5 cm, 54% above average; NOAA 2005). Our effort to use direct seeding as a method of regeneration proved impractical as a restoration treatment, even after sowing on two substrates and over 2 years with varying levels of moisture. Systematic surveys for natural regeneration within these gaps have so far not detected any natural regeneration. Although the disturbance severity was high in terms of material per hectare removed and soil disturbed, simply creating gaps mechanically without any subsequent artificial regeneration treatment was not sufficient for initiating a cohort of giant sequoia.

The density of seeds sowed in this study is far less than what can occur following a severe fire, where densities as high as 7,500 seeds/m^2 have been reported (Hartesveldt & Harvey 1967). The sheer quantity of seeds released by a severe fire is obviously difficult to simulate with an artificial sowing treatment. Although sowing costs are much lower than seedling planting costs, sowing appears to be much less reliable for cohort restoration when canopy gaps are not created with fire. Giant sequoia seedlings have been planted extensively beyond grove boundaries with success, including within gap–based silvicultural regimes where giant sequoia mortality in one case was lower than for five other native Sierran species (York et al. 2007). Planting giant sequoia seedlings within canopy gaps created as part of a restoration program can clearly be an effective treatment option.

Giant Sequoia Restoration — The Challenge of Managing for Long-Lived Pioneers

Emergence to a dominant canopy position following disturbance is a 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 (Grime 1979; Wright et al. 2000; Landis & Peart 2005), it follows that long-lived pioneers share rapid growth under high-resource environments as a common attribute (see Lusk 1999 for a possible exception). Although a generally positive relationship between growth and gap size applies for most tree species, the specific details of the relationship show a distinguishing characteristic of long-lived pioneer species. Two archetypical long-lived pioneer species, *Sequoiadendron giaganteum* and *Pseudotsuga menziesii* in the Pacific Northwest (Ishii & Ford 2002), are both relatively sensitive to gap size and have asymptotic relationships that saturate at distinctly large gap sizes (Fig. 1; Gray & Spies 1996). This relationship is consistent with the dependence of these long-lived pioneers on moderate or severe disturbances that create large canopy gaps (Spies et al. 1990; Stephenson 1994; Weisberg 2004). Quantifying the 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 applications. In the case of giant sequoia, creating a significant portion of gaps greater than 0.2 ha may be necessary if increasing canopy recruitment rate is an objective.

Severe, infrequent disturbances are usually assumed to be nonadaptive because they occur less frequently than the longevity of most organisms. For the longest-lived organisms that have life spans that are similar or slightly shorter than the return interval of these disturbances, however, large disturbances may be an adaptive force that selects for longevity (Pollmann 2004). While giant sequoia is undoubtedly adapted to low-severity, high-frequency surface fires (Kilgore & Taylor 1971), it is also adapted to very infrequent high-severity fires, which have occurred periodically in its range (Swetnam 1993) at greater frequencies than the multimillennia life span of giant sequoia (Stephenson & Demetry 1995). Canopy openings created by high-severity fires offer a competitive advantage to giant sequoia: mature individuals persist through the disturbance, and then fast-growing seedlings colonize the disturbed area and compete efficiently for large pools

Table 4. Some species from North America with long-lived pioneer life histories.

Species	*Forest Type*	*Longevity (yr)*	*Traits Noted in Literature*	*References*
Sequoiadendron giganteum	Temperate conifer	3,000+	Fast-growing, disturbance colonizer	Stephenson (1994)
Sequoia sempervirens	Temperate conifer	2,200+	Rapid growth after disturbance, long-lived, crown development mechanisms for persistence	Huston and Smith (1987); Sillett and Van Pelt (2007)
Pseudotsuga menziesii	Temperate conifer	1,000+	Dense foliage, crown development mechanisms for persistence	Ishii and Ford (2002); Van Pelt and Sillett (2008)
Taxodium distichum	Forested wetlands	1,000+	Nutrient-demanding, sprouts following disturbance	Keim et al. (2006); Effler and Goyer (2006)
Pinus strobus	Temperate conifer	450	Light-demanding, rapid growth (but delayed)	Huston and Smith (1987)
Betula alleghaniensis	Temperate hardwood	300+	Litter-free substrate required for establishment, moderate canopy gaps for recruitment	Houle and Payete (1990); Kneeshaw and Prevost (2007)
Liriodendron tulipifera	Temperate hardwood	300+	Establishes after gap creation and outgrows advanced regeneration	Huston and Smith (1987)
Liquidambar styraciflua	Temperate hardwood	300+	Colinizer of abandoned fields, rapid growth	Kormanik (1990); Bragg (2004)

of resources. Currently, prescribed fires are probably not reflecting the range of disturbance severity that occurred before current fire suppression policies (van Wagtendonk & Lutz 2007). For giant sequoia and other long-lived species around the world, severe disturbances are an important factor of their persistence and hence restoration. Numerous examples of these types of species can be found throughout the world's forests, including many in North America (Table 4). These species differ greatly in the type of disturbances influencing regeneration and longevity. For example, fire is commonly the both mid- and high-severity disturbance agent for giant sequoia (Kilgore & Taylor 1971; Swetnam 1993) although wind storms (e.g., Douglas-fir; Franklin et al. 2002; Lutz & Halpern 2006) and floods (e.g., bald cypress; Keim et al. 2006) influence both the persistence and the regeneration of other long-lived pioneers.

Treatments that restore or mimic the severity of disturbances that facilitate regeneration and recruitment of long-lived pioneers can be expected to meet great public scrutiny. Severe fires or mechanical treatments in giant sequoia groves, for example, can be visually striking events that often conflict with other objectives such as aesthetics or local air-quality standards. Despite these challenges, restoring severe disturbances can be particularly effective for meeting restoration goals (Fulé et al. 2004), especially where long-lived pioneer species exist.

Implications for Practice

- Disturbances that create distinct canopy gaps are necessary for giant sequoia regeneration.
- Seedling growth increases with gap size, but levels off around 0.2 ha. There is not, however, a corresponding relationship between gap size and mortality.
- Burned substrates increase initial growth rates compared with unburned substrates (bare soil).
- Greater water and/or nutrient availabilities continue to increase growth rates of planted giant sequoia even when light is greater than 70% of full sun.
- Restoration programs that include or mimic high-severity disturbances may be necessary for sustaining long-lived pioneer species.

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