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Release potential of giant sequoia following heavy suppression: 20 year results

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Abstract

We tested the release potential of suppressed giant sequoia (Sequoiadendron giganteum) saplings in a plantation that was overgrown with shrubs at Blodgett Forest Research Station, CA in the mixed conifer forest of the Sierra Nevadas. As an ancillary case study, we compared the shrub removal method of release with a clear-and-plant method in an adjacent stand. Measurements of various morphological traits were collected prior to shrub removal, then sapling height growth response was measured periodically after the release treatment. In general, giant sequoia responded quickly to the removal of competing shrubs, growing steadily for 20 years following treatment. Among the morphological traits considered, live crown ratio alone was the most important factor in predicting relative height growth following treatment. Other traits were correlated with release, but had lower importance values as indicated by a model selection procedure. The 16-year old saplings that were released in this study did not grow as large as 2-year old seedlings that were planted synchronously with release, but both methods resulted in merchantable-sized trees 20 years after treatment. Planted seedlings outgrew released seedlings by 27% in terms of stature and by 37% in terms of diameter. The released stand is projected with a growth model to take 12 years longer than the planted stand to grow to an average diameter of 38cm. The misperception of giant sequoia as having a low capacity for release may be related to its ambiguous categorization as a shade intolerant species.

Keywords: Sequoiadendron giganteum, release, shade tolerance, model selection

1. Introduction

Globally, the rising demand for forest products over the latter part of the 20th century was increasingly met with yields from plantation forests (Sedjo 1999). These plantations often utilize non-native species that are fast-growing and tolerant of local climates. One species with potential as a plantation-managed species is giant sequoia (Sequoiadendron giganteum (Lindl.) Buchholz). While not nearly as widespread as many other plantation species such as radiata pine (Pinus radiata D. Don), giant sequoia has been planted throughout western Europe (Alexandrov et al. 2002; Hartesveldt 1969; Knigge 1992; Melchior and Herrmann 1987), where it is noted for both its superior growth and its potential for use in intensive forest management (Knigge 1992). Interest in management of this species on several continents has been rekindled as plantation managers look for alternatives to traditional single-species plantations (e.g. Maclaren 2004). Closer to its native range consisting of disjunct groves on the western slopes of the Sierra Nevadas in California, giant sequoia is occasionally planted on both public (Stewart et al. 1994) and private land (Heald and Barrett 1999). As in Europe, it is not planted widely although it has potential as a fast growing tree, outperforming all associated species through the first decade even in small plantations (0.1- 1.0 ha; (York et al. 2004)).

Regardless of the species planted, the decision to initiate a forest plantation implicitly commits land managers to a series of treatments between regeneration periods that will ensure maintenance of rapid growth to meet target yields (Daniel et al. 1979). Attention to the details of treatments can prove to be influential over large landscapes as degraded forests are restored to biologically and economically beneficial areas (Lamb et al. 2005). Such intermediate treatments may include fertilization, pruning, and control of density or competing vegetation. Control of competing vegetation is especially critical where native shrub species can usurp resources, resulting in suppression or mortality of planted trees. Despite the best intentions of managers, however, plantations regularly become overrun with shrubs. Such conditions may arise when herbicide use is not an option, or it becomes too burdensome to control competing vegetation frequently enough to maintain high resource availability for planted trees. Other causes may stem from administrative difficulties, changes in ownership and policy, or simple neglect. While most tree species are vulnerable to shrub competition to some degree, the silvics of giant sequoia suggest that it may be especially prone to suppression (Weatherspoon 1990). Nevertheless, the species has an often-overlooked capacity to survive (if not grow) under conditions of low soil moisture and light availability (Stark 1968; York et al. 2003). Hence with plantations in general and especially where resource-demanding species such as giant sequoia are planted, managers may face the unwanted scenario of a plantation of suppressed saplings completely overgrown with shrubs.

This scenario was indeed the case for managers of Blodgett Forest Research Station in the Sierra Nevada range of California. Fifteen years after establishing a plantation of giant sequoia in the late 1960's, a canopy of shrubs approaching 100% cover was overtopping the planted saplings which were just 1 meter tall on average, a rate of growth far below acceptable management objectives. This situation presented uncertainty to managers about whether release of the existing stand of saplings was economically and biologically viable. Further, no criteria were available for indicating which individual trees had the greatest potential to release, if a release treatment were to be applied. To address these uncertainties, the stand of suppressed saplings at Blodgett Forest was used to set up a long-term management experiment to describe and quantify the capacity of giant sequoia individuals to release from heavy suppression.

While release from heavy competition is traditionally considered important as a successional mechanism mainly for shade tolerant species (e.g. Connell and Slayter 1977), the suppression and release process can profoundly influence successional outcomes for intolerant species as well (Wright et al. 2000). Quantifying release capacity and assessing morphological indicators of release potential thus provides practical information for plantation management but also provides insight that may be used for restoration or recruitment in less intensively managed areas (Ferguson et al. 1986; Harrington and Tappeiner 1997). In this paper we assess long-term (20 year) release potential as a general trait in giant sequoia, and attempt to find easily-evaluated morphological traits that can be used to predict future growth after release. As a companion to this primary objective, a nearby stand that was also overgrown with shrubs was completely cleared and re-planted to provide a relevant standard by which to compare the efficacy of the shrub release treatment.

2. Methods

2.1 Study site

Blodgett Forest Research Station (BFRS) is located on the western slope of the Sierra Nevada mountain range in California (38°52′N; 120°40′W). The study area lies within BFRS at an elevation of 1330 m. The climate is Mediterranean with dry, warm summers (14 to17 degrees C) and mild winters (0 to 9 degrees C). Annual precipitation averages 166cm, most of it coming from rainfall during fall and spring months, while snowfall typically occurs between December and March. Pre-suppression era median point fire interval in the area is 9-15 years (Stephens and Collins 2004). The soil developed from granodiorite parent material and is productive for the region. Soil productivity is relatively uniform across the study site and surrounding areas. Heights of codominant canopy trees typically reach 31 m in 50 years (BFRS data, http://nature.berkeley.edu/forestry/. March 20, 2005). Olson and Helms (1996) provided a detailed description of BFRS, its management, and trends in forest growth and yield.

Vegetation at BFRS is dominated by a mixed conifer forest type, composed of variable proportions of five coniferous and one hardwood tree species (Tappeiner 1980). The study site is located on a mild (5-10%) northeast facing slope. There are six native overstory tree species present: white fir (Abies concolor (Gord. & Glend.) Lindl. Ex Hildebr.), incense-cedar (Calocedrus decurrens Torr.), Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco var. menziesii), sugar pine (Pinus lambertiana Dougl.), ponderosa pine (Pinus ponderosa Dougl. ex Laws.), and California black oak (Quercus kelloggii Newb.).

In harvested openings throughout the forest, BFRS has planted giant sequoia since the mid-1960's. BFRS is not within an existing native grove, but is within the expanded range of past giant sequoia populations (Harvey 1985). An isolated native grove (Placer grove) exists approximately 48 kilometers to the north, while the closest grove to the south is within 200 kilometers. Climatic conditions are very similar between BFRS and native groves.

2.2 Treatments

The 1.6 ha study area was cleared in 1967 with a tracked dozer. The area was planted at various spacings in 1968 with 2-year old container-grown giant sequoia seedlings. Seeds were collected from within the Redwood Mountain grove in the middle of giant sequoia's native range. Following the planting, no vegetation control treatments were applied due to a lack of management resources. A dense shrub layer subsequently established dominance over the next 15 years. Shrub species were dominated by greenleaf manzanita (Arctostaphylos patula Greene), mountain whitethorn (Ceanothus cordulatus Kellogg), deer brush (Ceanothus integerrimus Hook. & Arn.), and bush chinquapin (Chrysolepsis sempervirens (Kellogg) Hjelmq.). Greenleaf manzanita, the dominant shrub species in the study area, effectively competes with conifer trees by depleting soil moisture (Busse et al. 1996; Conard and Radosevich 1981; Rose and Ketchum 2002). In addition to the reduction of soil moisture available to the giant sequoia seedlings, light availability was reduced, as many seedlings were completely overtopped by the 2 meter high, 15 year-old shrub canopy. Many saplings had thin and/or pale foliage- a condition also noted by Stark (1968), who experimentally reduced light available to saplings in an experimental plot in the species' northern range. Despite the extremely heavy shrub competition, survival of giant sequoia saplings was surprisingly high. Following mechanical removal of shrubs, enough live saplings remained to allow a thinning to an average density of 494 trees per hectare. The saplings remaining after the treatment averaged just under 2 meters tall. A thorough herbicide treatment (mixture of 2-4-D and Glyphosate) was applied 2 years after shrub removal to kill all of the sprouting stems. No follow up treatment was necessary to reduce shrub competition (i.e. saplings were “free to grow”).

Concurrent with the release treatment, an adjacent stand (4 hectares) was cleared with a tracked dozer and then planted with giant sequoia seedlings of the same origin. Shortly after planting, plots were established and monitored as in the released plantation. Shrub control treatments (mechanical and herbicide) were applied in a similar manner. Ponderosa pine trees that regenerated naturally outside the plots in both stands were measured and compared to confirm that soil productivity was similar between the two locations. This paired treatment was set up as an important reference since, even assuming saplings did release, newly planted seedlings may still have outgrown the released saplings despite their 15 year head start. In the past, foresters have been versed by silviculture text books in the futility of releasing shade intolerant species from heavy competition (e.g. Daniel et al. 1979; Smith 1986). Compiled descriptions of silvics for conifer species reported giant sequoia to be especially shade intolerant (Burns and Honkala 1990) and incapable of release (Schubert 1962). At the time of release, conventional thought would therefore have lead to a prediction that the released seedlings would perform poorly compared to the planted seedlings, perhaps simply resulting in another shrub dominated field or invasion from surrounding tree species.

2.3 Measurements and Analysis

Nine 0.04 ha permanent plots were established on a systematic grid and all trees (n=127) within plots were measured concurrent with the treatment and then 1 year, 12 years, and 20 years later for height and diameter at breast height (1.37m). The 1-year and 12-year data are presented, but because we are interested in long-term release potential, only the pre- and 20-year post treatment data are analyzed statistically. Prior to the release treatment, a number of candidate morphological traits were considered for measurement. Chosen measurements were those that were thought to be potentially indicative of growth potential following release, but could also be rapidly assessed in the field. Traits proving to be indicative of release could then be used in the future when selecting trees most capable of release. Many of the saplings were pale in color. This is also seen in giant sequoia during winter months, when nutrient in foliage is translocated to stems. Hence foliage quality (“pale” or “normal”) was included as a categorical variable with the expectation that pale trees indicated nutrient stress and therefore had a low probability of release. The second trait was live crown length, expressed as a ratio of total tree height. Live crown ratio presumably reflects the potential amount of leaf area available for photosynthesis upon release. The second and third variables were basal diameter and crown diameter, two measures of tree size that are easily assessed when operating in the field. Basal diameter was measured at 15 cm above the ground, and crown diameter was measured as the maximum crown diameter along the north-south axis of a tree’s projected canopy. The predictor variables therefore included 1 categorical variable (foliage quality), and 3 continuous variables (height to live crown ratio, basal diameter, and crown diameter).

At the time of release, saplings ranged in height from 0.6 to 3.8 meters. Because of the wide range in initial height and to account for these differences in initial height as they may contribute to post-treatment growth, we used relative height growth as the response variable. This removed the effect of the contributing variable of initial height by incorporating it into one collapsed response variable. This has a further benefit over including initial height as a predictor variable because it reduces the number of model parameters (i.e. reduces model complexity). Further, initial height can be assumed to be correlated with later height and is not a variable of interest (i.e. *given* similar heights, what other morphological features are important?). The response variable is, therefore, height growth for the 20 years following release, relative to initial tree height:

$$\underline{\mathrm{RELGRO} = (\mathrm{Height}_{t=20} - \mathrm{Height}_{t=0}) / \mathrm{Height}_{t=0}\,,}$$

Where RELGRO is relative growth and *t* is the number of years since the release treatment.

Given the objective of quantifying each variable's potential as an indicator of release, we chose a technique that could help quantify the relative contributions of each variable in explaining the observed data. In essence, the objective is to know which traits- or certain combinations of traits, are reasonable to consider when judging release potential in the field. The term "reasonable" inherently invokes the principle of parsimony. That is, we want the simplest possible way of explaining as much data as possible. A powerful tool recently emerging in ecology for doing such analyses is model selection (Johnson and Omland 2004). In this case, we use model selection to assess the different models that can be formed from the host of variables that were chosen to measure. Each variable and the possible combinations of variables form a set of multiple working hypotheses, an approach that stays true to the a priori framework of the study at the time of its initiation, when little was known about giant sequoia physiology.

We use generalized linear models to explain variance in the response variable with a set of candidate models. Because of the philosophical rational of limiting the number of candidate models to less than 40 (Burnham and Anderson 2002), we consider the variables to be additive instead of including interaction terms. Another reason for including only additive models is the benefit of having balance among the variables. Because results in model selection are inherently dependent on the set of candidate models, choosing certain interaction terms to include while excluding others would weigh certain variables disproportionately. Further, the intent is to assess individual characteristics of saplings in order to ultimately derive simple measures of release potential. Hence, the global model (the most complex) includes all four variables, and the other candidate models include all possible additive combinations of the variables (Table 1). Across all 15 candidates, each variable is represented equally.

To rank the models according to goodness of fit while penalizing for model complexity we used Akaike's information criterion (AIC) derived by Sugiura (1978). The application of AIC for statistical inference in ecological studies is described in detail by Anderson et al. (2000) and Johnson and Omland (2004). The criterion equation is:

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

where AIC is the criterion for model alternative *i*; RSS is the residual sum of squares after fitting the model; *n* is the sample size; and *K* is the number of parameters in the model. Thus, as model fit (quantified by RSS) increases AIC decreases, and as the number of parameters increases, AIC also increases (i.e. the model with the lowest AIC value is the "best" model). To perform model selection and to compare strengths of evidence, we evaluate AIC values for each candidate model in relation to the highest ranked model. To do this quantitatively, we compute Akaike weights, which give the likelihood that within the limits of the data and the set of alternatives, the given model is the most appropriate choice. Inference is guided by comparing the ratios of AIC weights for each species. Finally, to quantitatively compare each variable's overall predictability of growth response, we compute relative importance values for each variable.

Importance value is calculated as the sum of all Akaike weights for the models in which the given variable appears (Burnham and Anderson 2002).

To see if the clear-and-plant method was ultimately better than the release treatment in achieving larger average tree size, we measured the adjacent stand concurrently with the final measurement of the released stand. For this part of the analysis, inference is made from the difference between the stands and not individuals. Plots are therefore the experimental units, used to compare average performance of trees in the clear-and-plant stand with those from the released stand. Average height and diameter per plot of trees greater than 11cm dbh were compared between the two treatment areas (n = 9 plots in each area). The difference between the means of each treatment area and associated 95% confidence intervals were calculated for interpreting the difference between the two stands. This approach, instead of hypothesis testing, is used to allow a more objective assessment of the magnitudes of differences between the two treatments, rather than relying on a subjectively defined significance level assigned by the authors (Ford 2000; Stefano 2004).

Finally, both stands are grown using a stand projection model to put the treatment differences in a management context. The distance-independent growth simulator CACTOS (Wensel et al. 1986), calibrated with allometric equations developed from local stands, was used. CACTOS is the primary model used by industrial landowners in California mixed conifer forests for simulating growth and assessing yields over time. We simulated the growth of both stands until each stand surpassed an average tree size threshold. An average diameter at breast height of 38cm was chosen as the threshold since, given the local market, a first commercial entry would typically be made at or beyond this size threshold. The difference in time it takes for each stand to surpass the average diameter threshold is then considered the “cost” difference of the treatments.

3. Results

In general, giant sequoia released quickly and maintained rapid growth following the release treatment, although the degree to which saplings released varied widely (Fig. 1). Growth response was best explained by live crown ratio alone (Table 1). Some evidence for basal diameter and foliage quality as additional important variables is expressed in the second and third ranked models, but the primacy of live crown ratio becomes evident with the calculations of relative importance. When AIC weights are summed across all models which include it as a variable, live crown ratio has an importance value of 0.89. This compares to 0.49 for basal diameter, 0.42 for foliage quality, and 0.29 for crown diameter. A linear regression equation predicting relative growth from live crown ratio (Fig 2; adjusted $r^2 = 0.34$) has a slope that is far greater than zero ($CI_{95\%} = 13.1$ to 21.6 meters per unit increase in live crown ratio) and an intercept near the origin ($CI_{95\%} = -4.1$ to 1.2 meters). The residuals of the regression model are normally distributed. Twenty years after treatment, trees in the plantation that was cleared and planted were 27% taller and grew 37% more in diameter, on average, compared to trees that were released (Fig. 3). When growth is projected into the future, the released stand takes 12 years longer than the planted stand to reach the 38cm average dbh size threshold.

4. Discussion

Although typically considered to be shade intolerant, the giant sequoia saplings persisting beneath the shrub layer in this study were tolerant enough to survive the very low resource environment for many years. Since no areas were left untreated, we do not know the rate at which saplings may have survived and eventually outcompeted or outlived the shrub canopy. Shrub competition was, however, clearly reducing tree growth below levels of growth and recruitment set by management objectives, thus prompting the shrub removal treatment. The saplings retained the capacity to respond well to release, a trait usually not associated with intolerant species. Ambiguity in the concept of tolerance is a problem for giant sequoia, as it can be considered both tolerant and intolerant, depending on whether the term refers to survival or growth. Ambiguity in the tolerance concept also originates from variation in what is being tolerated. Light, moisture, and nutrient conditions can all limit growth, with the latter two factors becoming particularly important in drier forests- like that of the Sierra Nevada (Coomes and Grubb 2000). This is especially relevant for giant sequoia, which can be co-limited (in terms of growth) by light and water availability (York et al. 2003). Tolerance as a quantified trait should improve as incorporation of both growth and survival becomes more common in characterizations of species' ecological niches (e.g. Baraloto et al. 2005; Chen 1997; Kobe et al. 1995).

Typically, a trade-off is expected between a sapling's capacity for rapid height growth under high resource availability and its ability to survive under resource scarcity (Kobe et al. 1995, Kobe and Coates 1997). This trade-off does not appear to confine giant sequoia to the same degree as other species. It can grow faster than other associated canopy trees (York et al. 2004), yet here it also displayed a high capacity to survive under the dense shrub cover. Even for this species, considered to be a fast-growing pioneer (Stephenson 1994), the persist-and-release phase appears to be a relevant component of its life-history. The longevity with which giant sequoia seedlings can persist heavy shrub competition and the physiological adjustments necessary to adjust from the persistence to the release phase are potential areas of study that have relevance for restoration and management in native groves.

The rankings of best performing models suggest that release potential of giant sequoia is best predicted by live crown ratio (Table 1). Live crown ratio was also a good predictor of future height growth after release for trees of the species red fir (Abies magnifica A. Murr.), white fir, and Douglas-fir (Helms and Standiford 1985), all associates with giant sequoia. The relative importance values from the model selection procedure present a hierarchical guide to managers conducting intermediate treatments that aim to maximize growth or recruitment probability of certain individuals: All else being equal (i.e. similar height and growing environment), giant sequoia saplings with the best live crown ratio should have been selected first, followed by those with larger stem diameters, then those judged to have superior foliage quality. Crown diameter was the poorest predictor of height growth. Its value is further diminished because it is the most difficult to quickly estimate with accurately in the field.

Although they grew surprisingly well, the 15-year old released trees grew less overall following the treatment compared to the 2-year old seedlings planted after clearing the nearby stand. Whether the clear and plant method was worth the potential ecological cost of site disturbance and the economic cost of planting depends on the objectives for the plantation. When considering the time difference between the stands in reaching the merchantable size threshold to be a cost in terms of the number of extra years spent carrying a financial investment to maturity, the 12 year difference would likely be considered significant. In terms of biological cost to the tree in completing its life cycle, going through the suppression phase did not result in certain mortality but delayed canopy recruitment by a little over a decade. This time period is of course insignificant for giant sequoia individuals reaching their potential life-span of multiple millennia.

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Tables

Table 1. Performance of candidate models in predicting relative growth (RELGRO), 20 years following a shrub removal treatment in a heavily suppressed plantation at Blodgett Forest Research Station, CA.

Candidate Model Ranks	K_i	AIC_i	w_i	Evidence Ratio, w_1 / w_i
1. RELGRO = L	**1**	**143.12**	**0.2124**	
2. RELGRO = L+B	2	143.35	0.1893	1.1219
3. RELGRO = L+F+B	3	143.99	0.1375	1.5450
4. RELGRO = L+F	2	144.69	0.0969	2.1924
5. RELGRO = L+C	2	144.94	0.0855	2.4843
6. RELGRO = L+C+B	3	145.29	0.0718	2.9594
7. RELGRO = L+F+B+C	4	145.94	0.0518	4.0960
8. RELGRO = F	1	146.15	0.0467	4.5494
9. RELGRO = L+F+C	3	146.38	0.0416	5.1039
10. RELGRO = F+B	2	147.88	0.0197	10.8049
11. RELGRO = F+C	2	148.15	0.0172	12.3666
12. RELGRO = B	1	149.35	0.0094	22.5334
13. RELGRO = C	1	149.37	0.0093	22.7599
14. RELGRO = F+B+C	3	149.81	0.0075	28.3606
15. RELGRO = B+C	2	151.28	0.0036	59.1455

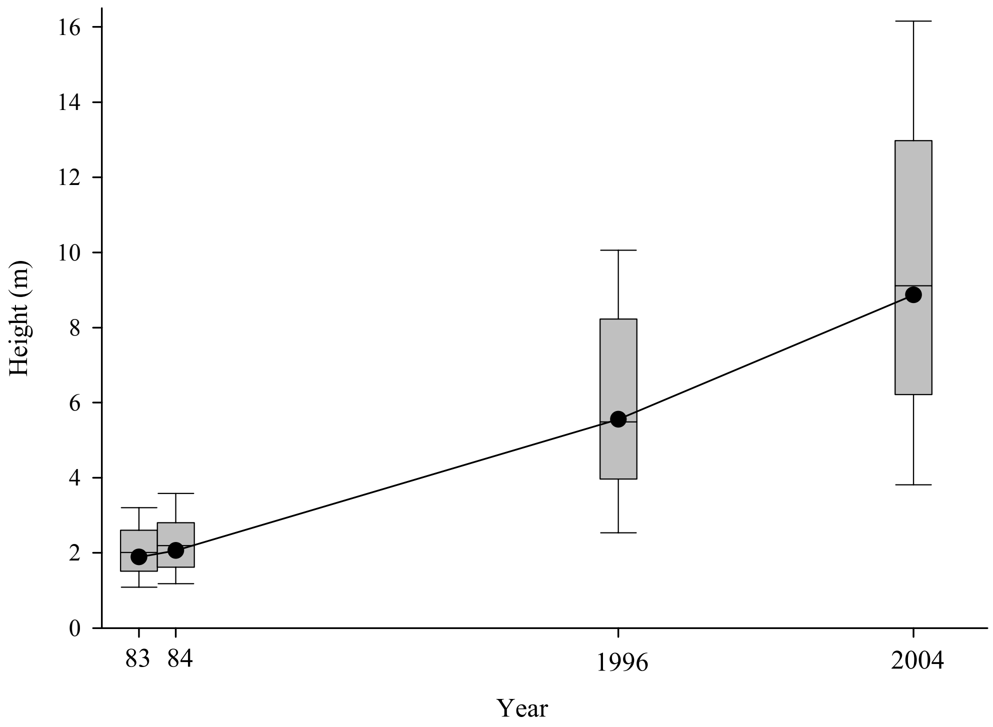
K_i= number of measured parameters in model ranked *i*; AIC_i= Akaike Information Criterion; w_i = Akaike weight (relative likelihood of model given the data and other candidate models). L = live crown ratio; B = basal diameter; F = foliage quality (“pale” or “normal”); C = Crown diameter.

Figure captions

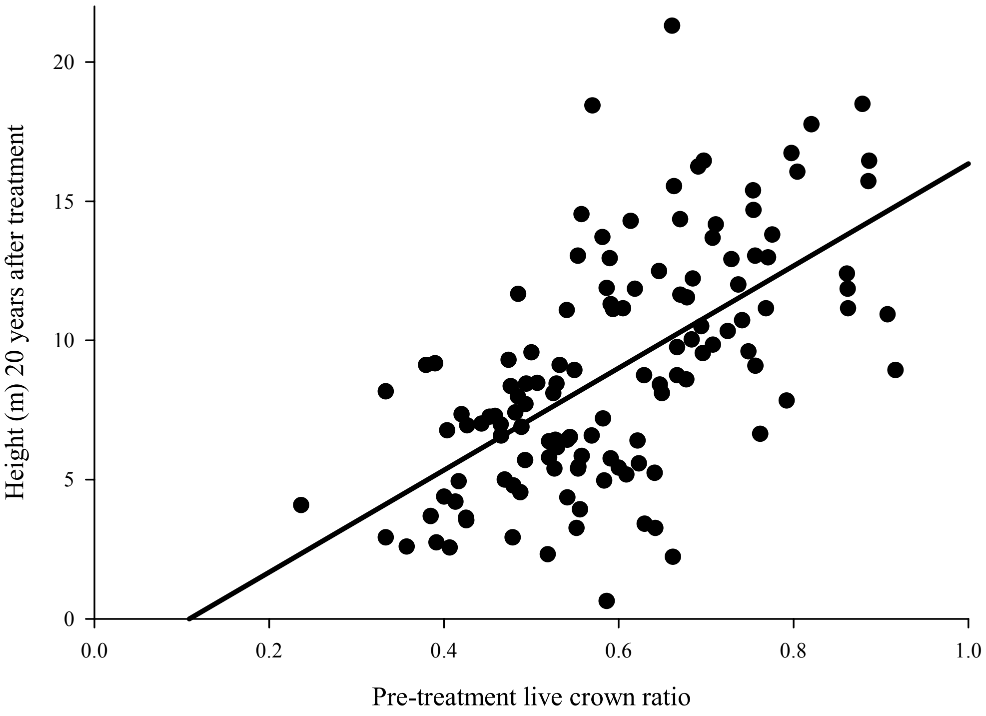
Figure 1. Height growth response of heavily suppressed giant sequoia saplings (n = 127) to a shrub removal treatment in a plantation at Blodgett Forest, CA. Box plots ends represent the 25th and 75th percentiles; whiskers represent the 10th and 90th percentiles; horizontal lines within the boxes represent medians. The line connects the height means (●) across years.

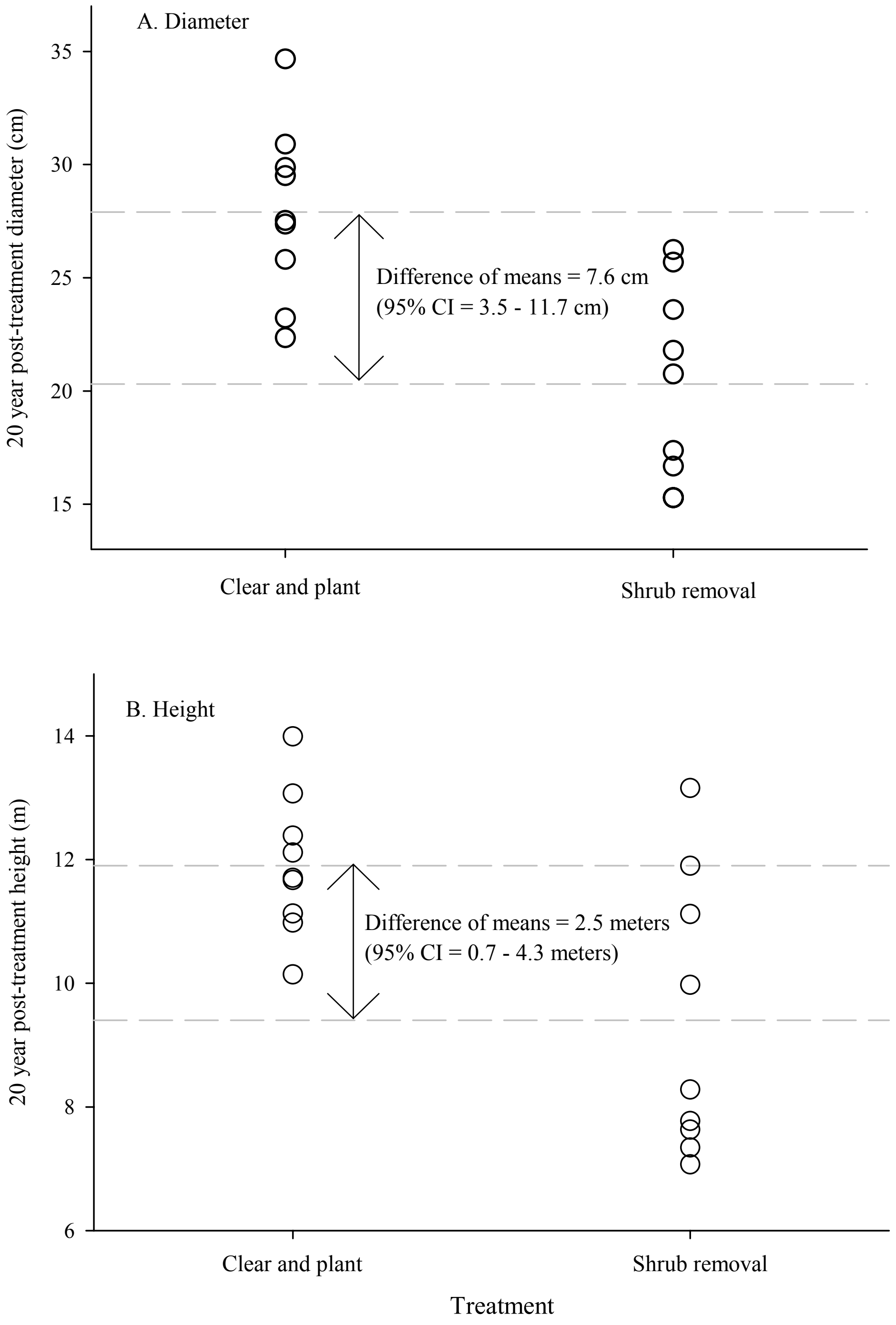
Figure 2. Effect of live crown ratio on the growth release of suppressed giant sequoia saplings following shrub removal at Blodgett Forest Research Station, CA. The line is a simple linear regression (adjusted r^2=0.34).

Figure 3. Comparison of release via shrub removal versus a clear-and-plant method of promoting a giant sequoia plantation at Blodgett Forest Research Station, CA. A = diameter growth comparison, B = height growth comparison. The horizontal lines represent the means from the two treatments. The 95% confidence intervals are for the difference in means (i.e. “significant” intervals do not include zero).



Height (m)
0
2
4
6
8
10
12
14
16
83
84
1996
2004
Year


Height (m) 20 years after treatment
0
5
10
15
20
0.0
0.2
0.4
0.6
0.8
1.0
Pre-treatment live crown ratio


A. Diameter
20 year post-treatment diameter (cm)
35
30
25
20
15
Difference of means = 7.6 cm
(95% CI = 3.5 - 11.7 cm)
Clear and plant
Shrub removal
B. Height
20 year post-treatment height (m)
14
12
10
8
6
Difference of means = 2.5 meters
(95% CI = 0.7 - 4.3 meters)
Clear and plant
Shrub removal
Treatment