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Silviculture in the Sierra Nevada Mixed-Conifer Forest for the 21st Century

By

Lauren E. Cox

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requirements for the degree of

Doctor of Philosophy

in

Environmental Science, Policy, and Management

in the

Graduate Division

of the

University of California, Berkeley

Committee in charge:

Professor John J. Battles, Chair
Professor Robert A. York
Professor Scott L. Stephens

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Abstract

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Climate change poses a profound risk to the functioning of forested ecosystems and past forest management approaches may no longer be appropriate for future forests. As trees vary in their vulnerability to climate change, it is essential to identify the most at risk species for conservation and refine management decisions for resistant tree species. In addition to managing for individual tree species, incorporating adaptive forest management approaches is essential for maintaining future forests. Over three chapters of my dissertation, I use long-term forest inventory data from different silvicultural experiments in the Sierra Nevada mixed conifer forest to evaluate potential management strategies for a changing future. My dissertation investigates three main questions: 1) how does planting density shape the trade-off between individual growth (maximize timber production) and stand-level productivity (maximize carbon sequestration) of giant sequoia, a climate vulnerable species? 2) how does herbivore protection and planting density impact the early survival and growth of incense-cedar, a climate resilient species? And 3) how does an operational femelschlag harvest affect the growth dynamics of Sierra Nevada mixed conifer tree species growing along gap edges? In chapter 1, I demonstrate the potential for incorporating giant sequoia into working forests to achieve different objectives, as they are able to produce merchantable timber at a young age and sequester large amounts of carbon in a relatively short period. In Chapter 2, I show that herbivore protection greatly increases the survival of young incense-cedar. Incense-cedar demonstrates the expected tradeoff between individual tree size and stand production, where narrow spacings yield smaller trees and higher stand-level production and wide spacings yield larger trees and lower stand-level production. Results from chapter 3 show that all mixed-conifer species may be successfully grown along the edges of group selections and most species will exhibit increased height and diameter growth after group expansion. Collectively, these three chapters present information necessary for evaluating forest management decisions to create a resilient future forest.

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INTRODUCTION

As changing climate and altered disturbance regimes are affecting forests in novel ways, past management approaches may not be appropriate for future forests. Managed forests sustain both individual species and future forest cover, thus it is essential to identify species that are threatened by increased disturbance as well as species that are resistant to disturbance to guide future planting efforts. Maintaining populations of both threatened and resistant species in managed forests requires information on the growth of these species. In addition to managing for individual tree species, understanding adaptive management approaches is essential for future forest management. Multi-cohort silvicultural systems such as group selection and an expanding group irregular shelterwood, also referred to as the German "femelschlag", show potential for increasing structural heterogeneity and increasing forest resilience. My dissertation investigates three main topics: 1) managing giant sequoia, a climate vulnerable species, for carbon and timber, 2) understanding early stand dynamics of incense-cedar, a climate resilient species, and 3) the effects of a femelschlag silvicultural system, an innovative approach in the Sierra Nevada designed to emulate natural disturbances and promote growth of native tree species. In this dissertation, I use long term experiments in the mixed conifer forests of the Sierra Nevada to evaluate potential management strategies for a changing future.

Chapter 1 focuses on giant sequoia, a famously massive tree species whose persistence is threatened by a changing climate and an altered disturbance regime. One approach for protecting threatened species is to incorporate them into working landscapes. In a forestry context, the objectives of a working landscape include the production of timber and the storage of carbon. Given its potential for rapid growth, an understanding of the growth-density relationships for giant sequoia is a necessity for planning future management for these common management objectives. To investigate the effect of initial planting density on both individual tree and stand level characteristics, I used repeated measures data from a 28-year-old giant sequoia spacing trial. After 28 years, survival among all spacing treatments was high. Individual bole volume increased with greater growing space allocated per tree. At the stand level, total aboveground carbon storage was similar across all spacing treatments. However, wider spacing treatments exhibited higher amounts of merchantable volume. These results indicate that giant sequoias are able to produce merchantable timber at a young age and sequester large amounts of carbon in a relatively short amount of time, supporting the contention that giant sequoia can "pay its way" in a working landscape.

Chapter 2 focuses on incense-cedar, a drought resistant conifer species native to the western United States that is host to few lethal pests and pathogens. Because incense-cedar has shown promise as a species adapted to future climate and disturbances, quantifying its survival and growth is important for defining its potential place within silvicultural prescriptions of the future. The objectives of this chapter are to understand 1) the impact of spacing and herbivore protectors on early seedling survival, 2) the impact on spacing on planting space occupancy after 18 years, 3) the impact of spacing on individual tree and stand characteristics. During the first

five years of growth, incense-cedar seedlings were grown in pairs, one with herbivore protection and one without, across a gradient of initial planting densities. Wider spacing had a minor and negative impact on seedling survival. In contrast, protecting trees from vertebrate herbivores using plastic mesh had a strong positive influence on seedling survival at age 3. After the 5th growing season, herbivore protection was removed and the less vigorous of the pair of seedlings was culled. After 18 years, 89% of planting spots were occupied by a live seedling. Although total occupancy differed by spacing treatment, there were no discernable trends with spacing width. Wider spacing treatments resulted in larger individual tree sizes and branch diameters. However, there was only a small gradient in canopy structure. All the trees had extensive live crowns; mean live crown ratios ranged from 89.4 to 97.8. As expected, stands with narrower spacing produced higher levels of stand-level bole volume. These results not only inform initial planting decisions, but also provide a basis to evaluate management decisions such as pruning young incense-cedar.

Chapter 3 focuses on the response of edge trees planted within gaps to an experimental femelschlag harvest implemented in a Sierra Nevada mixed-conifer forest. I consider the expanded gap experiment in two phases: 1) original group implementation through 12 growing seasons and 2) post gap expansion through the 21st growing season. We used edge tree height and diameter data for species planted in groups of increasing sizes (0.1-1 ha) through 21 growing seasons. After the 12th growing season, we found that edge trees of all species were considerably smaller than interior trees. Of edge trees, ponderosa pine were the tallest species, followed by giant sequoia, Douglas-fir, sugar pine, incense-cedar and white fir. All species of edge trees exhibited an increasing growth relationship with increasing group size during the 12th growing season. This trend demonstrates resources limitations along group edge environments and implies that edge tree growth would increase in larger groups (i.e. groups > 1.0 ha). One method to increase tree growth would be to release the edge trees by harvesting along group edges. During the 13th growing season, gaps were expanded along one edge in a femelschlag harvest. Light availability increased as a result of the gap expansion, though effects were more pronounced along southern edges that were released. Light availability along northern edges that were released was similar to the unreleased northern edges. During the 21st growing season, white fir exhibited the strongest response to the gap expansion. Trees growing along northern edges exhibited taller heights than those growing along southern released edges, despite the difference in initial live availability increase. Incense-cedar did not exhibit difference in height among gap edge position or release. These results provide insight for implementing natural disturbance based silvicultural designs in the Sierran mixed-conifer forest.

CHAPTER 1

Growth and form of giant sequoia (*Sequoiadendron giganteum*) in a plantation spacing trial after 28 years

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ABSTRACT

Giant sequoia is a famously massive and long-lived tree endemic to the Sierra Nevada of California, whose persistence is threatened by a changing climate and an altered disturbance regime. One approach for protecting threatened species is to incorporate them into working landscapes. In a forestry context, the objectives of a working landscape include the production of timber and the storage of carbon. Given its potential for rapid growth, an understanding of the growth-density relationships for giant sequoia is a necessity for planning future management for these common management objectives. To investigate the effect of initial planting density on both individual tree and stand level characteristics, we used repeated measures data from a 28-year-old giant sequoia spacing trial. After 28 years, survival among all spacing treatments was high (> 98%). Individual bole volume increased with greater growing space allocated per tree. Although initial relative growth rates based on bole volume differed among spacing treatments, relative growth rates were similar after 21 years. At the stand level, total stand volume was similar across all spacing treatments after 28 years. However, wider spacing treatments exhibited higher amounts of merchantable volume. After 28 years, stands of giant sequoia sequestered approximately 92.2 Mg ha^{-1} across all spacing treatments. Our results show that giant sequoias are able to produce merchantable timber at a young age and sequester large amounts of carbon in a relatively short amount of time, supporting that giant sequoia is a promising candidate species for planting for timber production as well as carbon sequestration.

INTRODUCTION

Understanding intra-specific competition and stand dynamics is essential to forestry (Hutchings and Budd 1981). Such knowledge informs initial tree planting design, timing and implementation of intermediate treatments, and other decisions needed to achieve specific management objectives (Drew and Flewelling 1979). One approach to quantifying these competition effects is through experimental density manipulations and long-term growth measurements (e.g., Harms et al. 2000). These spacing trials are commonly used to inform plantation forestry of the "best" initial planting spacing for a species. Although there may be no true optimal solution, data from these studies demonstrate tradeoffs between the expected higher stand-level growth of closer spacings and larger individual tree volume for wider spacings. These long-term spacing trials have been valuable resources for developing silvicultural tools for important timber species like

Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) as well as for other species throughout the western United States (McGown et al. 2015, Curtis et al. 2016).

Giant sequoia (*Sequoiadendron giganteum* (Lindley) J. Buchholz) is a long-lived pioneer species endemic to the western slope of the Sierra Nevada in California. Once widespread throughout the Sierra Nevada, the species' range has contracted to approximately 14,600 ha among 70 groves, although estimates vary (York et al. 2013a). More than a century of fire suppression has prevented sufficient recruitment of giant sequoia to maintain current populations (York et al. 2013a). Additionally, climatic changes pose a threat for the species, as increased frequency of hotter droughts is anticipated (Millar and Stephenson 2015). Giant sequoia groves are associated with higher levels of water availability. Warming temperatures without a corresponding increase in precipitation may exacerbate the vulnerability of giant sequoia groves, especially during multiyear droughts (Su et al. 2017). Other exogenous factors such as high severity wildfire and tourism will continue to impact giant sequoia groves into the 21st century (Jenkins and Brown 2020). Given these risks to giant sequoia persistence in its native groves, the species meets the criteria for prioritizing its conservation (Polasky et al. 2005 Potter et al. 2017).

Despite the apparent vulnerabilities of giant sequoia, the species has exhibited some resilience to global change that suggests promise for future conservation efforts. During 2012–2016, California experienced a severe drought that resulted in the death of over 147 million trees (CalFire and USFS 2019). Although giant sequoia is associated with high water availability, giant sequoia suffered relatively low mortality from the drought compared to other species (Stephenson et al. 2018; Sillett et al. 2019). Much of the drought mortality was concentrated in species (e.g., ponderosa pine) that also experienced insect attack and likely died from the additive effects of hotter drought stress and bark beetle attack (Stephenson et al. 2018). Giant sequoias are known to be resistant to insects and pathogens, although bark beetles (*Phloeosinus* spp.) in concert with other stressors can increase mortality (Nydick et al. 2018). More frequent hotter droughts and other climatic changes may alter the sequoia-insect dynamics and vulnerability to disturbances.

Although giant sequoia is not widely cultivated as a timber resource, there is the potential for incorporation of the species into mixed conifer forests of the Sierra Nevada where its associated species in native groves occur. Most native groves are managed for non-timber values by federal agencies (e.g., National Parks and National Monuments); however, some state and private grove locations have been actively managed for timber (Benson 1986; Dulitz 1994). Additionally, the species has been planted throughout western Europe and has exhibited potential for an intensively managed tree species (Knigge 1994; Alexandrov et al. 2002). Giant sequoia has several characteristics that make it a promising choice for a plantation species in the mixed conifer forest outside of native grove boundaries. In mixed species plantations, giant sequoia has exhibited higher survival rates than all other Sierra Nevada mixed conifer species (York et al. 2007). Compared to other species in mixed plantations, giant sequoia has shown higher productivity than competing conifers (Kitzmiller and Lunak 2012). Moreover, its wood properties suggest that it can be a commercially viable species (Piirto 1995). The introduction of giant sequoia into mixed conifer forests outside of native groves may not only achieve the objective of species conservation, but also add valuable timber resources to the landscape (Hansen et al. 1991, Polasky et al. 2005).

An alternative strategy to support the conservation of giant sequoia is to realize its carbon storage potential. Managing forests for carbon sequestration is a central component to many climate change mitigation plans (Fahey et al. 2010; Fargione et al. 2018). With the establishment of carbon markets, forest managers have access to reliable financial incentives. Because of their longevity, fast growth, and ability to reach extremely large sizes, giant sequoias are a promising candidate for species aimed at carbon sequestration (York et al. 2013b). In 2009, Sierra Pacific Industries, one of the largest timber companies in the United States, initiated a series of carbon sequestration projects. The first project aims to protect the genetic diversity of giant sequoia and expand the current range within California while also monetizing the gains in carbon storage (Lunak 2015). Based on the potential of giant sequoia to sequester carbon, Sierra Pacific Industries plans to maintain giant sequoias planted in this project in perpetuity.

The goal of this study is to investigate density-growth relationships in young giant sequoias to inform management for multiple objectives. Specifically, we ask: 1) How does initial planting density affect individual tree survival, size, and form? 2) How does initial planting density affect individual tree growth over time? 3) How does initial planting density affect stand volume production? And 4) How does initial planting density impact the trade-off between timber production and carbon sequestration? We rely on the proven empirical approach of a long-term spacing trial to answer these questions.

METHODS

Study Area

Blodgett Forest Research Station (BFRS) is a 1,763 ha research forest situated on the western slope of the central Sierra Nevada mountain range in California, USA (38°52N 120°40W). The study site is located within BFRS at an approximate elevation of 1,320 m. The regional climate is Mediterranean with warm, dry summers (14°–27° C) and mild winters (0°–9° C). Mean annual precipitation is 1,660 mm (BFRS data, https://forests.berkeley.edu/forests/blodgett). The majority of precipitation falls as rain during winter and spring. Snowfall accounts for approximately 30% of total precipitation. Soils are formed from andesitic parent materials (Heald and Barrett 1999). BFRS is representative of productive mixed conifer forests that occur between 1,200–1,700 m elevation along the western slope of the Sierra Nevada mountain range. The forest is composed of five coniferous and one hardwood tree species (Tappeiner 1980). Trees can grow to heights of 27–34 m in 50 years.

Giant sequoia does not occur naturally on BFRS. However, BFRS is just 16 km south of the northernmost native giant sequoia grove. The majority of native giant sequoia groves occur in the southern Sierra Nevada, a region that is similar in climate, soils, and topography. Seed for the study trees was collected from Redwood Mountain Grove, the largest existing grove, which is 290 km south of BFRS at Whitaker Forest (36.70°N 48.93°W).

Experimental Design

In 1989, giant sequoia seedlings were planted at nine densities, ranging from 2.1 – 6.1 m, with hexagonal spacing between planting spots (Table 1). Two seedlings were planted in each planting spot to ensure initial establishment at all locations, and the less vigorous seedling was culled in 1991. Spacing treatment areas ranged between 0.08 and 0.2 ha with wider spacings requiring larger treatment areas. Treatments were installed in a randomized block design. All spacing treatments were planted adjacent to one another. The edge rows of each spacing treatment were considered "buffer rows" (i.e., two parallel edge rows would separate study trees from different treatments) and these trees were not used in any analyses to control for edge effect. Spacing treatments were randomly assigned to a location within each of three blocks (Figure 1).

For each density treatment, we calculated the horizontal growing space available to each tree for use as a predictor variable. Growing space is defined as the amount of physical horizontal space allotted to each seedling at the time of planting. This value was calculated by dividing the area of the spacing treatment by the number of trees planted in that spacing treatment. Small growing space values correspond to higher tree densities (Table 1).

Field Measurements

We tracked giant sequoia survival and growth through year 28 via periodic measurements (seven intervals). At each interval, we measured height and diameter at breast height (DBH; breast height = 1.37 m) for all trees and noted tree status (live/dead; Table 1). During year 29, we randomly selected 210 trees across the nine spacing treatments (19-29 trees per treatment) to measure Girard form class, a standard method to describe the taper of the bole of merchantable trees. Girard form class is the ratio of inside bark diameter at 5.3 m (i.e., the height of the a merchantable log in the stem) to outside bark DBH (Mesavage and Girard 1946; Avery and Burkhart 2002). We measured DBH and outside bark diameter at 5.3 m using diameter tapes. Inside bark diameter at 5.3 m was calculated by multiplying outside bark diameter at 5.3 m by 0.9472, a correction factor based on local stem analysis of 23 giant sequoia trees of a similar size (York 2019). In addition to the Girard form class, we also calculated height to diameter ratios in this same set of trees to evaluate their stability and vulnerability to windthrow or snapping from snow stress.

Analytical Framework

To answer our specific questions, we considered results for both individual trees (n=2,141) and stands (n = 3 of each spacing treatment). For all analyses, we excluded trees on the edges of treatment areas to avoid interactions between spacing treatments. For analyses of individual tree characteristics (i.e., DBH, height, individual bole volume, and relative growth rate), we excluded all trees that had a dead or missing neighbor so that spacing around each tree remained constant throughout the 28-year sampling period. For stand characteristic analyses (i.e., stand volume, merchantable volume, and total aboveground carbon), trees with missing neighbors were included when calculating area-based means for each treatment area.

Survival Analysis

To calculate survival functions for giant sequoia trees across different spacing treatments over 28 years, we applied Turnbull's (1976) generalization of the Kaplan-Meier estimator (Gómez et al. 2009; Fay and Shaw 2010). We used weighted log-rank tests that employ a permutation procedure when there are many samples to compare survival curves. Survival analyses were run in R (http:// www.r-project.org/) using the ''interval'' library.

Individual tree characteristics

To describe stem size differentiation in each spacing treatment, we calculated the Gini coefficient (GC) based on height and DBH. The GC was originally developed to describe income inequities and has since been applied to describe the inequality of plant sizes (Weiner and Solbrig 1984). Values for the GC range between 0 and 1; a value of 0 indicates that all stems had the same size, whereas a value of 1 indicates that all stems had dissimilar sizes (i.e., a higher level of size differentiation). To test for difference size inequality, we only considered trees ≥ 2.54 cm DBH, the minimum DBH to calculate aboveground biomass following the protocol established by the Forest Inventory and Analysis National Program (FIA 2014).

To calculate individual tree bole volume, we developed a locally derived allometric equation (Supplementary Material B). This equation used 34 giant sequoias planted on Blodgett Forest Research Station that ranged from 8.1 to 15.0 m height and 22.9 to 45.0 cm DBH. We chose this equation based on the locality of the sampled trees and the lack of published equations on small giant sequoias. We based tree relative growth rates on individual tree volume calculations. To calculate annual relative growth rate (RGR), we used the following equation:

$$RGR = \frac{V_2 - V_1}{V_1 * (t_2 - t_1)}$$

where t_n is sampling year and V_n is individual tree bole volume for the *n*th sampling year.

To answer our questions on the effects of planting density on tree characteristics over time, we developed a set of generalized linear mixed models where growing space per tree and time since planting were fixed effects (Bolker et al. 2009). Models for DBH, height, individual tree volume, and relative growth rate included the random effect of individual tree identification nested within block to reduce spatial autocorrelation. For the log-linear model that included a quadratic time factor, we used both tree nested within block and block alone as random effects. Models for stand volume only included blocking as a random effect. Our set of candidate models included a power law model and log-linear relationships that include all combinations of growing space, time since planting, and their interactions. Two log-linear functions also included a quadratic term for time since planting. To correct temporal autocorrelation detected in the longitudinal data, we incorporated two correlation structures for each model: a first order autoregressive process and an autoregressive moving average process.

We implemented an information theoretic approach to compare model performance (Burnham and Anderson 2002). We calculated Akaike's information criterion (AIC), differences in AIC relative to the lowest AIC (ΔAIC), and AIC weights (w_i). For each model, we calculated the marginal and conditional R^2 for generalized linear mixed-effects models (Nakagawa and Schielzeth 2013). The marginal R^2 describes the variance explained by fixed effects whereas the conditional R^2 focuses on variance explained by both fixed and random effects. We inspected the residuals for each model to detect any heteroscedasticity and temporal autocorrelation. We selected the best model based on a combination of highest w_i and lowest temporal autocorrelation. Analyses were conducted in R using the "nlme" library.

Stand characteristics

We estimated bole volume, merchantable timber, and total aboveground carbon at the stand level, using each spacing treatment within the three blocks to represent a stand. Bole volume ($m^3\ ha^{-1}$) relied on the same local allometric equation for all trees ≥ 2.54 cm. Based on the tendency of giant sequoia to exhibit high degrees of taper and on past experience selling giant sequoia sawlogs at BFRS, we defined merchantable trees to be ≥ 30.0 cm DBH. For these trees , we calculated merchantable timber ($m^3\ ha^{-1}$) for each spacing treatment. To calculate total aboveground carbon, we used the locally derived bole volume equation and wood density documented by FIA (Wadell et al. 2014) to calculate stem biomass. We used regional biomass equations for giant sequoia developed by FIA (Waddell et al. 2014) to calculate bark and branch biomass. Total aboveground biomass included stem, bark, and branch biomass. Based on empirical carbon density derived from giant sequoia at both Whitaker Forest and another forest in the northern Sierra Nevada range, we multiplied total aboveground biomass by 0.544 g C/g biomass to convert tree biomass to tree carbon (Jones and O'Hara 2018).

To determine the effect of growing space on merchantable timber and carbon, we used a mixed effect model for data from year 28, as most treatments had not reached merchantable volume until the most recent sampling period.

RESULTS

Survival

After 28 years, 38 planting spaces had dead or missing trees across all spacing treatments. Since the last measurement at year 21, only 6 trees died. These 6 trees were all in the three narrowest spacing treatments. Survivorship of trees significantly varied by spacing treatment ($p < 0.005$, Figure S1). The narrowest spacing had the lowest probability of survival after 28 years (P(survival) = 0.965). Three treatments (28.3 m^2 (353 stems ha^{-1}), 23.6 m^2 (423 stems ha^{-1}), and 14.8 m^2 (676 stems ha^{-1})) had no dead or missing trees after 28 years.

Individual Tree Characteristics

Size differentiation based on both DBH (GC_{DBH}) and height (GC_{HT}) was greater among narrower spacing treatments than wider spacing treatments after 28 years (Figure S2). The GC_{DBH} ranged from 0.07 to 0.14 whereas the GC_{HT} ranged from 0.07 to 0.13. Across all spacing treatments, the GC_{DBH} peaked in years 5-7. However, the GC_{HT} for narrower spacings (3.7 – 7.4 m^2; 2,702 stems ha^{-1} – 1,347 stems ha^{-1}) peaked in year 21. The GC_{HT} for wider spacings peaked in years 5-7, following a similar pattern to the GC_{DBH} for all spacings.

Across all sampling periods, DBH increased with wider spacing treatments (Figure 2; Figure S3). Mean DBH of trees in the widest spacing was 2.3x larger than the narrowest spacing. Height also increased with wider spacing treatments (Figure 3; Figure S4). Mean height of trees in the widest spacing was 1.8x taller than the narrowest spacing treatment. The best model of DBH increment included a quadratic relationship by year with interactions between year and growing space for DBH. Autocorrelation was minimized with a moving average autoregressive process; variation was reduced by including a random factor of tree nested within block ($w_i = 0.73$; Table S1). For height, we also found a quadratic relationship by year with interactions between year and growing space with a moving average autoregressive process to be the best model. However, block without nesting was the random factor ($w_i = 1$; Table S2).

Similarly, individual bole volume increased with increasing spacing over time (Figure 4; Figure S5). The widest spacing exhibited mean bole volumes 7.8x larger than the narrowest spacing. The selected model of individual tree volume included a quadratic response by year and interactions between year and spacing treatments ($w_i = 0.71$; Table S3). The model included a moving average autoregressive process and a random blocking factor.

Prior to year 21, relative growth rate was distinctly different among spacing treatments with the widest spacing having a relative growth rate 1.8x greater than the narrowest spacing treatment (Figure 5; Figure S6). This magnitude of difference was maintained until year 21 when relative growth rates appeared to converge. During the final sampling period from year 21 to year 28, the relative growth rate of the widest spacing was only 0.8x that of the narrowest spacing treatment (Figure 5, inset). The selected model for relative growth rate included a quadratic response by year and interactions between year and spacing treatments ($w_i = 0.39$; Table S4).

Girard form class significantly differed by spacing treatment ($p = 0.04$; Figure 6). Trees in the three narrowest spacing treatments had lower Girard form class values (0.55, 0.60, 0.58), corresponding to higher degrees of taper. The 7.4 m^2 (1,347 stems ha^{-1}) spacing treatment exhibited the lowest degree of taper with a mean Girard form class value of 0.64. Across all spacing treatments, Girard form class values for individual trees ranged from 0.19 to 0.84. Height:diameter ratios across all spacing treatments in year 28 ranged from 42 to 52 (Figure 6). Trees in narrower spacing treatments exhibited higher height:diameter ratios than trees planted at wider spacings.

Stand Characteristics

Unlike trends in individual tree characteristics, stand level volume does not increase with increasing growing space per tree (Figure 7; Figure S7). After 28 years, the narrowest spacing treatment had the least stand bole volume whereas an intermediate spacing treatment (11.1 m^2; 897 stems ha^{-1}) had 1.3x greater stand volume, the highest of any treatment. Our selected model indicates a quadratic relationship by year with interactions between year and growing space ($w_i = 0.99$; Table S5).

Merchantable timber increased with increased growing space per tree and differences between spacing treatments were significant ($p < 0.0001$, Table 2, Figure S8). The 23.6 m^2 (423 stems ha^{-1}) spacing treatment yielded the highest amount of merchantable timber, 19.0x the amount of the lowest yielding spacing treatment (6.0 m^2; 1,654 stems ha^{-1}).

Total aboveground carbon was not significantly different across spacing treatments after 28 years ($p = 0.2$, Table 2, Figure S9). The intermediate 7.4 m^2 (1,347 stems ha^{-1}) spacing treatment yielded 1.2x the total aboveground carbon as the 14.8 m^2 (676 stems ha^{-1}) spacing treatment, which had the lowest total aboveground carbon.

DISCUSSION

After 28 years, diameters of giant sequoias increased with increasing spacing, similar to results from spacing trials of other species. (Harms et al. 2000; Curtis et al. 2016). After 30 years, ponderosa pine in stands with 32.4 m^2 growing space per tree (309 stems ha^{-1}) had diameters approximately 1.6x the diameter of trees in stands with 8.1 m^2 growing space (1,235 stems ha^{-1}; McGown et al. 2015). Giant sequoia trees with 28.1 m^2 growing space per tree (353 stems ha^{-1}) had diameters 1.7x larger than the diameter of trees with 7.4 m^2 (1,347 stems ha^{-1}) after 28 years (Figure 2; Figure S3). After 25 years, loblolly pine (*P. taeda* L.) stems in stands with 13.4 m^2 growing space per tree (747 stems ha^{-1}) had diameters 1.4x larger than stems in stands with 4.4 m^2 growing space (Amateis and Burkhart 2012). Giant sequoia trees with corresponding growing space area had the same magnitude difference in DBH (Figure 2; Figure S3).

Typically, height growth is not as strongly affected as diameter growth by spacing because of a higher prioritization of carbohydrate allocation (Hutchings and Budd 1981). However, the magnitude of the height response by giant sequoia is notable. Most other spacing trials found that heights were similar across spacings (Harms et al. 2000; Curtis et al. 2016). For example, for loblolly pine spacing trial at age 25, average height in a 13.4 m^2 spacing (747 stems ha^{-1}) was 1.1x taller than trees in a 3.3 m^2 spacing (Antón-Fernández et al. 2011). Heights of giant sequoia trees with 3.7 m^2 (2,702 stems ha^{-1}) and 14.4 m^2 (676 stems ha^{-1}) of growing space per tree differed by 1.5x (Figure 3; Figure S4). Even in spacing trials of Douglas-fir, ponderosa pine, and giant sequoia, the height of giant sequoias increased with wider spacings whereas the heights of ponderosa pines and Douglas-firs were relatively similar across all spacings after 20 years (Peracca and O'Hara 2008). The sensitivity of height growth in giant sequoia may be related to its growth habit as a pioneer species. Interestingly, the rate of height growth increased from year 21 to year 28

(Figure 3; Figure S4). Giant sequoia is a sustained growth species and is affected by factors during the current growing season (Gasser 1994). We speculate that the increased height growth is either from a carbon allocation effect or possibly from roots tapping into deep water sources.

Throughout 28 years, giant sequoias have maintained remarkably high survival rates and stands have not yet begun self-thinning. Peracca and O'Hara (2008) also documented high survival rates of giant sequoia relative to ponderosa pine and Douglas-fir. However, the lack of the onset of self-thinning raises the question of whether stands are differentiating or are likely to stagnate if mortality does not occur. The GC is one approach for describing stand differentiation in this context (Weiner and Solbrig 1984). In a 30 year-old ponderosa pine plantation, the GC for DBH ranged from 0.2 for a stand with 4.0 m^2 of growing space per tree (2,470 stems ha^{-1}) to approximately 0.07 at 64.9 m^2 growing space (154 stems ha^{-1}; McGown et al. 2015). Knox et al. (1989) noted increasing GC prior to the onset of self-thinning in loblolly pine followed by a decline in size inequality after the onset of self-thinning. A trend of increasing size differentiation may reflect a shift in stand development from size symmetric competition to size asymmetric competition (Weiner 1990). Although no spacing treatments have experienced competition-based mortality, more narrowly spaced treatments may have started to shift towards asymmetric competition (Figure S2).

Giant sequoia merchantability is limited by high degrees of taper that can result in delayed and inefficient production of sawlogs and high densities of small branches that increase the size of the defect core (i.e., the cylinder around the pith of the tree that contains branch stubs and occlusion scars) (York et al. 2013b; York 2019). Trees with higher taper tend to have higher live crown ratios. Thus, taper can be controlled by reducing live crown ratios through either manipulating growing space to reduce crown size or through reducing live crown through pruning. Typically, trees planted at narrower spacings are expected to have lower degrees of taper (Larson 1963). However, the giant sequoia in the three narrowest spacings exhibited a clustered pattern of low Girard form class values (i.e., high degrees of taper, Figure 6). After removing the smallest 20% of stems based on diameter at 5.3 m, these narrow spacings still exhibited a clustered pattern with a lower average form class value than the 7.4 m^2 (1,347 stems ha^{-1}) and 11.1 m^2 (897 stems ha^{-1}) treatments. We speculated that this result could be because of the small diameters of the bole at 5.3 m height used to define the Girard form class. Because these stems are still smaller than merchantable size, tree form may change as trees mature. To test the effects of pruning on reducing taper of giant sequoia, York (2019) measured giant sequoia trees that had been pruned to different heights, increasing the intensity of the treatment (2.0 m, 3.5 m, and 5.5 m in height). In giant sequoia that had been heavily pruned (5.5 m), the taper was significantly reduced compared to unpruned and less intensively pruned stems (York 2019). The Girard form class of intensely pruned stems corresponds to the Girard form class of the 7.4 m^2 (1,347 stems ha^{-1}) treatment (0.64; Figure 6). The average DBH of the unpruned trees in the 7.4 m^2 treatment was 25 cm whereas the DBH of the pruned stems was approximately 27 cm. Therefore, if achieving similarly sized trees with similar taper, planting at a 7.4 m^2 of growing space may be an alternative to pruning. However, manipulating spacing alone will not achieve dual objectives of lowered degree of taper and reduced defect core of pruning.

Height:diameter ratios may be used to assess tree stability and potential risk of mortality from windthrow. For multiple conifer species, a height:diameter ratio of 80 has been documented as a threshold for mortality from instability (Cremen et al 1982; Wonn and O'Hara 2001). Across all spacing treatments after 28 years, the height:diameter ratios of giant sequoias never exceeded 52 (Figure 6). Relative to both ponderosa pine and Doulas-fir, giant sequoia exhibit lower height:diameter ratios across a range of spacing treatments, exhibiting lower risk of mortality from windthrow or snow stress (Peracca and O'Hara 2008). In mixed species stands across Blodgett Forest, giant sequoia exhibited the lowest number of snapped stems after above average snowfall relative to California black oak (*Quercus kelloggii* Newberry), and white fir (*Abies lowiana* (Gordon & Glend.) A. Murray bis), ponderosa pine, and Douglas-fir (York and DeVries 2013). This stability can be attributed to both the relatively low height:diameter ratio (48; York and DeVries 2013) and the narrow crowns with numerous small branches characteristic of giant sequoia (York et al. 2013b).

Following initial planting, relative growth rates were high and growth rates among spacing treatments greatly differed. After 15 years, there is an inflection point in relative growth rates across all spacing treatments (Figure 4). This inflection point is reflected in changes in diameter over time. This year also marks a shift in GC_{HT} among spacings. Prior to year 15, the GC_{HT} of all spacing treatments were similar. However, in year 15, wider spacing treatments begin exhibiting lower levels of size inequities relative to narrower spacing treatments. During the most recent measurement interval, relative growth rates converge with only small differences among spacings (Figure 5). However, tree volumes vary widely by spacing in year 28 (Figure 4). These differences in growth rates after initial planting indicate that the initial spacing has long term impacts on the overall trajectory of tree size and stand production. The convergence of relative growth rate is likely because of the lack of mortality across all spacing treatments. Thinning treatments increase the relative growth rates of the surviving trees by increasing the growing space and resource availability of individual trees. Giant sequoias are known to respond positively to release treatments, even after heavy suppression (York et al. 2006, 2010). Although no thinning studies of giant sequoia monocultures have been published, understanding the response of a giant sequoia plantation to thinning relative to the growth of unthinned plantation would provide valuable insight to the effect of intermediate treatments on the growth and form of giant sequoia. We anticipate that relative growth rates would increase substantially with future mortality whether the cause is management intervention or self-thinning.

After 28 years, the expected tradeoff between individual tree size and overall stand production that has been documented in other spacing trials has not yet occurred in this study. In a 33-year-old Douglas-fir spacing trial, trees with 36 m^2 of growing space exhibited quadratic mean diameters 2.5x larger than the quadratic mean diameter of trees with only 1 m^2 of growing space (10,000 stems ha^{-1}). However, the total stand volume of narrowest spacing treatment (1 m^2) was 2.2x greater than the stand volume of the widest spacing treatment (36 m^2; 278 stems ha^{-1}); Curtis et al. 2016). For 28-year-old giant sequoia, the widest spacing (28.1 m^2; 353 stems ha^{-1}) produced the largest individual trees (Figure 4; Figure S5) and the stand volume was similar to that of narrower spacings (Figure 7; Figure S7). Based on our results, lower initial planting densities are preferable for management objectives of increasing tree size or overall stand volume production.

Although overall stand-level bole volume was not strongly impacted by spacing treatments, merchantable timber was greater at wider spacings because of the larger individuals produced by wider initial planting densities. Based on FIA protocol, a merchantable tree is defined as having a DBH ≥ 25.4 cm (FIA 2014). However, the high degree of taper for giant sequoia necessitates a larger minimum diameter for merchantability. We selected a 30- cm diameter threshold based on past management experience at BFRS. Giant sequoia yield falls within the predicted yield for young growth of the related coast redwood trees (*Sequoia sempervirens* (D.Don) Endl.) based on empirical yield tables (Lindquist and Palley 1963). However, the maximum projected yield for young growth coast redwood is approximately 5.4x greater than the maximum in the giant sequoia spacing study. For the highest quality sites, coast redwood yield tables indicate average densities of trees ≥ 26.7 cm DBH of 16.5 m^2 growing space per tree (606 stems ha^{-1}) and 543 m^3 ha^{-1} of merchantable timber at age 30. In the 23.8 m^2 spacing treatment that yielded the most merchantable timber after 28 years, all trees were ≥ 26.7 cm and total density was only 423 trees ha^{-1}.

Carbon sequestration is an increasingly common management objective for the purpose of climate change mitigation (Griscom et al. 2017, Forest Climate Action Team 2018). The development of cap-and-trade carbon markets has provided potential for economic returns on planting trees specifically for the management goal of carbon sequestration (Daniels 2010). Giant sequoia is a promising species to plant for goals of carbon sequestration based on its longevity and relatively fast growth rate. This alternate management objective would allow for trees to be planted in areas that may not be able to be treated or harvested easily, such as in riparian corridors or on steep slopes. After 28 years, stands of giant sequoia sequestered approximately 92.2 MgC ha^{-1} across all spacing treatments. Based on Forest Inventory and Analysis (FIA) data from the database version 1.8.0.0.1, the mean amount of aboveground carbon across all inventory plots in the Sierra Nevada mixed conifer forest was 111 MgC ha^{-1} and the 99th percentile was 377 MgC ha^{-1} of aboveground carbon. Considering the young age of the giant sequoia spacing trial, our results show that giant sequoia are able to sequester large amounts of carbon in a relatively short amount of time, evidence that giant sequoia is a promising candidate species to include when managing for carbon sequestration.

Although still in the early phase of this spacing study to consider future timber and carbon projections, our results provide information on the effect of planting density decisions and management implications for early stand tending methods for incorporating giant sequoia into plantation settings. Our results indicate that giant sequoias are able to produce merchantable timber at a young age, making it a promising species to incorporate into timberlands for the purpose of harvesting for future revenue. One potential deterrent to planting giant sequoia for timber is the tendency of young giant sequoia to have dramatic taper. However, planting at wide spacings in combination with pruning early on during stand development should result in large sawtimber trees as early as 20 years with reduced taper and thus less wood wasted during the milling process. Alternatively, planting at a 7.4 m^2 (1,347 stems ha^{-1}) may be achieve a similar taper to intense pruning. For the purpose of carbon sequestration, planting density should not significantly impact the total amount of carbon sequestered by a giant sequoia stand during early years of development. Additionally, survival of giant sequoia is high across all stand densities and may provide an opportunity to commercially thin prior to self-thinning while maintaining trees on the site for continued carbon sequestration.

Giant sequoias are under-studied compared to other commercial species of Sierra Nevada mixed conifer forests. Results from this spacing study provide valuable information on density-growth relationships for giant sequoia that are necessary to inform early stand management decisions. However, several limitations should be considered when interpreting these results. The volume equation (Supplement 2) was developed from trees in a mixed species stand that had been pre-commercially thinned. Although these conditions differ from the pure species spacing trial, this equation is representative of young giant sequoia at Blodgett Forest. Other published allometric equations focus on old giant sequoia (e.g., Sillett et al. 2019) or rely on equations developed for coast redwood (FIA 2014). Another potential source for misapplication of results is using these data for projections on different sites as Blodgett Forest is a relatively productive site in the Sierra Nevada. Additionally, an economic analysis of planting and pruning activities is necessary to inform decision-making. Despite these limitations, general trends exhibited by giant sequoia planted at different densities provide insight for achieving different management objectives.

Under a changing climate, the role of plantations is expanding, with increasing opportunities to mitigate climate change (Paquette and Messier 2010). Managing for multiple objectives will be increasingly common and incorporating charismatic species in plantation settings may be one way to meet multiple management objectives, including timber production, carbon sequestration, and species conservation. Incorporating giant sequoia into younger, managed stands is one avenue for not only meeting a variety of management objectives for revenue, but also conserving genetic lines of giant sequoia. Although the management of young coastal redwoods has been met with controversy (Rodrigues 1996), the active management of the species has ensured its maintenance on the landscape and the conservation of the gene pool. A similar approach may also be successful for giant sequoia. To effectively incorporate tree species into working forests for conservation and market-based values, a solid understanding of the species' stand dynamics and development of silvicultural tools is necessary. An increasing variety of management objectives and decision-making processes opens new avenues for incorporating vulnerable species into working forests.

ACKNOWLEDGEMENTS

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R. Heald designed the original study. R. Heald and J Pettigrew conducted dimensional analysis of stem form that we used to develop the local volume equation. Blodgett Forest Research Station provided labor for all treatments and previous measurements.

TABLES

Table 1. Initial planting treatment description for a giant sequoia spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Density and mean trees per plot are based on initial planting treatments and do not account for any mortality throughout 28 years. Growing space is defined as the amount of physical horizontal space allotted to each seedling at the time of planting.

Growing Space (m^2)	Spacing (m)	Density (stems ha^{-1})	Mean Trees per Plot
3.7	2.1	2,702	193
4.8	2.4	2,081	160
6.0	2.7	1,654	143
7.4	3	1,347	122
11.1	3.7	897	41
14.8	4.3	676	35
18.9	4.9	528	36
23.6	5.5	423	24
28.3	6.1	353	27

Table 2. Merchantable timber ($m^3\ ha^{-1}$) and Aboveground Carbon ($MgC\ ha^{-1}$) for giant sequoia after 28 years in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

Growing Space (m^2)	Merchantable Timber		Aboveground Carbon[1]	
	Mean ($m^3\ ha^{-1}$)	Standard Error	Mean ($MgC\ ha^{-1}$)	Standard Error
3.7	0	0	82.0	7.7
4.8	5.7	2.5	102.6	4.3
6.0	5.0	2.5	86.8	8.1
7.4	17.4	11.8	99.0	8.5
11.1	56.6	16.2	104.1	8.0
14.8	51.2	1.4	83.5	1.4
18.9	79.9	3.4	92.3	2.8
23.6	100.1	12.4	93.9	7.8
28.3	98.5	22.3	85.4	12.8

[1] A wood carbon density of 0.544 g C/g biomass was used to calculate aboveground carbon of giant sequoia (Jones and O'Hara 2018)

FIGURES

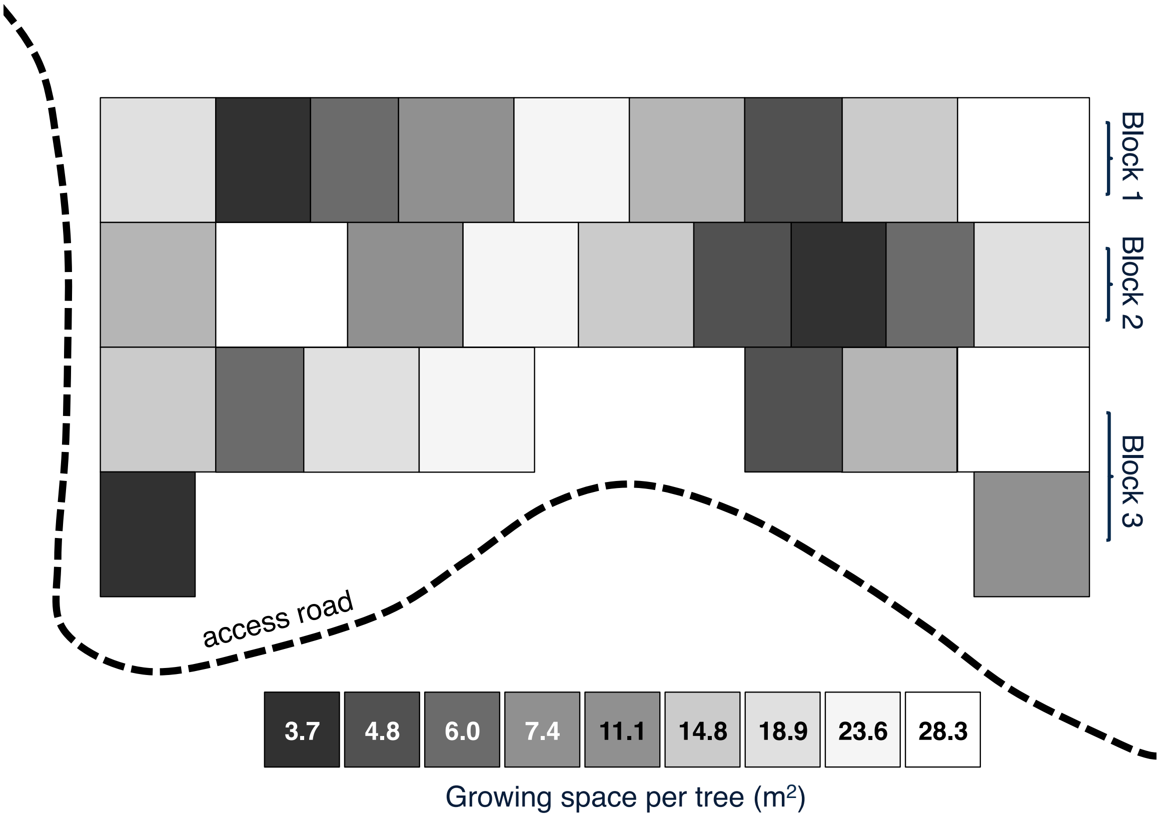

Figure 1. Map of giant sequoia spacing study at Blodgett Forest Research Station in the central Sierra Nevada. Each block contains a replicate of each spacing treatment. Blocks are arranged from north (Block 1) to south (Block 3) to avoid potential unequal shading from adjacent stands to the south. Small growing space values correspond to higher tree densities.

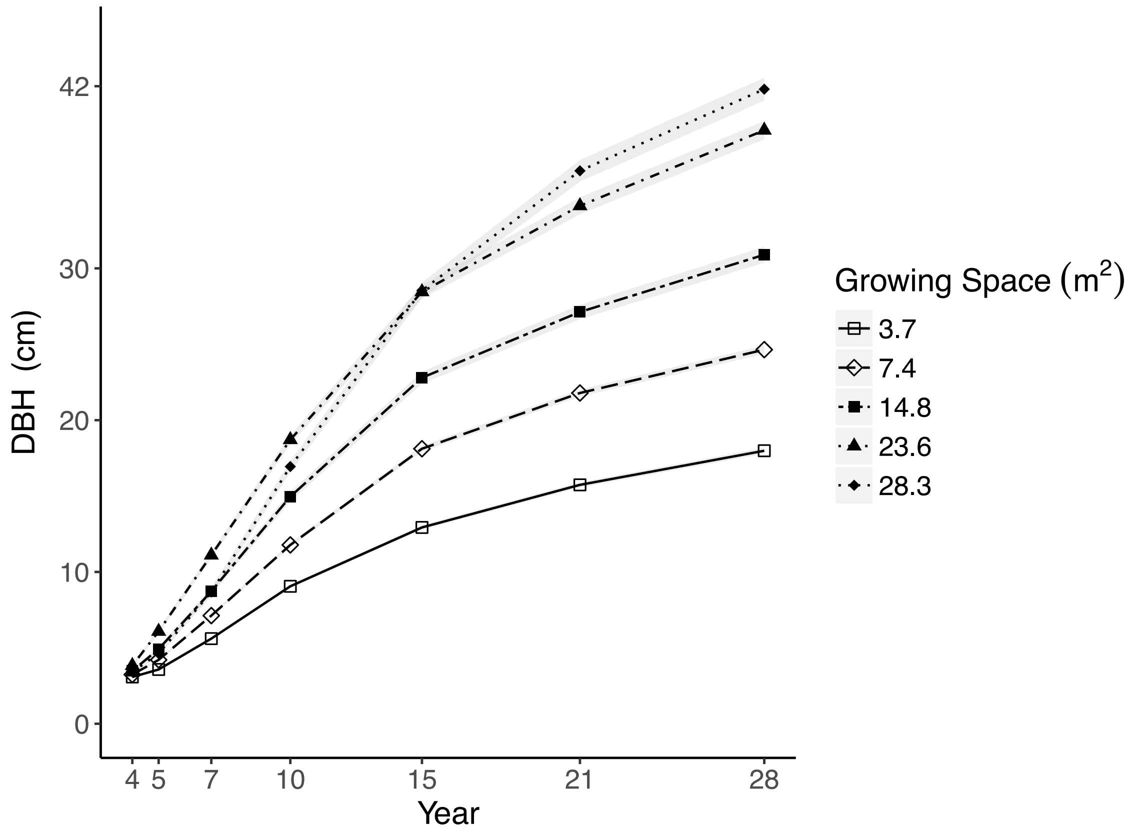

Figure 2. Diameter at breast height (DBH, cm) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. Shaded ribbons indicate standard error. Data for all nine treatments found in supplementary material.

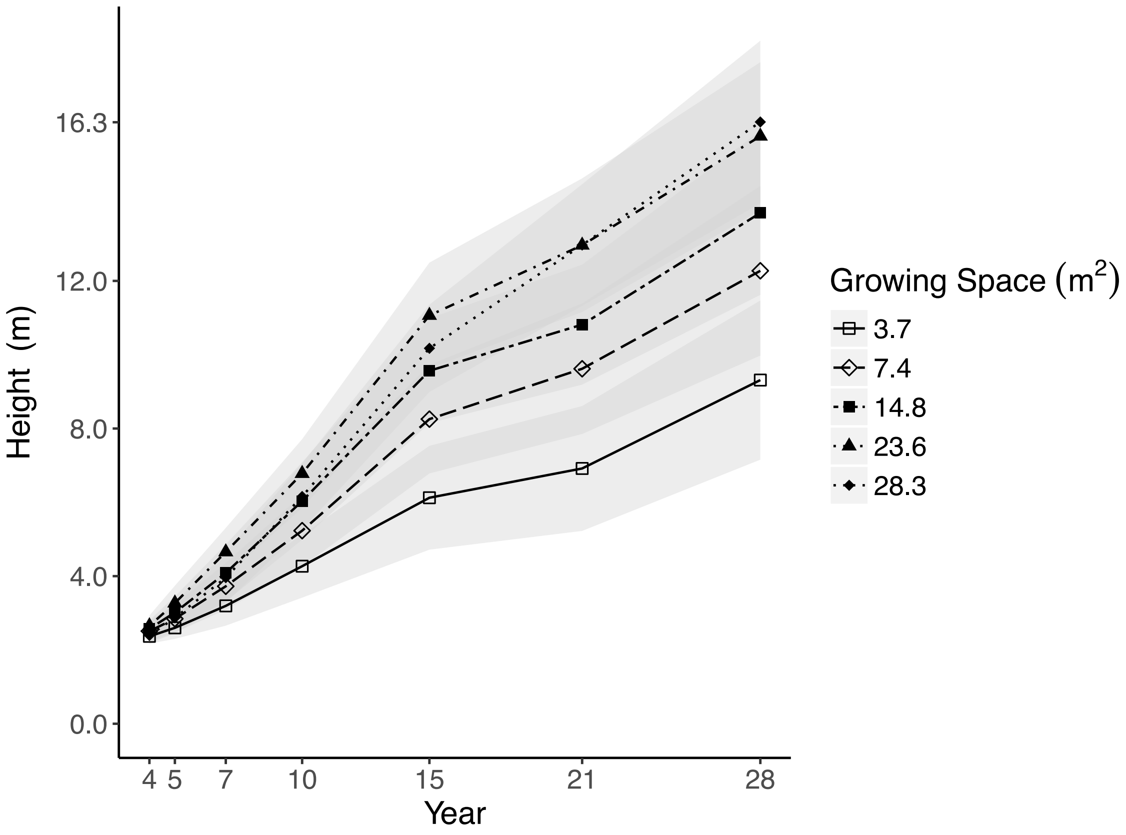

Figure 3. Height (m) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. Shaded ribbons indicate standard error. Data for all nine treatments found in supplementary material.

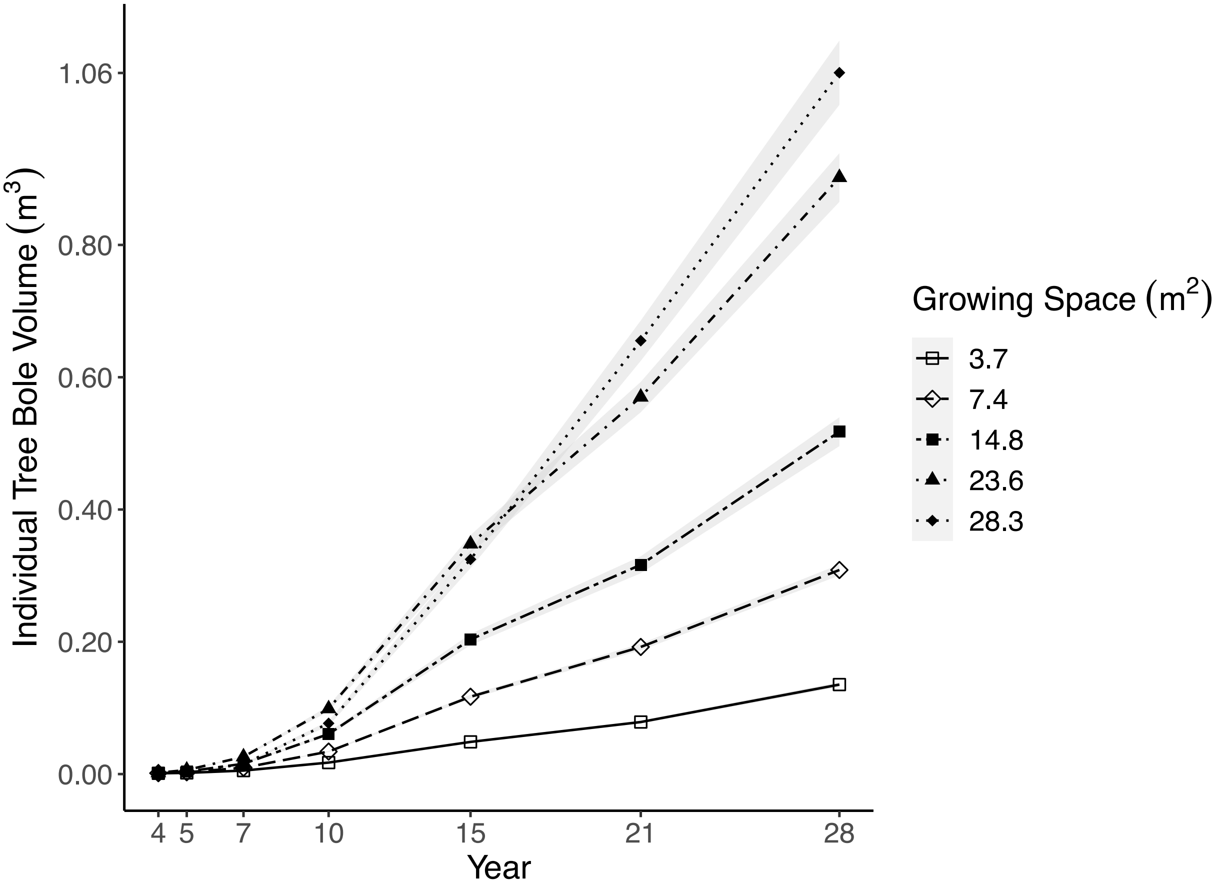

Figure 4. Mean bole volume of trees in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. Shaded ribbons indicate standard error. Data for all nine treatments found in supplementary material.

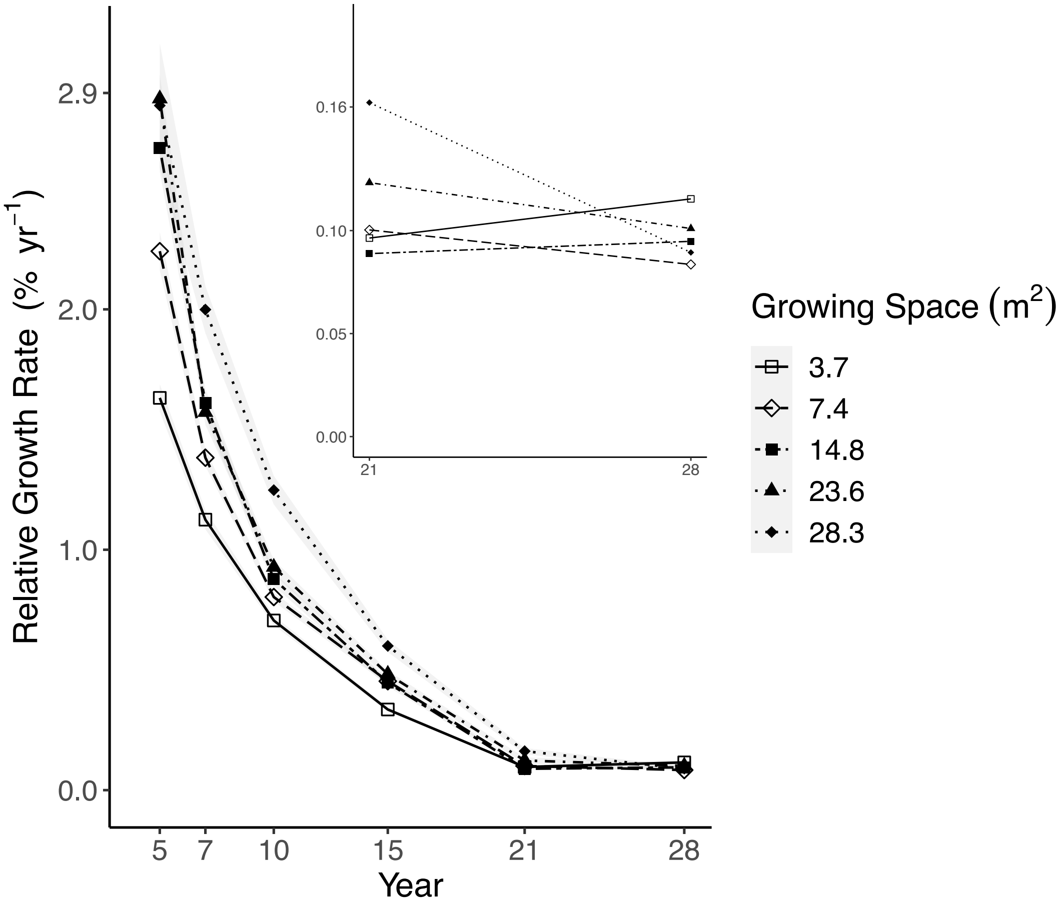

Figure 5. Relative growth rate based on bole volume of trees in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. Shaded ribbons indicate standard error. The inset shows relative growth rates based on bole volume during the most recent sampling period. Data for all nine treatments found in supplementary material.

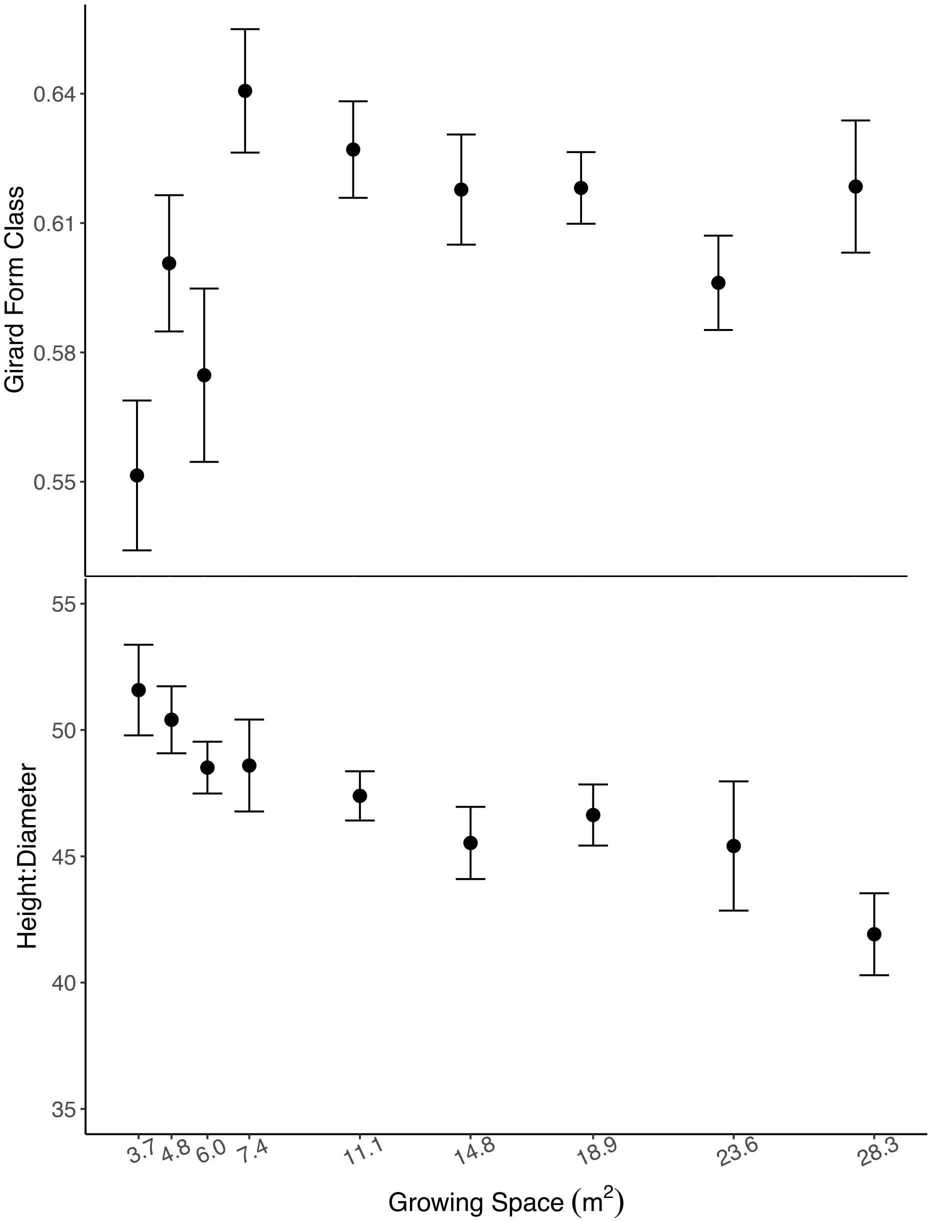

Figure 6. Girard form class and height:diameter ratio for a subsample (n=210) of giant sequoia in a spacing trial at Blodgett Forest, CA. Bars indicate standard error. Growing space indicates initial planting density treatment.

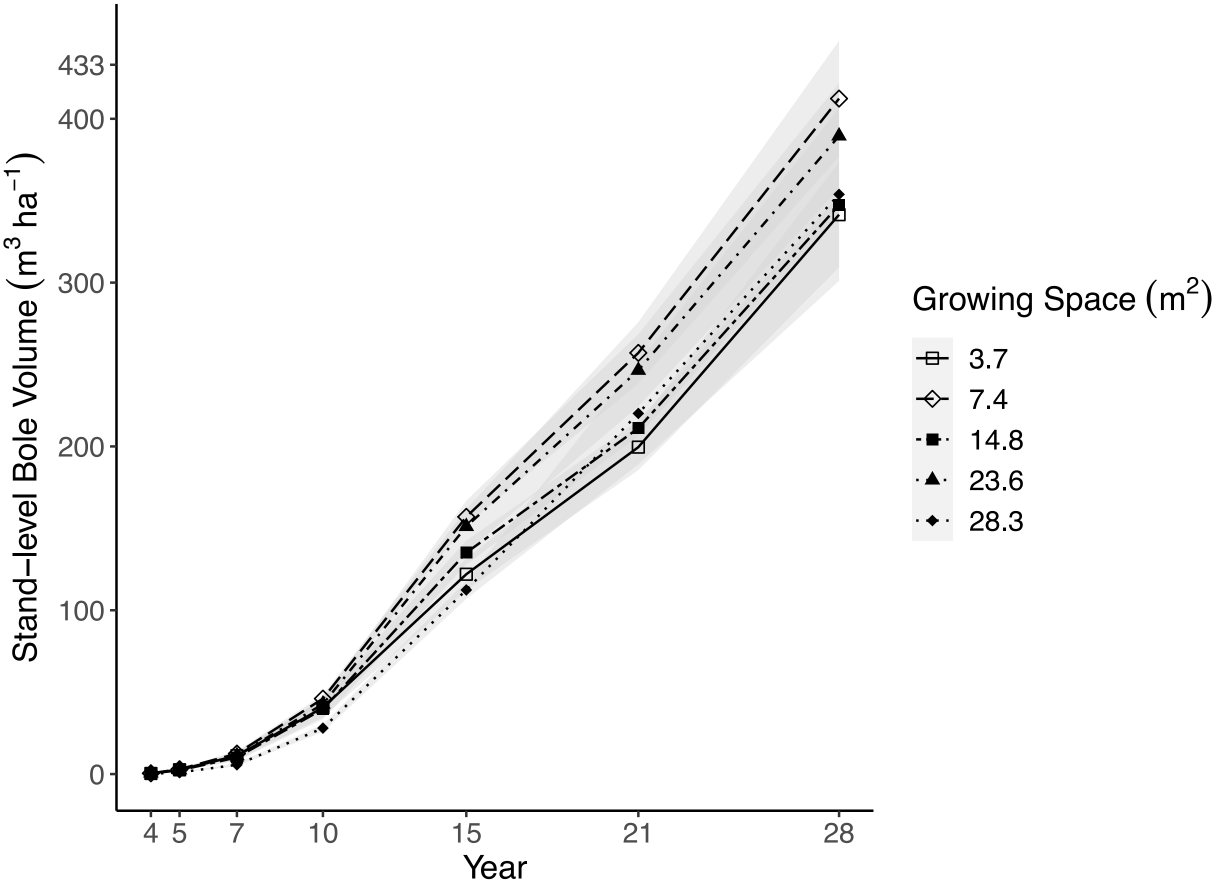

Figure 7. Mean stand bole volume in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. Shaded ribbons indicate standard error. Data for all nine treatments found in supplementary material.

TRANSITION FROM CHAPTER 1 TO CHAPTER 2

The role of plantations is expanding and present potential opportunities to mitigate climate change. Incorporating climate vulnerable species into plantation settings is one option for meeting management objectives such as timber production or carbon sequestration. In Chapter 1, I found that giant sequoia planted in a spacing trial exhibited high rates of survival after 28 years regardless of initial planting density. Giant sequoia deviated from the expected tradeoff between individual trees size and stand production. There is an expectation that wide spacings will result in lower levels of stand production. However, for giant sequoia, even the widest spacings had stand production levels similar to narrow spacings. Thus, managers may be able to achieve either high levels of carbon sequestration or merchantable timber when planting at wide spacings. Actively managing giant sequoia is one approach to ensure that it persists on the landscape and its gene pool is conserved.

Whereas giant sequoia is a vulnerable, charismatic species endemic to the Sierra Nevada mixed conifer forest, incense-cedar is a co-dominant species in the mixed conifer forests that span most of the west coast mountain range in the United States. Both species are understudied compared to other associated commercial timber species such as ponderosa pine and Douglas-fir. In Chapter 1, I demonstrated the potential of giant sequoia to be incorporated into working forests and presented information that can guide managers to achieve objectives related to merchantable timber or carbon sequestration. In Chapter 2, I used long-term data from an 18-year-old spacing trial to investigate stand dynamics of young incense-cedar. In addition to analyzing individual and stand-level growth, I tested the impact of herbivore protection on incense-cedar seedlings and explored the potential of pruning young incense-cedar to meet timber and fire risk reduction objectives. Although this spacing trial is younger than the giant sequoia spacing trial, the results are valuable for informing initial planting density and serve as a basis to evaluate future management decisions such as pruning.

CHAPTER 2

Effect of initial planting density and herbivore exclusion on incense-cedar survival and growth after 18 years

ABSTRACT

Incense-cedar is a drought resistant conifer species native to the western United States that is host to few lethal pests and pathogens. Because incense-cedar has shown promise as a species adapted to future climate and disturbances, quantifying its survival and growth is important for defining its potential place within silvicultural prescriptions of the future. The objectives of this study are to understand 1) the impact of spacing and herbivore protectors on early seedling survival, 2) the impact on spacing on planting space occupancy after 18 years, and 3) the impact of spacing on individual tree and stand characteristics. The presence of mesh tubing herbivory protection had a strong positive influence on seedling survival (96% survival with protection; 92% survival without protection) whereas increased spacing had a slight negative influence on seedling survival. After 18 years, 89% of planting spots were occupied by a live seedling. Although total occupancy differed by spacing treatment, spacing treatment is unable to predict occupancy. Wider spacing treatments resulted in larger individual tree sizes and branch diameters. Mean live crown ratios ranged from 89.4 to 97.8, indicating a lack of differentiation. Stands with narrower spacing produced higher levels of stand-level bole volume. Our results inform initial planting decisions and provide a basis for future management decisions.

INTRODUCTION

The global change drivers of warming climate and altered disturbance regimes pose a profound risk to the functioning of forested ecosystems by increasing the morbidity and mortality of trees (Seidl et al. 2017; Anderegg et al. 2020). As the western US is projected to have more frequent, hotter droughts putting future forests at risk for mass fire events (Millar and Stephenson 2015; Stephens et al. 2018), managers are tasked with implementing adaptive management strategies to foster ecosystems that are able to accommodate these changes (Millar et al. 2007). One approach is to manage for tree species that can provide some of the same functions that maladapted species provided and are more likely to persist in the projected future climate (Nagel et al. 2017).

Incense-cedar (*Calocedrus decurrens* (Torr.) Florin) is a shade tolerant, drought resistant species that is host to few lethal insect pests and pathogens (Powers and Oliver 1990). The species is native to mixed-conifer forests of mountain ranges spanning from northern Oregon to Baja California. Incense-cedar is one of four species in the *Calocedrus* genus (the only one native to North America) and is within the *Cupressaceae* family – the same as giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz). Like giant sequoia, the root systems of incense-cedar are well-developed and support arbuscular mycorrhizae. This characteristic has been attributed to increased drought tolerance for other tree species (Augé 2001). Slow-growing relative to the majority of their associates on productive sites, incense-cedar competes well on dry, hot slopes and may outgrow other species on poor sites (Powers and Oliver 1990). The commercial value of timber from incense-cedar is high, and includes uses for furniture, fencing and siding. However, relative to other timber species of the mixed-conifer forest, little applied research has been done that is relevant to the management of incense-cedar growth and yield.

Among the dominant tree species in the Sierran mixed-conifer forests, incense-cedar has demonstrated a remarkable ability to persist under novel conditions. Not only has incense-cedar density increased as a result of the past century of fire suppression, but it also experienced relatively low mortality through the 2012-2016 drought (Fettig et al. 2018; Restaino et al. 2019). After prescribed fires, incense-cedar has exhibited high survival rates compared to other conifer associates, second only to giant sequoia (Bellows et al. 2016; Stephens and Finney 2002). Incense-cedar has shown promise as a candidate for assisted migration in recent provenance trials (Young et al. 2020). Because this species has shown promise as a potential species adapted to future climate and disturbances, quantifying its survival and growth is important for defining its potential place within silvicultural prescriptions of the future.

Knowledge of intra-specific competition is a basic need for informing tree planting designs and implementing young stand management treatments to achieve specific objectives (Drew and Flewelling 1979; Hutchings and Budd 1981). Spacing trials are long-term experiments designed to the quantify the effects of initial planting density, which is the first decision that must be made along a sequence of potential interventions during young stand development. Such trials are important because they identify tradeoffs between stand-level growth and individual tree size. For example, spacing trials have been used to develop silvicultural decision-making tools for important timber species, including ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Although incense-cedar is currently a valuable harvested wood product in the western United States (California Department of Tax and Fee Administration 2021; Pong and Cahill 1988), no spacing trials on the species have been published. Given its potential to thrive in future climates, understanding its silvics is a critical knowledge gap for climate adaptive practices.

Management strategies that promote the survival and early growth of planted trees can confer long-term advantages in stand productivity (Ponder 2003). However, the value of these investments (e.g., tree shelters to promote survival; maintaining wide spacing to promote early growth) must be quantified to inform the development of effective and efficient practices. The primary goal of this study is to understand the impacts of different management strategies on young stand dynamics of incense-cedar. We divided our research questions into three categories that reflect key aspects of reforestation: establishment, early individual growth and survival, and early stand production (Figure S1).

Specifically, we ask:

Establishment

1) How does spacing affect seedling survival?
2) How does herbivore exclusion affect early survival?
3) What are the interactive effects of spacing and herbivore exclusion?

Early Individual Growth and Survival after 18 years

4) How does spacing affect occupancy?
5) How does spacing affect individual tree size (diameter, height, and bole volume)?
6) How does spacing affect crown form (live crown ratio)?
7) How does spacing affect branch form (density and diameter)?

Early Stand Production

8) How does spacing affect stand level volume and biomass production?

Answering these questions will not only inform initial planting decisions but also provide the basis to evaluate future management decisions such as the potential value of pruning in young incense-cedar stands.

METHODS

Study area

The spacing trial is established at Blodgett Forest Research Station (BFRS), a 1,763 ha research forest in the central Sierra Nevada, California, USA (38°52N 120°40W). The elevation of the study site is approximately 1295 m. The regional climate is Mediterranean, characterized by a summer drought period and mild winters. Most precipitation occurs during the winter and spring, averaging 1,660 mm annually. Average summer temperatures range between 14° and 27° C while average winter temperatures are between 0° - 9° C (BFRS data, https://forests.berkeley.edu/forests/blodgett). Soils are formed from andesitic parent materials (Heald and Barrett 1999).

BFRS is composed of five coniferous and one hardwood tree species: sugar pine (*Pinus lambertiana*), ponderosa pine, white fir (*Abies lowiana*), incense-cedar, Douglas-fir, and California black oak (*Quercus kelloggii*). The forest is representative of a productive mixed-conifer forest that occurs between 1,200–1,700 m in elevation on the western Sierra Nevada slope. Trees at BFRS are able to reach 27-34 m in height in 50 years (BFRS data, https://forests.berkeley.edu/forests/blodgett). Between 1750 and 1900, median composite fire intervals at the 9–15 ha spatial scale were 4.7 years with a fire interval range of 4–28 years (Stephens and Collins 2004).

Experimental design and field methods

In 1999, incense-cedar seedlings were planted at nine increasingly wide spacings, ranging from 2.1 – 6.1 m hexagonal spacing between planting spots (Table 1). Spacing treatments were randomly assigned to a location within each of three replicates or blocks (i.e., a randomized block design, Figure 1). Two seedlings were planted in each planting spot to increase the chance of at least one surviving seedling at each spot (Figure 2). In 2000, plastic tubing (made by Vexar) was installed on one of each seedling pair to protect against small mammal browsing. To protect seedlings from large mammal browsing (primarily deer and cattle in this area), high fencing was installed around the entire study area. All seedling heights were recorded in 2000. In 2003, Vexar tubing was removed and seedling vigor was recorded on a scale from 1 to 5. A vigor of 1 to 3 indicated a living plant (1 being the most vigorous); a vigor of 4 and 5 indicated a dead or missing plant, respectively. During winter of 2003, extra seedlings planted in 1999 surrounding the official spacing study were transplanted into planting spots with dead and dying seedlings (i.e., live seedlings with low vigor). In 2005, for planting spots with two live seedlings, the least vigorous tree was culled so that only one tree remained per planting spot. Vigor and height of the remaining seedling was recorded. During summer 2018, we surveyed all trees in the spacing study and noted their vigor, diameter at breast height (DBH; cm; at 1.37 meters above ground), and height (m). We also noted the height to the base of live crown (m) for each tree. In addition, for each tree in the two innermost planting rows of each spacing treatment, we counted the number of branches in the first 30 cm above breast height (1.37-1.67 m aboveground) and measured the diameter of the branch closest to breast height on the western side of each bole. (Figure 2). Branch diameter was measured with calipers at the branch collar.

Analytical approach

To answer our specific questions about the effect of initial planting density, we calculated the horizontal growing space of each spacing treatment to use as a predictor variable. We defined growing spaces as the amount of physical horizontal space allocated to each planting spot. Small growing spaces correspond to high tree planting densities (Table 1). For all analyses, we excluded "guard trees" along the borders of each spacing treatment to avoid interactions between treatment areas. All analyses were conducted in R (R Core Team 2021).

Establishment

Questions 1-3 focus on the effect of planting density and Vexar tubing on seedling survival. We quantified survival by calculating the survival rate three years after the Vexar tubing was installed (i.e. survival from 2000 to 2003, Fig. 2). Each planting spot in this analysis included a matching treatment pair of two seedlings, one with Vexar tubing and one without. Planting spots without a matched treatment pair were excluded from this analysis. This data subset included 4,076 seedlings planted across 2,038 planting spots. Annual survival was calculated as a discrete rate (Sheil et al. 1995); results were summarized as a function of Vexar and spacing treatments. We estimated uncertainty by obtaining confidence intervals of survival using profile likelihood (Eitzel et al. 2015). To test for treatment effects on survival, we fit a logistic regression using a generalized linear mixed-effects model (function "glmer", Bates et al. 2015) with Vexar tubing and spacing as fixed effects and block as a random effect.

Early Individual Growth and Survival

The next part of our analysis focused on the number of planting spots occupied by a live tree in 2018 (Question 4). We defined occupancy as a planting spot with at least one live stem present. All planting spots (n=2,115) were included in this analysis. To describe the effect of spacing on planting spot occupancy in 2018, we fit a logistic regression using a generalized linear mixed-effects model (function "glmer", Bates et al. 2015) with spacing treatment as a fixed effect and block as a random effect. We calculated confidence intervals for binomial probabilities.

Our analysis of individual tree characteristics and crown form focused on field data collected in 2018 (Questions 5 and 6). We excluded all trees that had dead or missing neighbors to ensure that growing space was consistent for each tree within the spacing treatment. Additionally, we excluded all planting spots with multiple live stems (i.e. planting spots with transplants that were never culled) and trees that forked below breast height (i.e. were measured as multiple stems in one planting spot) so that each planting spot included in the analysis only had a single live stem. To estimate individual bole volume, we used the cubic volume equation for incense-cedar from the USFS Forest Inventory and Analysis program (Wadell et al. 2014). To analyze the effect of spacing on individual characteristics and crown form, we implemented an information theoretic approach to compare model performance (Burnham and Anderson 2002). We chose four candidate models to compare for each response variable: a simple linear equation, a log-linear fit, a quadratic fit, and a Michaelis–Menten fit (asymptotic fit). For each model, we calculated Akaike's information criterion (AIC), differences in AIC relative to the lowest AIC (ΔAIC), and AIC weights (w_i). We inspected the residuals for each model to detect any heteroscedasticity. For the analysis of live crown ratio, we implemented a logit transformation on the proportion data to meet the assumption of normally distributed residual terms (Warton and Hui 2011). The best model was selected based on w_i. For models with ΔAIC values ≤ 2, we selected the model with the fewest parameters. Analyses were conducted in R using the “nlme” library (Pinheiro et al. 2021).

Branch density and diameter analysis included a subsample of 384 trees across all spacing treatments (Question 7). We excluded all planting spots with multiple live stems and trees that were forked below breast height. All trees that had dead or missing neighbors were also excluded so that growing space was consistent within the spacing treatment. We implemented an information theoretic approach similar to that used for the individual tree and crown form, developing four simple models to compare. However, because of the reduced sample size of this data, the random blocking effect was not included.

Early Stand Production

To answer our final question regarding stand level biomass production (Question 9), we calculated the area-based biomass production mean for each treatment replicate within the three blocks (n=3; Figure 1). For this analysis, trees with missing or dead neighbors were included when calculating stand level means for each treatment. We used estimated bole volume to calculate an area-based average to describe stand-level bole volume production. To calculate total biomass for all trees, we used the wood density and bark and branch biomass equations documented by FIA (FIA 2014). Total aboveground biomass for each tree was calculated by summing stem, bark, and branch biomass. Stand-level biomass estimates were calculated as area-based means across the three blocks. To test for differences among spacing treatments, we implemented an information theoretic approach, comparing the linear, log transform, quadratic, and Michaelis-Menten model fits.

RESULTS

Establishment

Seedling survival averaged 94% per year across all spacing and Vexar treatments. An additive mixed-effects logistic model best indicated that both spacing and Vexar had significant effects on seedling survival (Figure 3). The presence of Vexar had a positive influence on seedling survival (96% survival with Vexar; 92% survival without) whereas spacing had a slight negative influence on seedling survival (Figure 3; Table S1).

Early Individual Growth and Survival

After 18 years, 1,895 of 2,115 planting spots (89%) were occupied by a live seedling. Although total occupancy differed by spacing treatment ($p < 0.001$), spacing treatment is unable to predict occupancy (Figure 4). Occupancy was similar between the widest and narrowest spacings, whereas intermediate treatments had lower occupancies. The widest spacing treatment (29.1 m^2 spacing) exhibited 92% occupancy whereas the narrowest spacing exhibited 94% occupancy. The 15.0 m^2 and 23.9 m^2 spacing treatments exhibited the two sparsest occupancies of 74% and

78%, respectively. The 19.3 m^2 treatment exhibited the highest percent occupancy with 95% of planting spaces occupied by a live tree.

Wider spacing treatments resulted in larger DBH (Figure 5a). The mean diameter of the widest spacing (29.1 m^2 spacing) was 2.1 times greater than the mean diameter of the narrowest spacing. Height also increased at wider spacings (Figure 5b). The mean height of the widest spacing was 1.6 times taller than the mean height of the narrowest spacing. For both diameter and height, a log transform model was the best fit (Table S3).

As expected, we found this same trend of increasing tree size at wider spacings held for individual volume as well. At the widest spacing, mean tree volume was 2.5 times larger than the narrowest spacing (Figure 5c). For all individual volume, linear and quadratic model fit the data equally well; for simplicity, we report results from the linear model.

Mean live crown ratios ranged from 89.4 (3.5 m^2 spacing) to 97.8 (29.1 m^2 spacing) with wider spacing treatments corresponding to larger live crown ratios (Figure 6). A non-linear mixed-effects model indicated that growing space had a significant effect on live crown ratio and followed a Michelis-Menten fit. The range of live crown ratios was narrow across all spacing treatments and crown lifting has only just begun in the narrowest spacing treatment.

Branch diameter was also best described by a Michelis-Menten fit (Figure 7a). Mean branch diameter closest to breast height (1.37 m) in the widest spacing treatment (29.1 m^2 spacing) was 1.9 times larger than mean branch size in the narrowest spacing. The relationship between branch density and growing space was best described by a quadratic fit, though the range for branch densities was small (7.3 – 6.3 branches per 0.3 m along bole; Figure 7b)).

Early Stand Production

Stands with narrower spacing generally produced higher levels of stand-level bole volume (Figures 8a and 8b). However, the most productive spacing was the third narrowest treatment (6.0 m^2 spacing) and the least productive spacing treatment was the second widest (23.9 m^2 spacing). Based on predicted values, the narrowest spacing treatment (3.7 m^2 spacing) produced 5.5 times more volume (m^3 ha^{-1}, Figure 8a) and biomass (Mg ha^{-1}, Figure 8b) than the widest spacing treatment. For both stand- level volume and biomass production, a log transform relationship was the best fit.

DISCUSSION

Establishment

Early survival of planted seedlings is essential and management strategies such as herbivore exclusion are effective in increasing survival. For young incense-cedar seedlings, the presence of protective tubing during the first three years after planting increased the likelihood of seedling survival (Figure 3). Anthony et al. (1978) demonstrated that Vexar is effective in protecting other conifer species such lodgepole pine (*P. contorta* Douglas), ponderosa pine, and red fir (*A. magnifica* A. Murray bis) from small herbivores, with 4 times less mortality experienced by seedlings in Vexar tubing. However, Vexar tubing is not consistently effective in reducing browsing by large mammals and conifer seedling survival (Brandeis et al. 2002). Rather than protective tubing, the fence installation around the entire study area prevented browsing by large mammals in the incense-cedar spacing trial. Other studies have shown that tree shelters may also alter the microclimate around the seedling to promote seedling growth (Ward et al. 2000; Keeton 2008). However, the type of protective barrier influences the degree of this microclimate alteration (Ward et al. 2000). Our results indicate that incorporating Vexar as an early stand management strategy coupled with fence installation may help ensure survival for incense-cedar seedlings by excluding both large and small herbivores.

Early Individual Growth and Survival

After 18 years, 89% of planting spots had a live stem across all spacing treatments. Although the spacing treatments had a significant effect on planting spot occupancy, occupancy could not be predicted using planting spacing. The lack of predictive power of spacing treatments coupled with subtle effect of spacing on live crown ratio suggests that young tree mortality is not because of intraspecific competition or self-thinning. For other spacing trials of conifer species, the onset of self-thinning has not occurred until after 30 years after planting. At age 20, a ponderosa pine spacing trial had 97.5% occupancy (Oliver 1990). For Douglas-fir, even after 35 years, only the narrowest spacing treatments (1 m^2 and 4 m^2) had less than 20% total occupancy (Curtis et al. 2016). However, a giant sequoia spacing trial at BFRS had 98.3% occupancy after 28 years (Cox et al. 2021). Although incense-cedar mortality in this spacing trial cannot be attributed to intraspecific competition, other stochastic factors may have resulted in the death of study trees.

After 18 years, the rate of increased DBH growth of incense-cedar as a function of spacing fell within the range reported from similar studies of co-existing species. To compare responses, we calculated the spacing gradient as the widest spacing divided by the narrowest spacing and then expressed the growth-to-spacing ratio as the spacing gradient divided by the growth increment (Table 2). Larger values of growth-to-spacing ratios indicate a more sensitive response of species to initial planting spacing. After 20 years, ponderosa pines with 24.1 m^2 of growing space exhibited diameters 1.9 times larger than trees with 2.4 m^2 and Douglas-fir exhibited diameters 1.7 times as large (Peracca and O'Hara 2008) – a growth to spacing ratio of 0.19 and 0.17 respectively. The mean DBH of giant sequoia with 28.3 m^2 growing space was 2.4 times the mean DBH of trees with 3.7 m^2 after 22 years (York et al. 2013b) – a growth-to-spacing ratio of 0.32. For incense-cedar, we reported a growth to spacing ratio of 0.27 (Figure 5a).

As has been documented in most other tree species, the impact of initial planting density on incense-cedar height was weaker than the effect on diameter (Figures 5a and 5b). This effect is likely carbohydrate allocation is prioritized to height growth over diameter growth, leading to differentiation in diameter before height differentiation occurs (Hutchings and Budd 1981). Although the magnitude of difference among spacing treatments was greater for diameter than height, incense-cedar exhibited a greater difference in height growth among spacing treatments compared to other associated species – a growth to spacing ratio of 0.20 (Table 2). At age 20, ponderosa pines with 24.1 m^2 of growing space exhibited heights 1.1 times larger than trees with 2.4 m^2 and Douglas-fir exhibited heights just 0.82 times as large (Peracca and O'Hara 2008) – a growth to spacing ratio of 0.11 and 0.08, respectively. Western white pines (*P. monticola* Douglas ex D. Don) with 36 m^2 of growing space had heights 1.1 times taller than threes with 4 m^2 growing space at age 16 (Bishaw et al. 2003) – a growth to spacing ratio of 0.12. In contrast, heights of giant sequoia with 28.3 m^2 growing space were 1.8 times the height of those with 3.7 m^2 growing space at age 22 (York et al. 2013b) – a growth to spacing ratio of 0.24. Thus, the notable effect of spacing on incense-cedar height growth is not as pronounced as giant sequoia, but greater than the effect of spacing on other Sierra Nevada mixed-conifer associates. The larger effect of spacing on height for both incense-cedar and its relative, giant sequoia, may be attributed to their sustained growth habit, where shoot growth is influenced by the current environment rather than the resources available during the prior growing season (Gasser 1994; Harry 1987).

All trees grown in forested conditions will experience crown recession as trees grow and compete for limited resources. Trees grown at closer spacings are expected to experience natural pruning and crown recession earlier than trees grown at wider spacings (Smith and Reukema 1986). After 18 years, the live crown ratios of incense-cedar are large across all spacing treatments. However, the narrowest spacing treatment (3.7 m^2) has a lower mean live crown ration than the wider spacings (Figure 4). In contrast, 20 year-old ponderosa pine exhibited live crown ratios less than 70% even at 37.2 m^2 growing space (Peracca and O'Hara 2008). The difference in crown recession may be attributed to the relative shade tolerance of incense-cedar compared to ponderosa pine along with differences in crown morphology (Garber et al. 2008). More shade tolerant tree species often exhibit greater live crown ratios as they can maintain foliage under the shade of their own crowns for longer periods than less shade tolerant trees. The delayed crown recession in incense-cedar increases the risk the vulnerability of trees to injury and mortality from fires. Pruning lower limbs from is a useful management tool to reduce the likelihood of mortality from low severity fires (Bellows et al. 2016).

The number and size of branches influences wood quality. Depending on the management objectives for a stand, managers may wish to prune lower limbs to improve wood quality or decrease stem taper. Incense-cedar are known to have persistent lower dead branches (Powers and Oliver 1990), which form loose knots that reduce lumber value. However, overall branch density across all spacings (7 branches from 1.37 to 1.67 m above ground) is less than the branch density of giant sequoia (10.8 branches from 1.37 to 1.67 above ground; York et al 2013). Branch diameter for incense-cedar increased with increased growing space, similar to the trend between DBH and growing space. Branch diameters in the widest spacing treatment (29.1 m^2) were 1.9 times larger than those in the narrowest spacing treatment, whereas diameters differed by a magnitude of 2.1 (Figures 5a and 7a). Despite differences in shade tolerance and branch size, the influence of spacing on ponderosa pine branch diameter was similar to incense-cedar. After 20 years, branches of trees with 30.1 m^2 growing space were 2.0 times larger than branches of trees with 3.3 m^2 growing space (Oliver 1990). In the incense-cedar spacing trial, branch diameter approached the asymptote of 37.7 mm at the widest spacing (Fig 7a), indicating that planting at even wider spacings would have minimal impact on branch size while increasing individual tree volume.

Many of the stems that were alive after 18 years were forked below breast height. Of the 2,115 total planting spaces, 1,895 were alive. Of the living stems, 16% were forked below breast height. Potential causes of the forked stems include disease such as incense-cedar broom rust (*Gymnosporangium libocedri*), or frost or browsing killing the apical meristem, resulting in deformations. Such defects may influence which timber products are able to be produced. For example, if a tree is forked at the base, it would be processed as two individual stems, likely with smaller diameters. Although forked stems may grow together to form one bole throughout the lifetime of the stand, this is a potential consideration if planning for timber production.

Early Stand Production

An expected tradeoff exists between individual tree size and stand production. Narrower spacing treatments are expected to yield smaller trees with higher stand-level volumes, whereas wider spacings yield larger trees with smaller stand-level volume (Assmann 1970; Long and Smith 1990). This incense-cedar spacing trial demonstrates this expected tradeoff. Generally, planting at wider spacings would be recommended for meeting the objective of timber production of large, individual trees whereas narrower spacings are more suitable for biomass production, carbon sequestration, or wood products that can be derived from smaller logs (e.g. poles or fence boards). After 18 years, incense-cedar trees across all spacing treatments have not yet reached the minimum threshold of 30 cm for merchantable timber (Figure 5a), although individual bole volume increases linearly with spacing (Figure 5c). Thus, we infer that planting at wider spacings will produce larger, merchantable trees sooner than narrower spacings. However, specific recommendations on achieving timber production goals will best be evaluated in the future. Aboveground biomass accumulation across all spacings was modest (Figure 8b). The relationship between stand production and initial planting density will be measured over time to demonstrate trends over full rotation ages.

We are unaware of any peer-reviewed publications on thinning experiments for incense-cedar. However, we may draw some inferences based on the results from this spacing study. After 18 years, competition related mortality had not yet occurred, so thinning to prevent mortality is likely unnecessary at this stage of stand development. However, it is apparent that trees planted at the widest spacings will reach merchantable sizes earlier than those at narrower spacings. Therefore, thinning may be used to promote larger individual tree size. As incense-cedar maintains persistent low crowns, thinning early during stand development may also be used to create a stand structure that reduces the risk of high severity fire.

Incense-cedar is understudied relative to other commercial Sierra Nevada commercial conifer species. Our results provide information on early survival and density-growth relationships that may be used to inform early management decisions. However, several limitations these results reflect incense-cedar growth at only one site. Blodgett Forest Research Station is a productive forest (high site) in the Sierra Nevada which should be considered when applying these results to other sites. Survival differed across spacing treatments and the low survival in the 15.0 m^2 spacing treatment caused us to remove it from our analyses, leaving a gap in our spacing treatment gradient. The cause of this increased morality in an intermediate spacing treatment is not readily apparent. We suspect that the lower survival is because of microclimate differences or a stochastic event such as frost. Additionally, the 6.0 m^2 spacing treatment exhibited unexpectedly high individual tree sizes in two of the three replicates, resulting in high mean values. Despite this variability, our results demonstrate general trends exhibited by incense-cedar planted at increasing spacing that may be used to direct early management decisions.

The results from our spacing trial support other studies that demonstrate the climate readiness of incense-cedar. Despite some early seedling mortality, after 18 years – four of which were during an epic drought – overall occupancy of the spacing trial was 89%. After the 2012–2016 drought, Restaino et al. (2019) found that incense-cedar experienced less mortality than the pine species, likely because of fewer lethal pests present. When investigating the impacts of fuel reduction treatments on drought-related mortality, Steel et al. (2021) found that incense-cedar exhibited the lowest mortality of all species at just 3%. In a provenance trial, low-elevation incense cedar seedlings not only exhibited high survival (97%), but also outperformed other species in stem volume (Young et al. 2020). The results from our study demonstrate the potential for incense-cedar to be planted for either timber production or carbon sequestration. Other early stand management strategies such as pruning and thinning may be implemented to create more resilient structures that are less vulnerable to high severity fires.

Conclusion

Incense-cedar is a co-dominant species in the mixed conifer forests that spans most of the west coast mountain range in the United States. Despite its prevalence and potential market value, the species is understudied compared to other associated timber species such as Douglas-fir and ponderosa pine. As climate change continues to threaten the future functioning of forests, prioritizing native species, such as incense-cedar, that are well adapted to hotter, drier climates is one potential method for managing for resilient future forests. New provenance trials have indicated that incense-cedar is a promising species for future forests (e.g., Young et al. 2020). The use of Vexar to protect seedlings during establishment should promote their chance of survival. Results after 18 years of growth indicate that incense-cedar generally follows expectations for individual tree growth and stand production. Because of the persistence of lower limbs on incense-cedar, pruning may be considered not only to reduce fire-related injury and mortality, but to improve wood quality to meet timber production objectives. The trajectory of these stands and individuals indicates the potential for timber production and carbon sequestration. As future droughts and fires impact the composition of western forests, managing for incense-cedar may prove to be a winning strategy for a resilient future forest.

TABLES

Table 1. Initial planting treatment description for an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Density and mean trees per plot are based on initial planting treatments and do not account for any mortality throughout 18 years.

Growing Space (m^2)	Spacing (m)	Density (stems ha^{-1})	Mean Trees per Plot
3.7	2.1	2,684	215
4.8	2.4	2,073	160
6	2.7	1,661	49
7.5	3	1,335	138
11.2	3.7	895	34
15	4.3	668	30
19.3	4.9	519	29
23.9	5.5	418	25
29.1	6.1	343	25

Table 2. Comparison of tree growth responses to different initial planting spacings. Spacing gradient is defined as the widest spacing divided by the narrowest spacing. Growth differential is the difference in tree size between the widest and narrowest spacing. The growth-to-spacing ratios are calculated by dividing the spacing gradient by the growth differential. Larger values of growth-to-spacing ratios indicate a more sensitive response of species to initial planting spacing.

Species	Spacing Gradient	DBH Growth Differential	HT Growth Differential	DBH:Spacing ratio	HT:Spacing Ratio
Incense-cedar	7.9	2.1	1.6	0.27	0.20
Ponderosa pine[a]	10	1.9	1.1	0.19	0.11
Douglas-fir[a]	10	1.7	0.82	0.17	0.08
Giant sequoia[b]	7.6	2.4	1.8	0.32	0.24
Western white pine[c]	9	1.3	1.1	0.14	0.12

[a] Peracca & O'Hara (2008)

[b] York et al. (2013b)

[c] Bishaw et al. (2003)

FIGURES

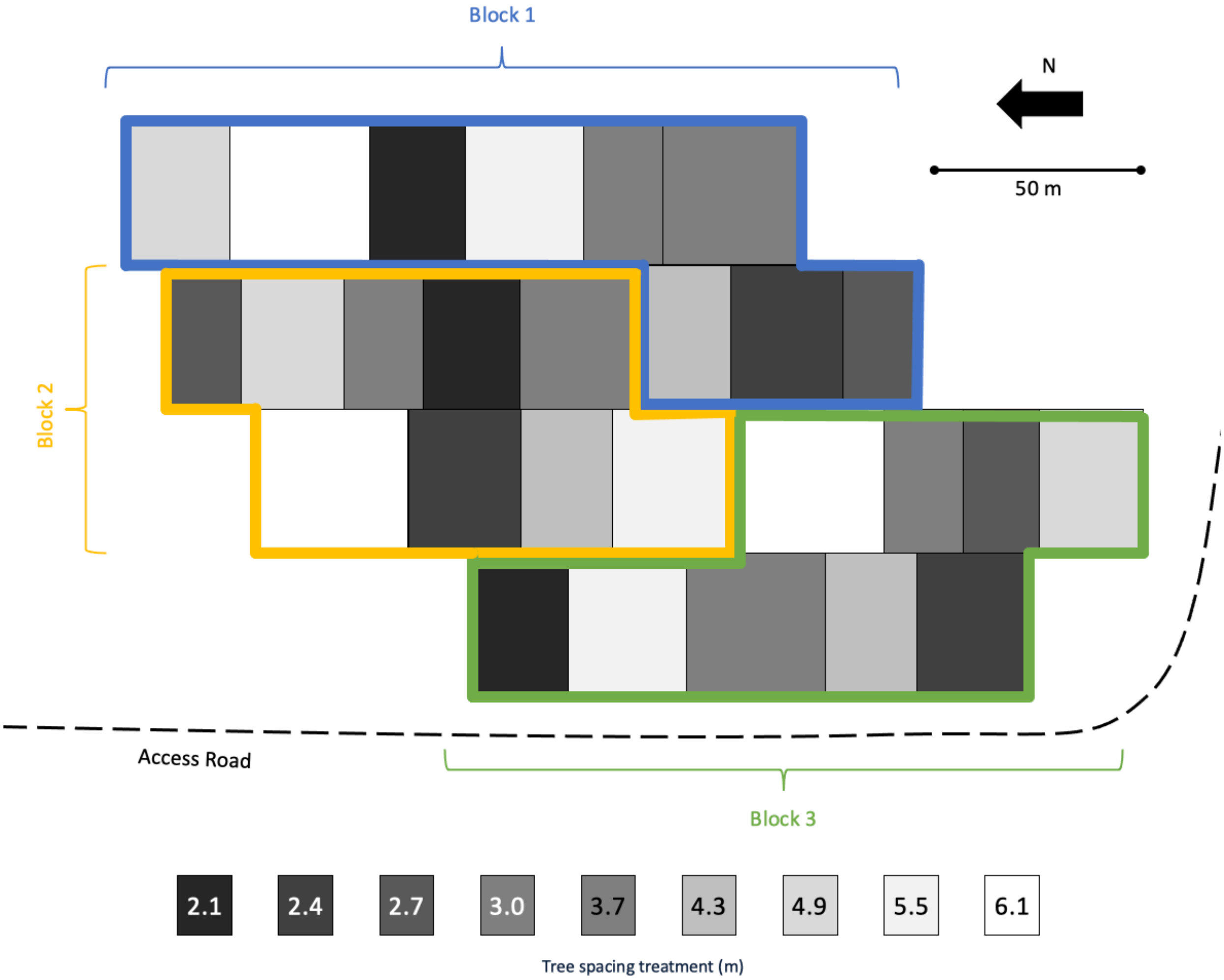

Figure 1. Map of an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Each block contains a replicate of each spacing treatment. Small growing space values correspond to higher tree densities.

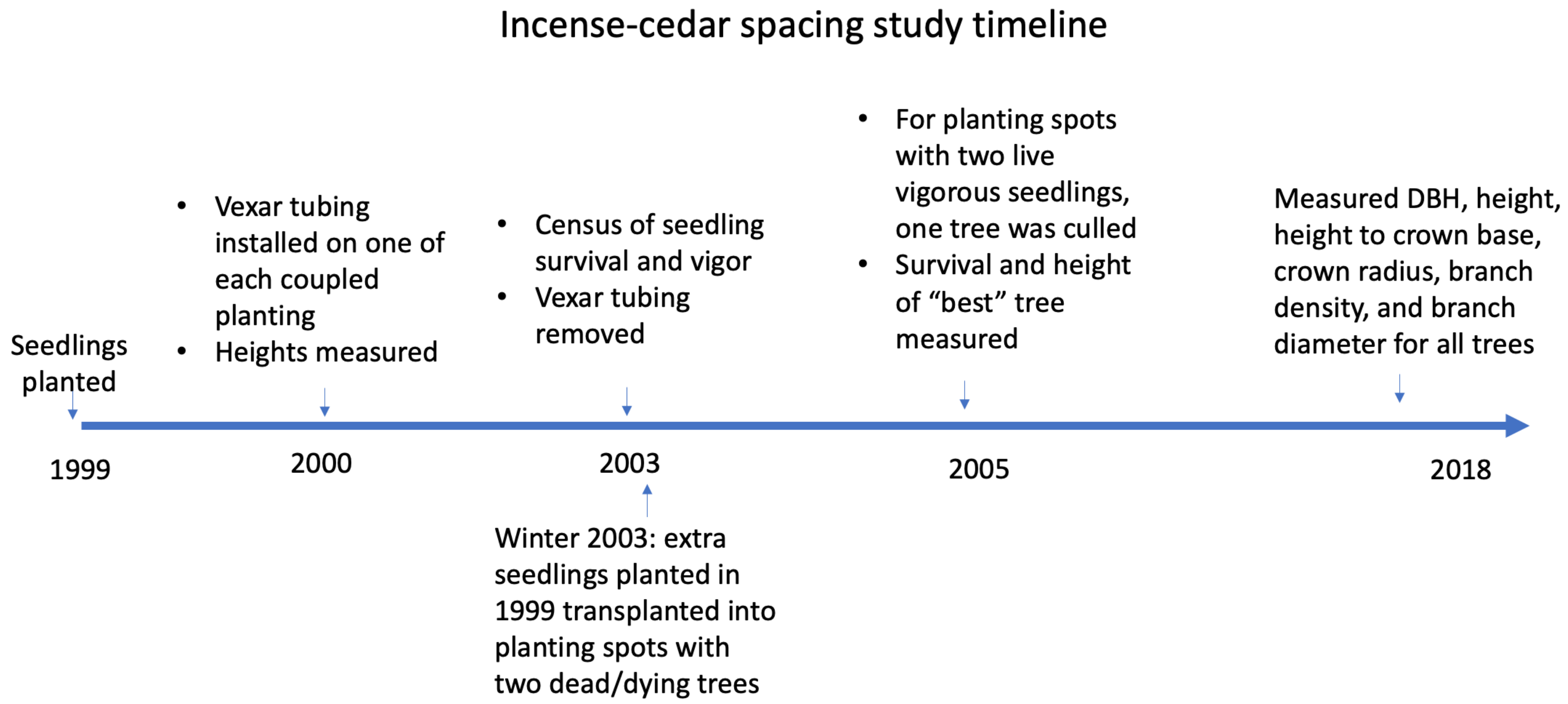

Figure 2. Timeline of incense-cedar spacing trial treatments and measurements at Blodgett Forest, Sierra Nevada, CA.

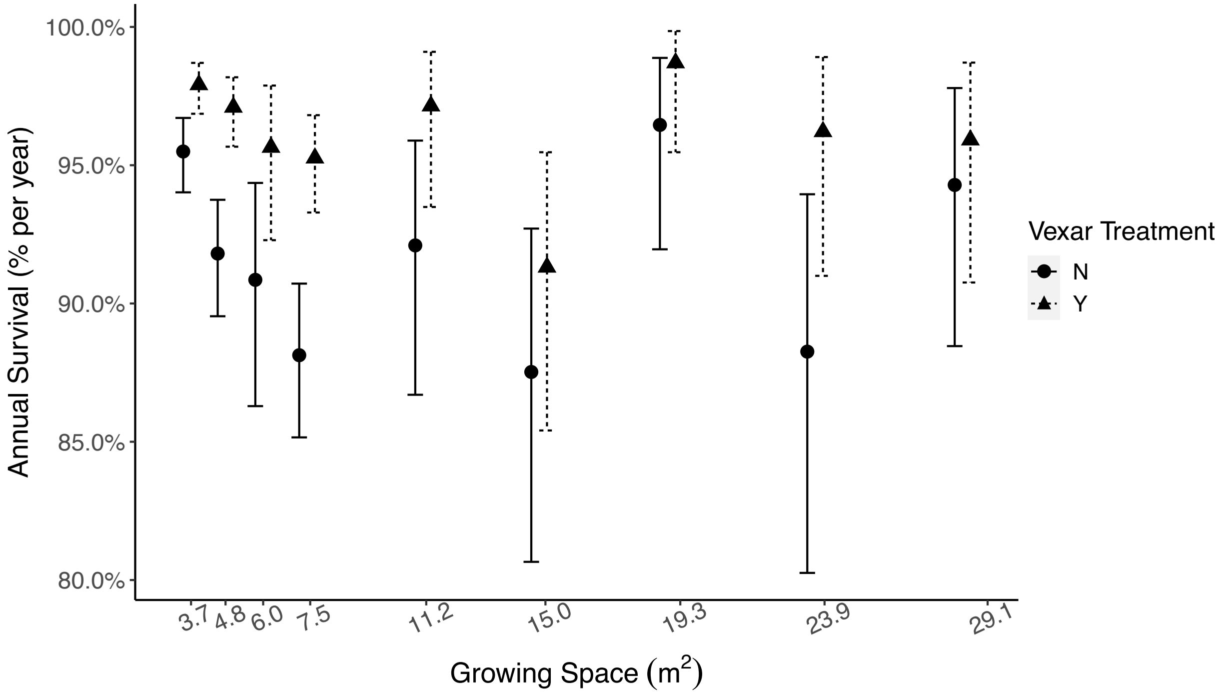

Figure 3. Survival of incense-cedar seedlings from 2000-2003 in spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Error bars represent profile likelihood confidence intervals.

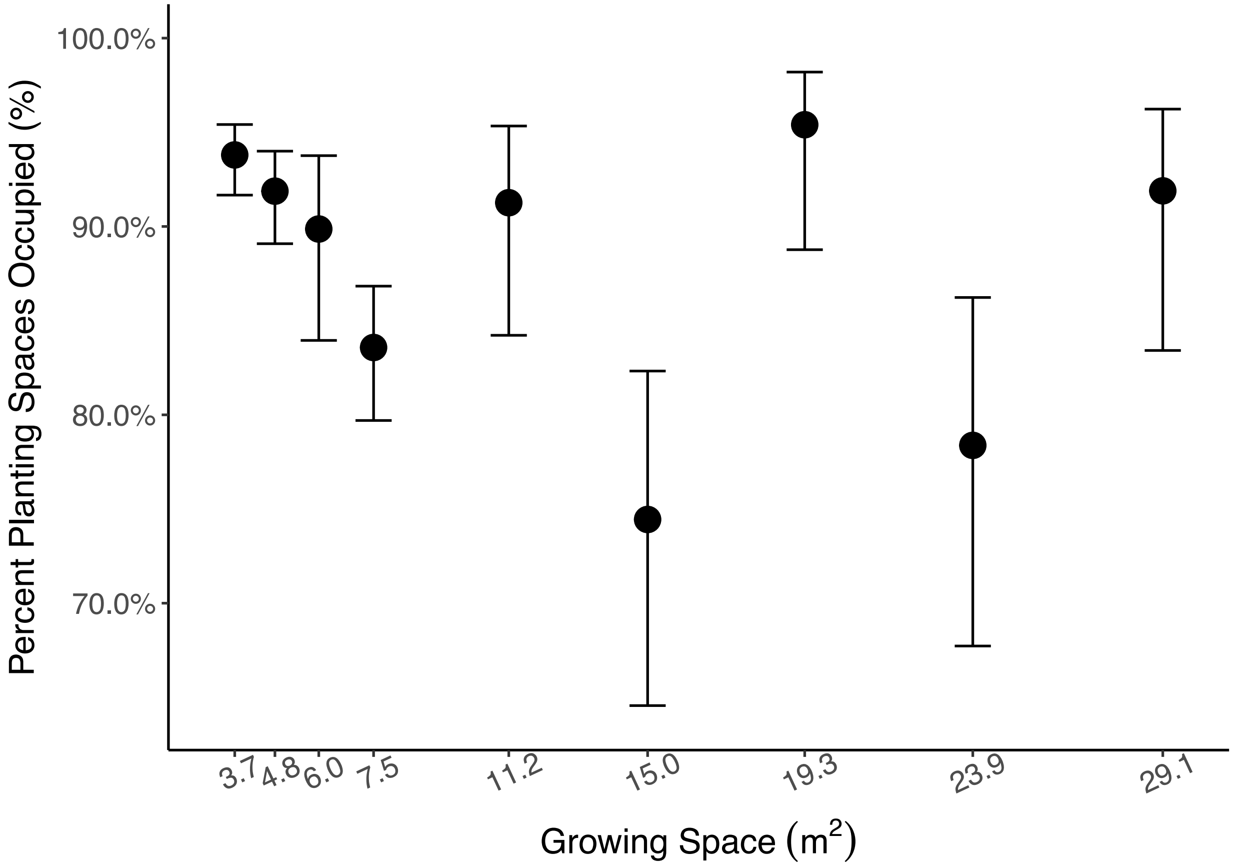

Figure 4. Occupancy of planting spots in 2018 in an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Error bars represent 95% confidence intervals.

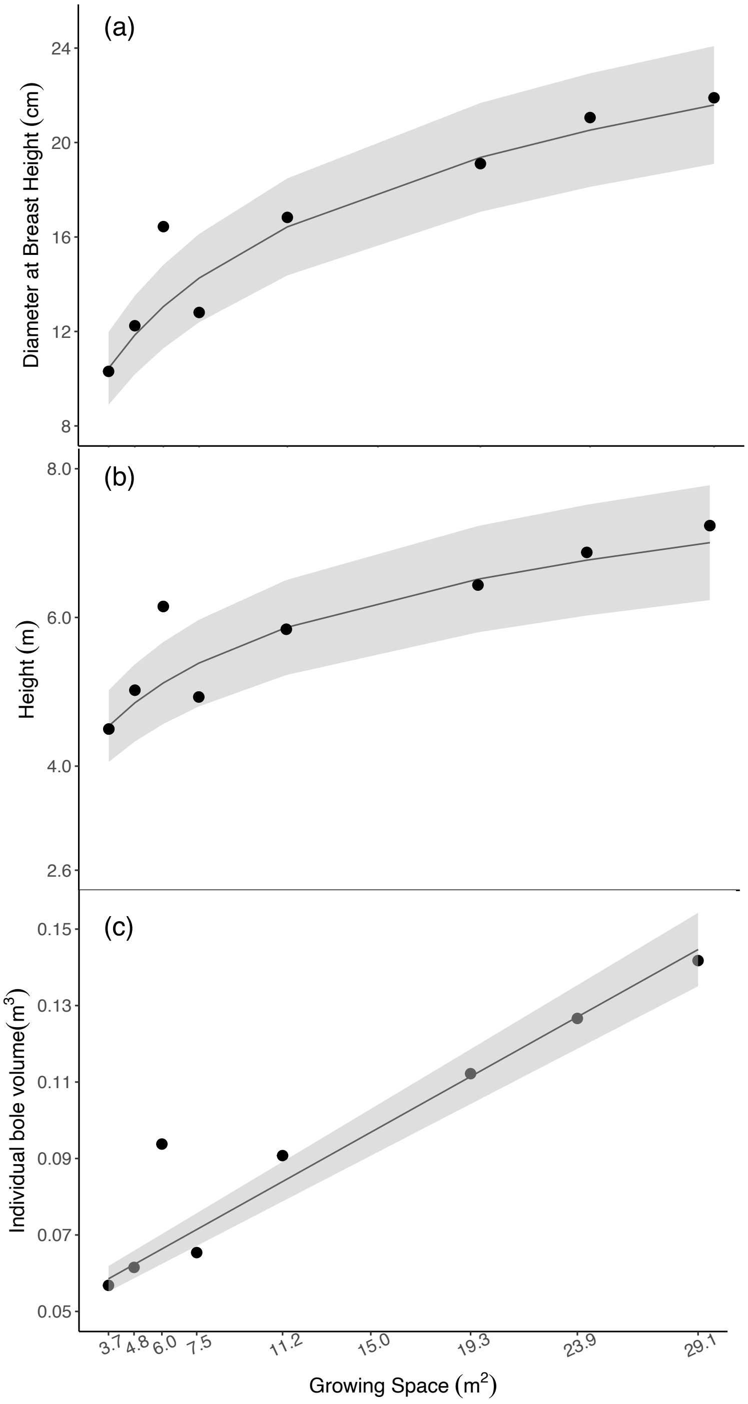

Figure 5. Individual tree characteristics after 18 years in an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. (a) Diameter at breast height (DBH; cm), height (m), and (c) individual bole volume (m3) for incense-cedar across all spacing treatments. The 15.0 m2 spacing treatment was excluded because of low sample size left in the treatments from mortality. Shaded ribbons represent 95% confidence interval for the best fit model. The y-axis reflects a 3x difference in magnitude for each variable.

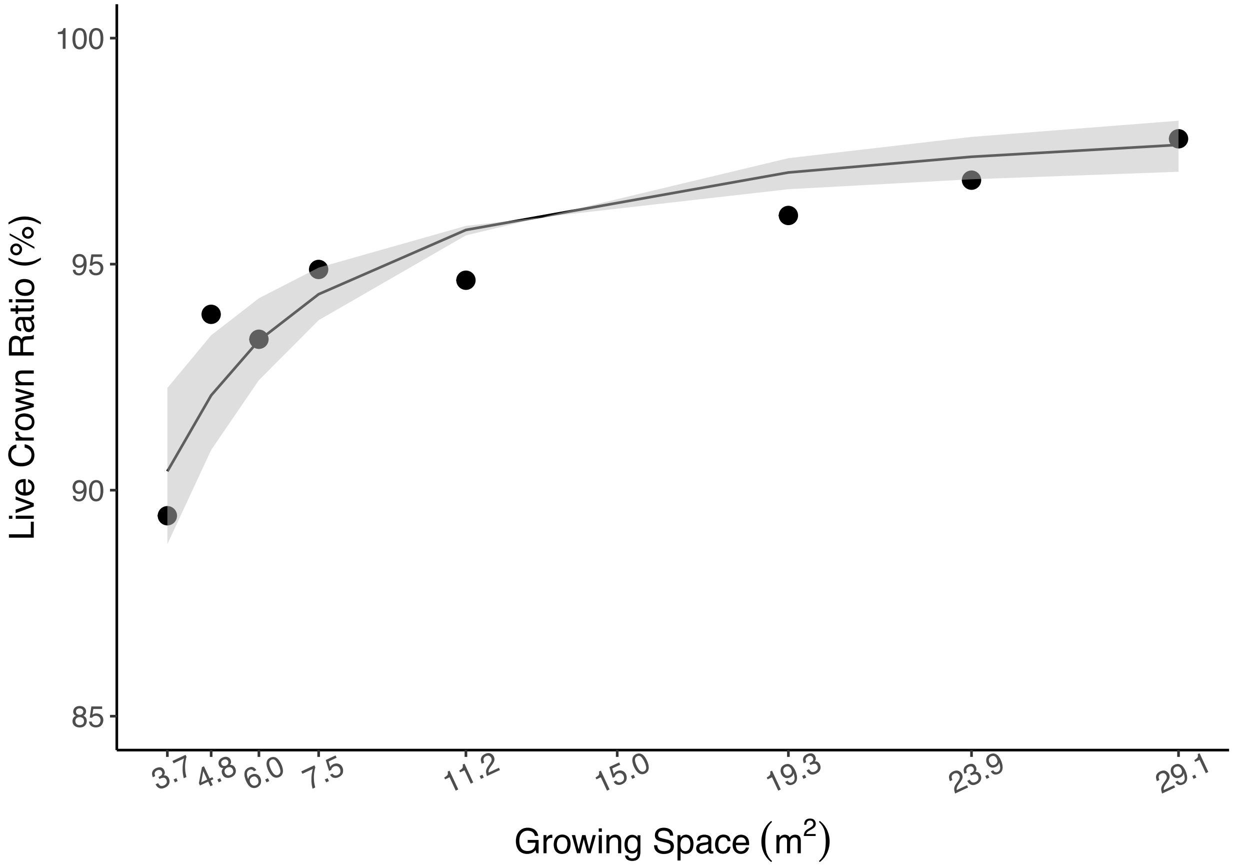

Figure 6. Live crown ratio in an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. The 15.0 m2 spacing treatment was excluded because of low sample size left in the treatments from mortality. Shaded ribbons represent 95% confidence interval for the best fit model.

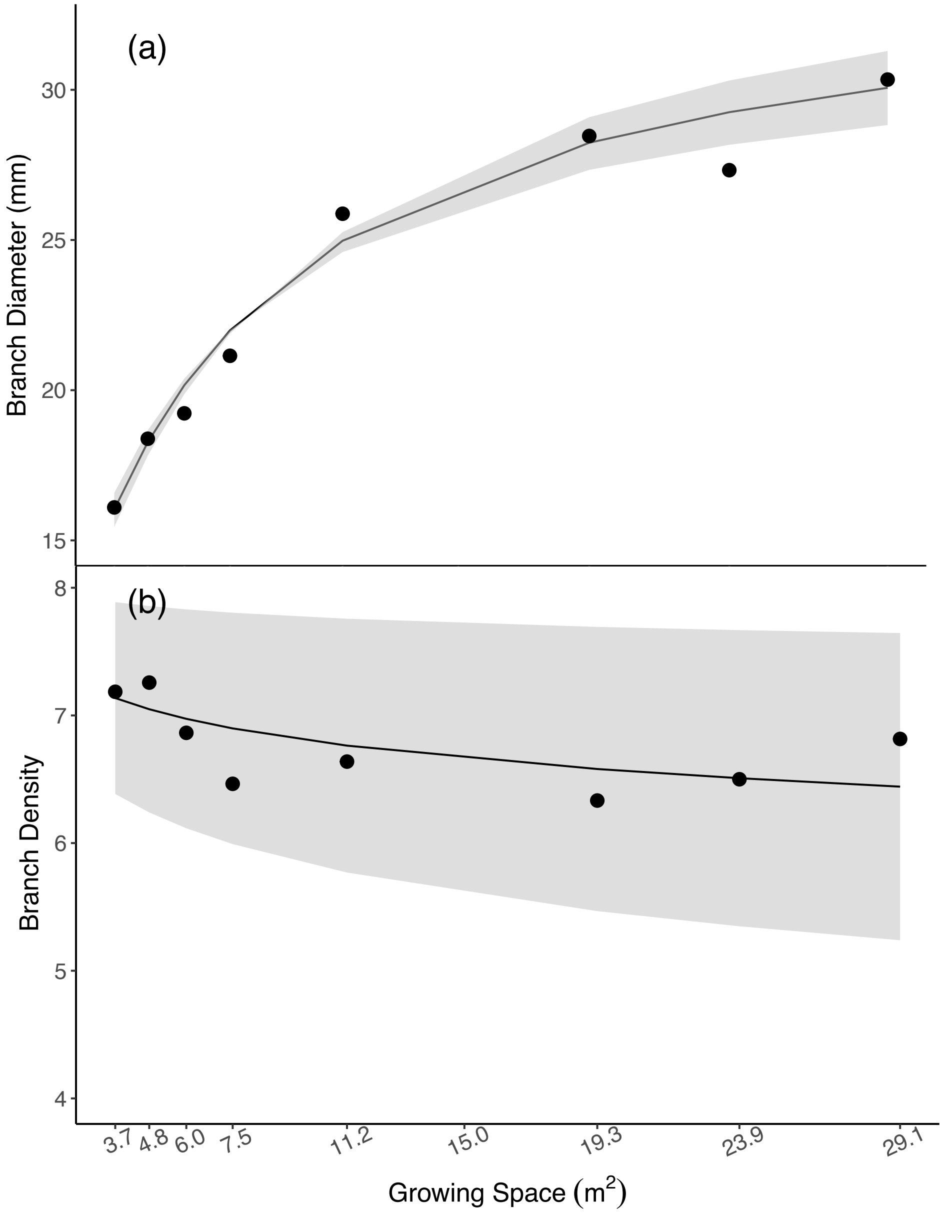

Figure 7. (a) Branch diameter (mm) and (b) density for a subsample of incense-cedar trees (n=384) in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. The 15.0 m2 spacing treatment was excluded because of low sample size left in the treatments from mortality. Shaded ribbons represent 95% confidence interval for the best fit model.

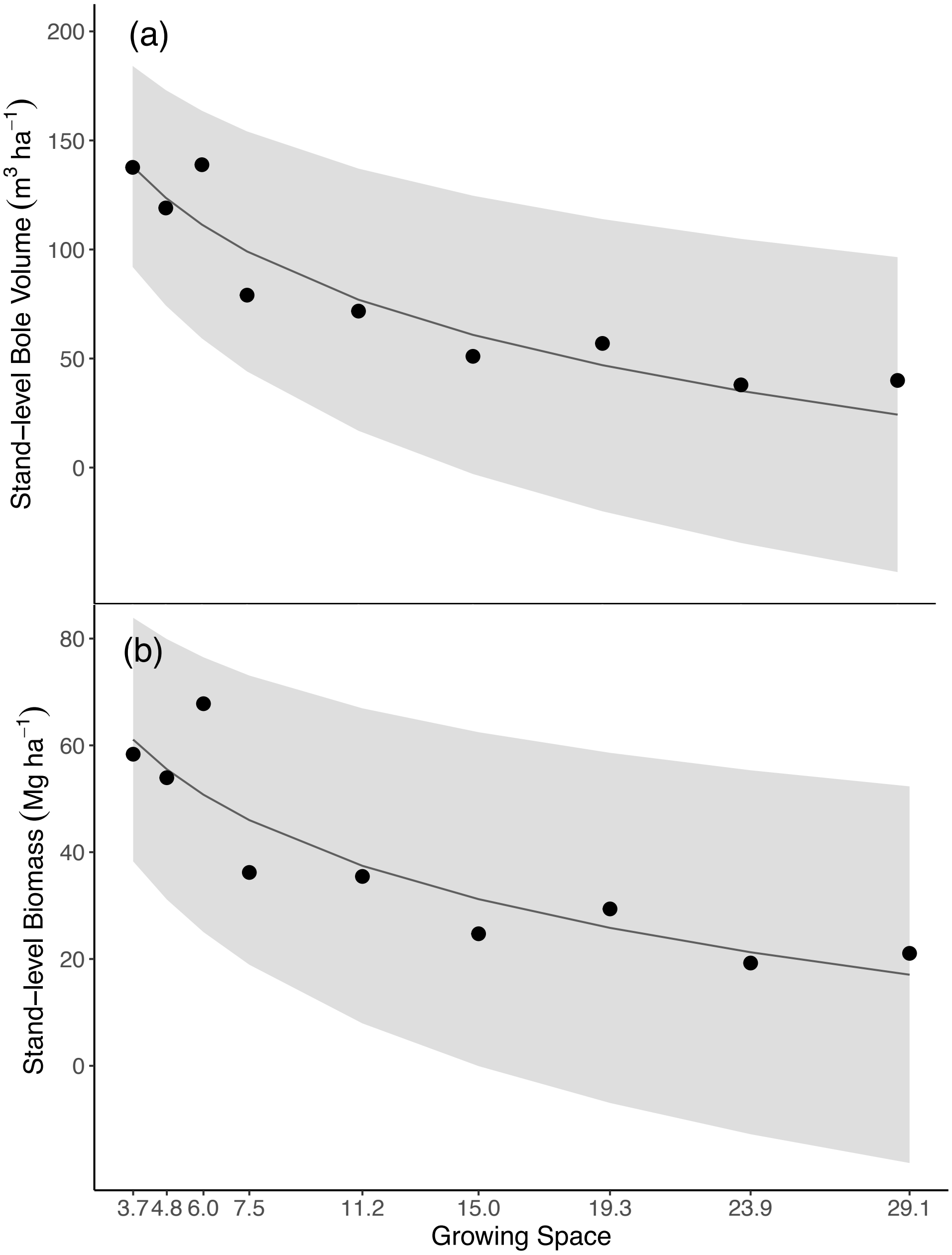

Figure 8. (a) Stand-level volume (m3 ha-1) and (b) biomass (Mg ha-1) production in an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Shaded ribbons represent 95% confidence interval for the best fit model.

TRANSITION FROM CHAPTER 2 TO CHAPTER 3

Incense-cedar, a drought resistant species native to the Sierra Nevada mixed conifer forest that is host to few lethal pests and pathogens, has shown promise as a species adapted to future climates and disturbances. One adaptive management strategy is to manage for tree species that can provide similar services that maladapted species provide but are more likely to persist under future climate conditions. Quantifying the survival and growth of climate resilient species is important to define its place in adaptive silvicultural prescriptions. In Chapter 2, I investigated the young stand dynamics of incense-cedar to inform early stand management decisions. I found that herbivore protection had a strong influence on seedling survival. After 18 years, the crowns of incense-cedar had not yet lifted, posing a potential fire risk that might be mitigated with pruning. However, unlike giant sequoia studied in Chapter 1, incense-cedar exhibited the expected tradeoff between individual tree size and stand production. While wider spacings produced larger individuals, narrower spacings produced higher levels of stand-level bole volume.

Managed forests sustain both individual species and future forest cover. 1t is essential to identify species that are threatened by increased disturbance as well as species that are resistant to disturbance to guide future planting efforts. Likewise, developing and testing innovative silvicultural treatments to increase stand heterogeneity and resilience of forests is important for planning future management decisions. In Chapter 3, I investigate the effects of an operational femelschlag harvest on the growth dynamics of mixed conifer species planted along group selection edges. This silvicultural treatment was designed to emulate the low to mixed severity fires that had historically maintained Sierra Nevada mixed conifer forests. For Chapter 3, I consider the expanded gap experiment in two phases: 1) original group selection harvest through 12 growing seasons and 2) post femelschlag harvest through the 21st growing season. Within the original groups, both giant sequoia and incense-cedar were planted along with other associated conifer species. The results from this study provide information about the growth of incense-cedar and giant sequoia in a managed mixed species, multi-aged stand and may be used to inform future gap-based silvicultural treatments in mixed conifer forests.

CHAPTER 3

Growth dynamics of mixed-conifer tree species inform gap-based silviculture

ABSTRACT

Emulating natural disturbance patterns through gap-based silviculture is one approach to restoring structural heterogeneity and maintaining species diversity in Sierra Nevada mixed conifer forests. Examples of gap-based approaches include group selection and expanding gap or femelschlag harvests. This study investigates the growth dynamics of young edge trees in an expanding gap system in two phases: 1) initial group openings through 12 growing season and 2) post gap expansion through the 21st growing season. We used edge tree height and diameter data for species planted in groups of increasing sizes (0.1-1 ha) through 21 growing seasons. After the 12th growing season, we found that edge trees of all species were considerably smaller than interior trees, indicating a need for release. Of edge trees, ponderosa pine were the tallest species, followed by giant sequoia, Douglas-fir, sugar pine, incense-cedar and white fir. Based on hemispherical photograph analysis, we found light availability increased after the femelschlag harvest during the 13th growing season, though effects were much more pronounced along southern edges that were released. Light availability along northern edges that were released was similar to the unreleased northern edges. After release, trees growing along northern edges exhibited taller heights than those growing along southern released edges, despite the difference in initial light availability increase. Incense-cedar did not exhibit difference in height among gap edge position or release. Our results provide insight for implementing natural disturbance based silvicultural designs in the Sierran mixed-conifer forest.

INTRODUCTION

Managing forests to emulate natural disturbance patterns has become an increasingly common management approach aimed to promote structural heterogeneity and increase forest resilience (Long 2009; Puettmann 2011; Lafond et al. 2013; Hessburg et al. 2019). Gap-based silviculture is one example of a multi-cohort method to achieve these objectives (Kern et al. 2017; York et al. 2021). Gap-based systems involve removing trees either as individuals or in groups for the purpose of regeneration. During an initial entry, gap openings are situated within an intact mature forest matrix with further scheduling of harvests guided by the natural disturbance regime. Examples of such silvicultural systems include group selection and irregular expanding group shelterwood, or the German “femelschlag” approach. The group selection system creates distinct canopy gaps by removing multiple trees during each harvest entry while a femelschlag harvest regenerates new cohorts by gradually expanding the gaps created in the first cutting cycle until the entire stand is regenerated (Raymond et al. 2009). The femelschlag system reduces potential damage to young trees because harvesting equipment does not make repeat trips into areas that are regenerated, thereby protecting regeneration for long periods. This system promotes the heterogeneous structure of the group selection system while protecting regenerating areas in the stand and releasing trees that regenerated in previously made groups. Both group selection and femelschlag approaches are designed to balance timber production with ecological sustainability and are potential methods for emulating natural disturbances in different regions (Arseneault et al. 2011; McNab and Oprean 2021). These systems may contribute to multiple objectives, such as regenerating desired tree species (Leak and Filip 1977; Coates 2000), maintaining a diverse and structurally complex forest (Raymond et al. 2018; Rogers et al. 2020), and supporting wildlife habitat (Homyack and Haas 2009) while also producing merchantable timber.

One potential concern with a gap-based approach is the reduced productivity resulting from edges produced by small canopy openings. We define the edge of a gap as the area along the boundary of the harvested opening where there is the potential for competitive interaction between the young trees in the gap and the mature trees in the matrix. Trees planted along edges of gap openings have been shown to exhibit slower growth than trees planted closer to the interior where resource availability is higher (Gray and Spies 1996; McNab and Oprean 2021; York et al. 2003). One option to mitigate these edge effects is a femelschlag harvest to release the trees planted along the gap boundary. Such an operation is expected to provide increased growing space to trees planted within original gaps and may be easier to implement than additional distinct gaps because of existing infrastructure (i.e. skid trails and landings) from the original gap formation.

Throughout the past century, fire suppression in the Sierra Nevada mixed-conifer forests has created high-density, homogenous forests structures more heavily dominated by shade tolerant species such as white fir and incense-cedar (Safford and Stevens 2013; Dolanc et al. 2014). In this forest type, a gap-based silviculture approach is one method to restore heterogenous forest structures and increase ecosystem resilience (Seidl et al. 2014). Prior to fire suppression practiced throughout the 1900s, the mixed-conifer forests were described as multi-aged structures characterized by patches of trees interspersed among a relatively open, fire-maintained landscape (Safford and Stevens 2013). The low to mixed-severity fire regime that had maintained Sierran forests was characterized by a high frequency of small gaps and few large gaps (Collins and Stephens 2010). Gap sizes ranging from 0.5-1.0 ha have been shown to be large enough to match the productivity of even-aged plantations while also increasing the coarse scale heterogeneity once maintained by frequent fire (York and Battles 2008). When restoring or emulating a natural disturbance regime in the Sierra Nevada mixed conifer forest, pyrosilviculture, incorporating prescribed fires into stand management, is essential and gap-based silvicultural designs may create stand structures that are better able to accommodate future prescribed fires (York et al. 2021). To effectively implement gap-based silviculture, it is essential to understand not only the impacts of initial group openings, but also the effects of subsequent group openings and their relation to decisions made in previous cutting cycles.

The goal of this study is to understand the impacts of expanding gap silviculture on the growth dynamics of trees in the Sierran mixed conifer forest. Specifically, we asked the following questions:

1) How did gap size affect tree growth by species after 12 years and did this differ between gap edge and gap center?

   After 12 years, we expected that gap size would have an impact on the growth of planted trees and that the size of trees would differ between gap edge and gap center. Prior to gap expansion, we anticipated shade intolerant species would perform better in gap centers.

2) How did the light environment change on edges after expansion?

   We hypothesized that the expansion would significantly increase the available light for edge trees. Given the sun path in temperate regions of the northern hemisphere, the effect on the light environment is expected to be less for expansions on the north side of the gap.

3) What was the effect of the expansion on the growth of edge trees within the gap?

   Tree growth should differ between released edges and edges that were not released. We anticipated a weaker response of trees growing along northern released edges compared to southern released edges. We also expected shade intolerants to have a stronger response than the shade tolerant species because of their sensitivity to light availability.

METHODS

Study area

Blodgett Forest Research Station (BFRS) is a 1,763 ha research forest in the central Sierra Nevada, California, USA (38°52N 120°40W). The elevation of the study site is approximately 1220-1310 m. The regional climate is Mediterranean, characterized by a summer drought period and mild winters. Most precipitation occurs during the winter and spring, averaging 1,450 mm annually. Average summer temperatures range between 14° and 27° C while average winter temperatures are between 0° - 9° C (BFRS data, https://forests.berkeley.edu/forests/blodgett). The soil is developed from granodiorite parent material and is highly productive for the region. Between 1750 and 1900, median composite fire intervals at the 9–15 ha spatial scale were 4.7 years with a fire interval range of 4–28 years (Stephens and Collins 2004). BFRS is representative of the productive mixed-conifer forest occurring between 1,200–1,700 m in elevation on the western Sierra Nevada slope. Currently, trees at BFRS are able to reach 27-34 m in height in 50 years (BFRS data, https://forests.berkeley.edu/forests/blodgett). Similar to much of the Sierra Nevada range (Beesley 1996), the site was clearfell harvested in the early 1900s and allowed to naturally regenerate from trees remaining on the site. Dominant native tree species at BFRS include Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco var. *menziesii*), incense-cedar (*Calocedrus decurrens* Torr.), ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.), sugar pine (*P. lambertiana* Dougl.), white fir (*Abies concolor* [Gord. & Glend.] Lindl. Ex Hildebr.) and California black oak (*Quercus kelloggii* Newb.). Managers at BFRS have also planted giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz), a species whose range once included BFRS, though not currently naturally occurring on the site (Harvey 1986).

Experimental Design

The expanding gap experiment at BFRS is divided into two phases: 1) original gap implementation via group selection, and 2) first gap expansion or femelschlag harvest. The original group selection harvest was designed to study the influence of opening size on seedling growth within the openings. This first phase included a regeneration treatment and intermediate treatments to control both non-tree and inter-tree competition. During the summer of 1996, three replicates of four circular opening sizes (0.1, 0.3, 0.6, 1.0 ha) were harvested. These opening sizes corresponded to group diameter:tree height ratios of 1, 1.8, 2.6, and 3.2. The groups occupied 15% of the 34-ha study area that was situated on a 10–25% north-facing slope. Within each opening, an even mixture of six conifer species were planted in rows with a wagon wheel design (Figure 1). Eight “spokes” extended from drip lines along group edges into the group center along each cardinal and intercardinal direct. Douglas-fir, incense-cedar, white fir, and ponderosa pine were planted from bare root stock. Sugar pine and giant sequoia were from container stock. Seedling sizes were similar across all species at the time of planting. During the spring of 2000, competing vegetation was controlled using herbicide and during summer 2003 natural regeneration occurring in between planting rows was culled. After the 7th growing season, trees were thinned from an original planting spacing of 3 m to a spacing of 4.5 m to reduce inter-tree competition. Additional information about the implementation and results from the first phase of the group selection experiment is described in York et al., (2003, 2004, 2007).

The second phase of this experiment included an expanding gap or femelschlag regeneration treatment during the summer of 2012. Surrounding ten of the original groups, an additional gap was created to “release” the edge trees along one side of the original group (Figure 1). These expansions ranged between 0.35–0.75 ha and occupied 11% of the 34 ha study area. Unlike original group openings, the location of these expansions was determined by the existing group openings and features in the intact matrix. The shape and size of the expansion varied but were designed to border an equal number of groups on the north edge and south edge, releasing the edge trees planted in the first harvest entry. The implementation of these expansions is an example of an operational femelschlag in the Sierra Nevada mixed conifer forest.

Field Measurements

For our analysis, we focused only on the edge trees of the original groups as these trees were competing for more limited resources during the first phase and are expected to show the greatest response to release with a harvest. Edge trees are defined as those planted in the three outermost rows of the original groups (9 m inward from the drip line). In the 3rd, 5th, 7th, and 12th growing seasons, all edge trees were measured for height (m). Most recent measurements were used to assess the effect of original group size on the growth of edge trees.

During summer 2012, hemispherical photographs were taken at the end of planting rows, where were directly under the driplines of the surrounding mature trees. Planting rows were “released” if the expansion was adjacent to the spoke and “reference” if the matrix remained adjacent to the spoke (Figure 1). The released and reference categories were considered the treatment during the second phase of the expanding gap experiment. Photographs were taken immediately pre and post femelschlag harvest to capture the change in light availability after the harvest. Film photos were taken 1 m above the ground with a Nikon 35-mm camera and a Nikkor fish eye lens (8 mm f /2.8). To minimize the effects of direct lighting, all photos were taken near dawn or dusk when isotropic skylight conditions prevailed. 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).

In the 15th and 21st growing seasons, we measured the height and diameter at breast height (DBH; cm; 1.37 m above ground) of edge trees. To describe the location of each tree within a group, we calculated a “northness” index using the equation:

$$Northness = \cos(asp)$$

where *asp* is the azimuth (radians) of the corresponding planting row. To assess the effect of gap expansion on edge trees, we used height (m) and DBH increment between the 15th and 21st growing seasons and absolute height and DBH during the 21st growing season.

Data Analysis

During the first phase of the group selection experiment, groups served as the experimental unit (n=12). To determine the effect of group size on tree size after 12 years of growth after the initial group formation, we developed a set of candidate models and implemented an information theoretic approach to compare model performance. Our set of candidate models included a linear model, a power law model, a quadratic model, and a saturating model using the Michelis-Menten equation. The linear and power law models indicated that height increased with increasing group size. The quadratic and saturating models indicated that height did not steadily increase with group size and that maximum tree heights were achieved within the 0.1–1 ha group size range. To account for a small sample size, we used a modified Akaike's information criterion (AICc) to rank model performance. In addition, we calculated the difference in AICc values (ΔAICc) and the AIC weight (w_i). Models with ΔAICc values of less than two are considered to have less support (Burnham and Anderson 2002). To describe the general trend (i.e. increasing height growth with group size or slowing height growth with group size), we summed the w_i values of the linear and power models and the quadratic and saturating models.

To determine the effect of release treatment on light conditions, we used an analysis of covariance (ANCOVA) model. Pre-treatment light condition of each photograph location was included as the covariate and post treatment %TTR was the response variable. We included the northness of the corresponding row and treatment (reference v. released) as independent variables.

For the second phase of the expanding gap experiment (i.e., after the femelschlag harvest), individual edge trees receiving either "released" or "reference" treatments served as the experimental unit (n=643). Each edge tree was assigned a northness value based on its location within the gap. To assess the femelschlag harvest, we implemented an ANCOVA approach using the height in the 12th growing season (last measurement pre-expansion) as a covariate. The height and DBH increment between the 15th and 21st growing seasons and the 21st growing season height and DBH were used as response variables in two separate models. Independent variables included species, northness, treatment (i.e. reference or released), and original group size. All analyses were conducted in R (R Core Team 2021).

RESULTS

After 12 growing seasons, trees planted in the center of groups were 1.9 times taller than trees planted along group edges (within 9 m of mature trees; Figure 2). In the center of groups, giant sequoia were the tallest trees, followed by ponderosa pine, Douglas-fir, incense-cedar, sugar pine, and white fir (Figure 2b). In contrast, ponderosa pine were the tallest trees along group edges, followed by giant sequoia, Douglas-fir, sugar pine, incense-cedar, and white fir (Figure 2c).

For all species of trees growing along group edges, increasing models of tree growth (linear and power) outweighed models indicating slowed growth (quadratic and saturating; Table 1). Sugar pine exhibited the narrowest margin of weight between increasing and slowing growth models. A linear fit was the best model ranking for both Douglas-fir, giant sequoia, and incense-cedar (Figure 3). However, the linear fit was only marginally better than the power law model for giant sequoia and incense-cedar (Table S1). A power law fit was the best model ranking for both ponderosa pine and white fir, though support was not substantially better than the linear fit for either species (Figure 3). The asymptotic model was the best fit model for sugar pine, though support was not substantially better than the power law fit or linear fit (Figure 3, Table S1).

Treatments significantly increased the amount of light available on the group edges but the impact diminished substantially for releases on the north edges (Figure 4, Table S2). Across all positions within a group, mean %TTR for reference edges was 37% and mean of 60% for released edges (Figure 4). However, this treatment effect was driven by expansions along the southern edge. Mean %TTR for reference edges (not harvested) on the south side of gaps was 19%; mean %TTR for southern released edges was 63%, a more than threefold increase in light availability. In contrast there was no effect of the release on light availability along the northern border: reference edges had 52 TTR and released edges had 48% TTR. However, it is important to note the overall higher light levels (~50% TTR in all cases) along the northern edge.

For height increment between the 15th and 21st growing season, there was a significant effect of species ($F_{5,\,219} = 9.8$, $p < 0.001$), treatment ($F_{1,\,219} = 41.0$, $p < 0.001$), and northness ($F_{1,\,219} = 33.2$, $p < 0.001$) on height growth when controlling for pre-treatment tree height (Figure 5, Table S3). In addition, there were complex interactions among the independent variables (Figure S1, S5). Across all species and northness values, edge trees grew 2.6 m in height along reference edges and 3.4 m in height along the released edges between the 15th and 21st growing seasons. Ponderosa pine exhibited the greatest difference in height increment between north and south locations along released edges, with southern released edge height increments measuring 2.6 times taller than the height increment of trees along northern released edges (Figure S1). The height increment of incense-cedar trees along southern released edges was 0.96 times the height increment of those along northern released edges (Figure S1). Height increment across all species along southern released edges was 1.4 times larger than height increment along southern reference edges (Figure 5c).

For diameter increment between the 15th and 21st growing seasons, we found a significant effect of species ($F_{5,\,172} = 7.2$, $p <0.001$) and treatment ($F_{1,\,172} = 132.2$, $p<0.001$) and complex interactions among independent variables after controlling for pre-treatment diameter (Figure 5, S2, S6, Table S4). Douglas-fir diameter increment along released edges was only 1.3 times larger than the diameter increment of Douglas-fir along reference edges, whereas ponderosa pine diameter increment along released edges was 2.0 times larger than that of reference ponderosa pine trees (Figure 5b). Diameter increment along southern released edges was 2.0 times larger than diameter increment along southern reference edges. The diameter increment along northern released edges was 1.4 times larger than northern reference edges (Figure 5d).

After 21 growing seasons, including the seven years after the gap expansion, we found a significant effect of species ($F_{5,\,270} = 9.3$, $p < 0.001$), treatment ($F_{1,\,270} = 21.3$, $p = <0.001$) and northness ($F_{1,\,270} = 22.2$, $p < 0.001$) on edge tree height when controlling for pre-treatment tree height (Figure 6, S3, S7, Table S5). Original group size did not have a significant effect on tree height after 21 growing seasons and gap expansion. Across all species and treatments (reference and released), trees along the northern edges were 1.3 times taller than trees on the southern edge. White fir exhibited the greatest difference in tree height by position in gap with released edge trees along the northern edges measuring 2.0 times taller than trees along southern edges. Incense-cedar trees along northern released edges were just 0.94 times as tall as those along southern released edges (Figure S3). For trees along released edges, ponderosa pines were the tallest, followed by giant sequoia, Douglas-fir, sugar pine, white fir, and incense- cedar (Figure 7).

We found a significant effect of species ($F_{5, 218} = 10.8$, $p < 0.001$) and treatment ($F_{1, 218} = 93.7$, $p<0.001$) on diameter of edge trees after 21 growing seasons when controlling for pre-treatment height (Figure 6, Table S6). Interactions among independent variables were complex (Figure S4, S8). White fir exhibited the greatest difference in diameter between released edges and unreleased edges, whereas Douglas-fir exhibited the smallest difference (Figure 6). White fir along released edges had diameters 1.5 larger than white fir along reference edges. Among released white fir edge trees, those along northern edges had diameters 2.0 times larger than those along southern edges (Figure S4).

DISCUSSION

Effect of Original Gap Size on Edge Tree Growth

Our analysis of tree heights during the 12th growing season focuses on edge trees which have been shown to exhibit lower growth rates than trees planted in the center of groups (e.g., Coates 2000; McNab and Oprean 2021; York et al. 2003). Sipe and Bazzaz (1995) compared the response of maple (*Acer* spp.) to position within gap. The relatively shade intolerant striped maple (*A. pensylvanicum* L.) and red maple (*A. rubrum* L.) grew approximately twice as tall in group center positions than edge positions in large groups (0.03 ha), whereas the response of the shade tolerant sugar maple (*A. saccharum* L.) was not as pronounced. McNabb and Oprean (2021) found that yellow poplar (*Liriodendron tulipifera* L.) in the center of gaps were approximately twice as tall as edge trees 10 years after gap implementation and approximately 1.3 times as tall after 20 years. The results from our analysis showed a persisting edge effect on tree height, though the magnitude of this effect varied by species (Figure 3). In an earlier analysis of the Sierra Nevada group selection experiment, after four growing seasons giant sequoia exhibited the greatest difference between center and edge position among the shade intolerant and mid-tolerant species. They were approximately 1.5 times taller in the center of group openings than at the southern edge of groups and 1.2 times taller than those long the northern edge (York et al. 2003). After 12 growing seasons, giant sequoia in the center of group openings were 2.4 times taller than those growing along group edges (Figure 3). The difference in height between center and edge trees also increased for ponderosa pine and Douglas-fir from the 4th growing season to the 12th growing season. After 12 years, center trees were approximately 1.8 times taller than edge trees for both ponderosa pine and Douglas-fir (Figure 3). However, during the 4th growing season, Douglas-fir planted in the center of gaps were approximately 1.2 times taller than southern edge trees whereas ponderosa pine planted in the center of gaps were approximately 1.4 times taller than southern edge trees (York et al. 2003).

After 12 years of growth, we found increased tree heights with increased group size for edge trees across all species, a relationship that has been documented in other forest types (e.g., Coates 2000; Gray and Spies 1996). The six species planted in groups spanned a shade tolerance gradient, with white fir as the most shade tolerant species to ponderosa pine and giant sequoia as the most shade intolerant species. As groups create a sharp gradient in resource availability, we expected species of different shade tolerances to perform differently. Shade intolerant species such as giant sequoia and ponderosa pine are more sensitive to increases in light availability compared to shade tolerant species such as white fir and incense-cedar. Our analysis of the response of edge tree height to group size indicated that increasing models, such as a linear or power law relationship, were appropriate for describing all species (Table 1; Table S1). Sugar pine, a mid-tolerant species, was the only species that had a saturating model as the best fit. However, the saturating fit was only marginal better than the linear or power law relationships (Table S1). We expect that the increasing growth relationship is unique to trees along group edges and that trees grown in the center of gaps would exhibit asymptotic relationships as light availability is higher in gap centers. Based on analysis of all trees (combined center and edge) during the 7th growing season, tree height growth exhibited a saturating relationship with group size (York et al. 2007). In contrast, the increasing growth relationships of edge trees during the 12th growing season demonstrate that resources are limited in group edge environments and imply that edge tree growth would increase in larger groups (i.e. groups > 1.0 ha). Because of this, releasing the edge trees through a femelschlag harvest is a promising option for increasing tree growth.

Effect of a Femelschlag Harvest on Light Availability

Gaps produce a steep gradient in resource availability and provides a range of conditions that are suitable for multiple species (Ricklefs 1977; Canham et al. 1990; Diaci 2002). Releasing group edges through expansions may be implemented to increase growth of edge trees while regenerating a new cohort in the stand. The increased light availability will vary based on the shape and orientation of the group and the expansion, along with the composition of the surrounding matrix (Marquis 1965; Canham et al. 1990). In northern hemisphere temperate forests, light availability tends to be more limited on southern edges of group openings as shade cast by trees in the matrix limits the amount of light that is able to access trees within the group. After the femelschlag implementation, we saw a considerable increase in light availability along the released southern edges (Figure 4). However, there were no differences in light for reference and released edges for groups expanded on the northern side. Based on the latitude and position of these groups on a north facing slope, the northern edge of groups are expected to receive more light than the southern edges of groups (Canham et al. 1990; Diaci 2002). When expansions occur on the northern side of groups, removing the trees along the drip edge should increase light availability directly above edge trees within the group. However, our results did not indicate any difference between reference and released edges along northern edges. Shade cast by trees growing in the center of the gap (to the south of the north edge trees) are taller than those growing along edges (Figure 2) and may continue to influence the light availability of trees along the northern edge. In contrast, when expansions occur on the southern edge, the trees in the center of the gap would not have influence over light availability along the southern edge as they do not block direct light to the southern edge. The results from our hemispherical photograph analysis indicate that implementing gap expansions along the southern edge would be most effective for increasing light availability along original gap edges (Figure 4).

Notably, other factors may limit the response of tree growth other than light availability. Competition from shrubs (Montgomery et al. 2010), belowground water and nutrient limitations (Walters et al. 2014), and differences in microclimates may also influence tree growth. However, shrub competition has been controlled throughout the implementation of this study and is unlikely to influence our results. Unlike trees planted in the center of the original groups, competition between group edge trees and mature trees in the adjacent matrix is higher. Earlier analyses of the first phase of this experiment found that trees along the southern and northern edges of the gaps exhibited higher levels of moisture stress that trees in the center of gaps (York et al. 2003). Although soil moisture and water potential of different species were not measured in this iteration of analyses, moisture availability may influence the height response of edge trees to both original gap size and gap expansion.

Effects of Femeschlag Harvest on Edge Trees

The increase in resource availability created by the femelschlag harvests resulted in increased growth for edge trees. Height and diameter increment were both greater along released edges compared to relative edges across all northness values (Figure 5). The increased growth along the northern edge of gaps occurred despite the lack of increased light (Figure 4), indicating that the femelschlag harvest increased other resources like belowground water and nutrient availability. The difference in diameter increment between released and reference edges was greater than the difference in height increment, especially along the southern edge. This difference in response of diameter and height increment may be attributed to carbohydrate prioritization height growth over diameter growth (Hutchings and Budd 1981). If resources or growing space are limited, trees will grow in height but limit diameter growth. Large height responses to competition are expected only under high levels of competition. The relatively large response of diameter growth emphasizes the sensitivity of diameter to increased resource availability and the effect of the femelschlag.

Tree species reacted differently to being released by the gap expansions. White fir exhibited the greatest difference in mean absolute height and diameter between released and reference edges whereas Douglas-fir exhibited the smallest difference (Figure 6). Oliver and Dolph (1992) found that white fir exhibited the strongest response to release compared to all other mixed-conifer associates. Although white fir growing on reference edges exhibited similar heights and diameters across all positions (i.e. northness values), heights and diameters of white fir growing on released edges differed by position (Figure S3, S4). Northern edges that had been released had white firs that were almost twice the size of white firs growing on southern released edges (Figure 6), despite no difference in light availability between northern released edges and reference edges (Figure 4). This demonstrates the species' ability to persist in shaded conditions and respond to increases in resources other than light that may limit plant growth, such as belowground water availability and nutrients. The minimal response of Douglas-fir is unexpected. After release, Douglas-fir has been shown to respond almost as strongly as white fir (Oliver and Dolph 1992). One potential explanation for this minimal response is a "growth shock" to release, during which Douglas-fir may allocate more to root growth or foliage replacement after release (Kneeshaw et al. 2002).

Ponderosa pine is a drought adapted and shade intolerant species (Oliver and Ryker 1990). It not only exhibited the largest trees 12 growing seasons after original group implementation but responded positively to gap expansions and it is on a trajectory to maintain its dominance (Figures 6, 7). In contrast, Oliver and Dolph (1992) found that ponderosa pine had the smallest height increment after release. Based on response to gap expansion and large size of edge trees, it is clear that producing merchantable ponderosa pine is possible using gap-based silviculture, even in small original group sizes if relying on artificial regeneration (Figure S7, S8). However, initial growth of ponderosa pine lagged behind other species. One drought adaptation strategy is prioritizing root elongation over shoot growth (Kozlowski et al. 2012). The ponderosa pine seedlings in this study likely employed this strategy, leading to a delayed stem growth.

Unlike other species, incense-cedar did not exhibit a strong height or height increment response to release treatment, position along group edge, or original group size (Figure 5, 6, S3, S7). The root systems of both incense-cedar and giant sequoia support arbuscular mycorrhizae which may increase drought tolerance of the species (Augé 2001; Begum et al. 2019). Additionally, both species have sustained growth, responding to the current environmental conditions rather than the conditions present during the prior growing season, allowing them to more readily adapt to growing conditions (Gasser 1994; Harry 1987). Relative to incense-cedar, giant sequoia exhibited taller trees along northern released edges (Figure 6). However, compared to ponderosa pine and white fir, neither incense-cedar nor giant sequoia experienced a direct relationship with release and northness. The difference of shade tolerance between incense-cedar and giant sequoia may explain the difference between their responses. However, the unique characteristics of sustained growth and arbuscular mycorrhizae may explain the volatility of their results.

Conclusion

Gap-based silviculture provides a promising method to achieve multiple objectives in the Sierra Nevada mixed-conifer forest. This is the only study of an operational femelschlag harvest in the Sierra Nevada mixed-conifer forest. Our results indicate that all mixed-conifer species may be successfully grown along edges of original groups and most species will exhibit increased height and diameter growth after gap expansion. One common concern of managers is the ability to regenerate shade intolerant species using a gap-based approach. In group selection systems, there have been documented shifts towards shade tolerant species after multiple cutting cycles (Rogers et al. 2020). However, a femelschlag approach may maintain shade intolerant species in the stand through repeated release treatments. After 21 years of growth and release, it is apparent that ponderosa pine can be successfully regenerated using a femelschlag approach, even along the edges of relatively small groups. When planting trees along the edges of groups, shade tolerant white fir responded the strongest to gap expansion. Incense-cedar did not respond to position within the group or strongly to the release, but it persisted. One consideration is that the edge trees analyzed in this study are also the edge of the matrix for the new gap (Puettmann et al. 2009). Future management activities within the gap expansions may impact the growth of these edge trees. These results provide some long-term insight into the operational implementation of a femelschlag system in the Sierra Nevada.

TABLES

Table 1. Combined AICc weights of models indicating increasing growth and slowing growth of edge trees planted in experimental groups at Blodgett Forest in the central Sierra Nevada. Linear and power models were used to describe an increasing growth trend; quadratic and saturating models were used to describe a slowing growth trend.

Species	Weight of Increasing Growth Models	Weight of Slowing Growth Models
Douglas-fir	0.89	0.11
giant sequoia	0.76	0.24
incense-cedar	0.74	0.26
ponderosa pine	0.83	0.17
sugar pine	0.54	0.45
white fir	0.89	0.11

FIGURES

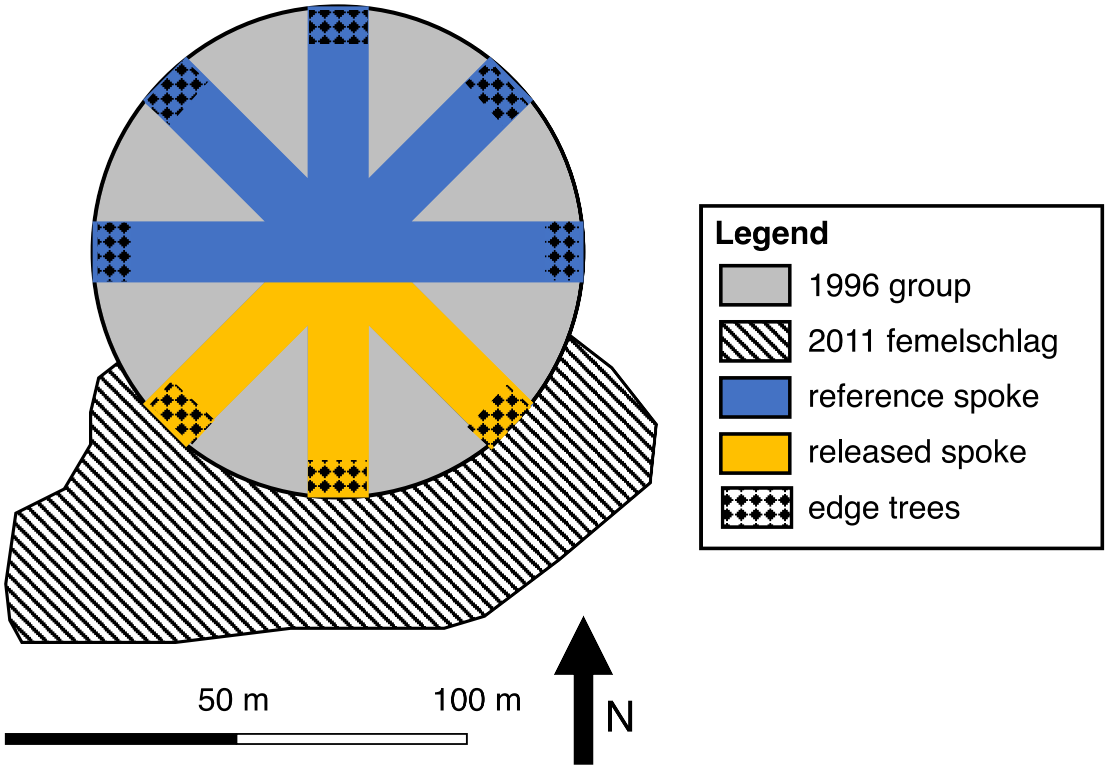

Figure 1. Map of one example of the group selection and femelschlag harvests at Blodgett Forest in the central Sierra Nevada.

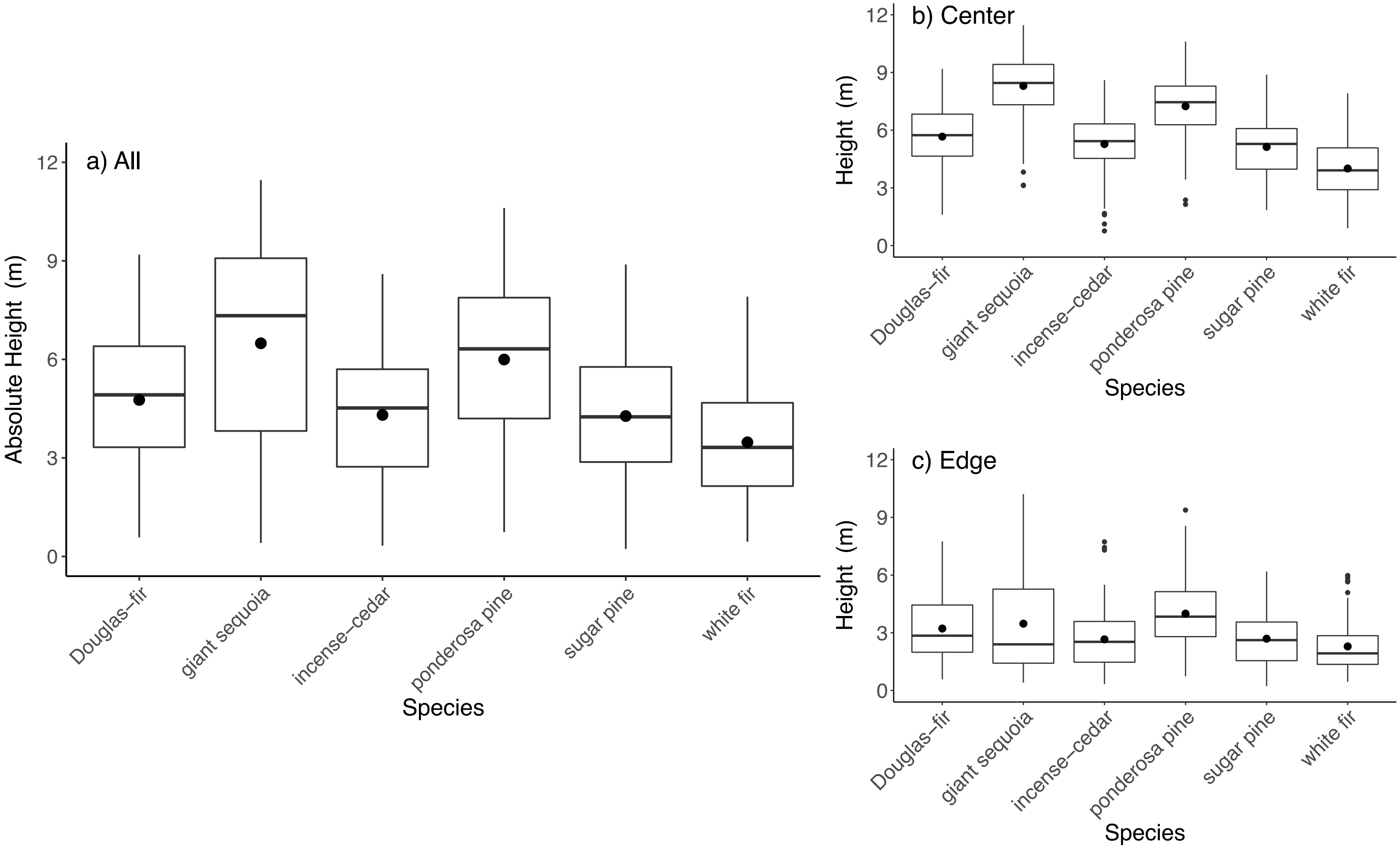

Figure 2. Mean tree height of (a) all trees within original groups, (b) trees planted in the center of groups, and (c) trees planted along edges of groups after 12 years of growth at Blodgett Forest in the central Sierra Nevada.

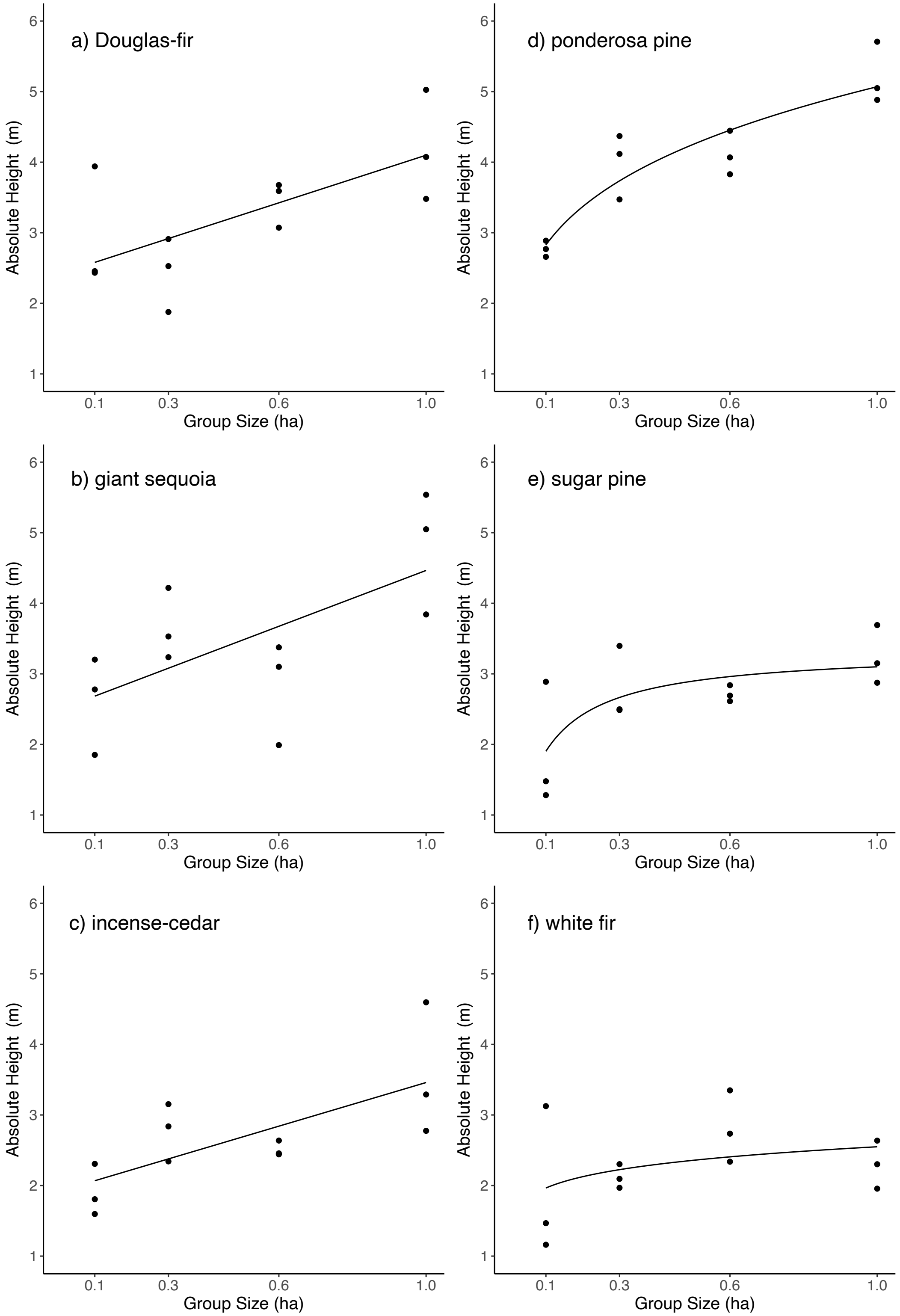

Figure 3. Edge tree height responses to gap size in experimental groups after 12 years at Blodgett Forest in the central Sierra Nevada. Predicted curves are displayed for the best model fit.

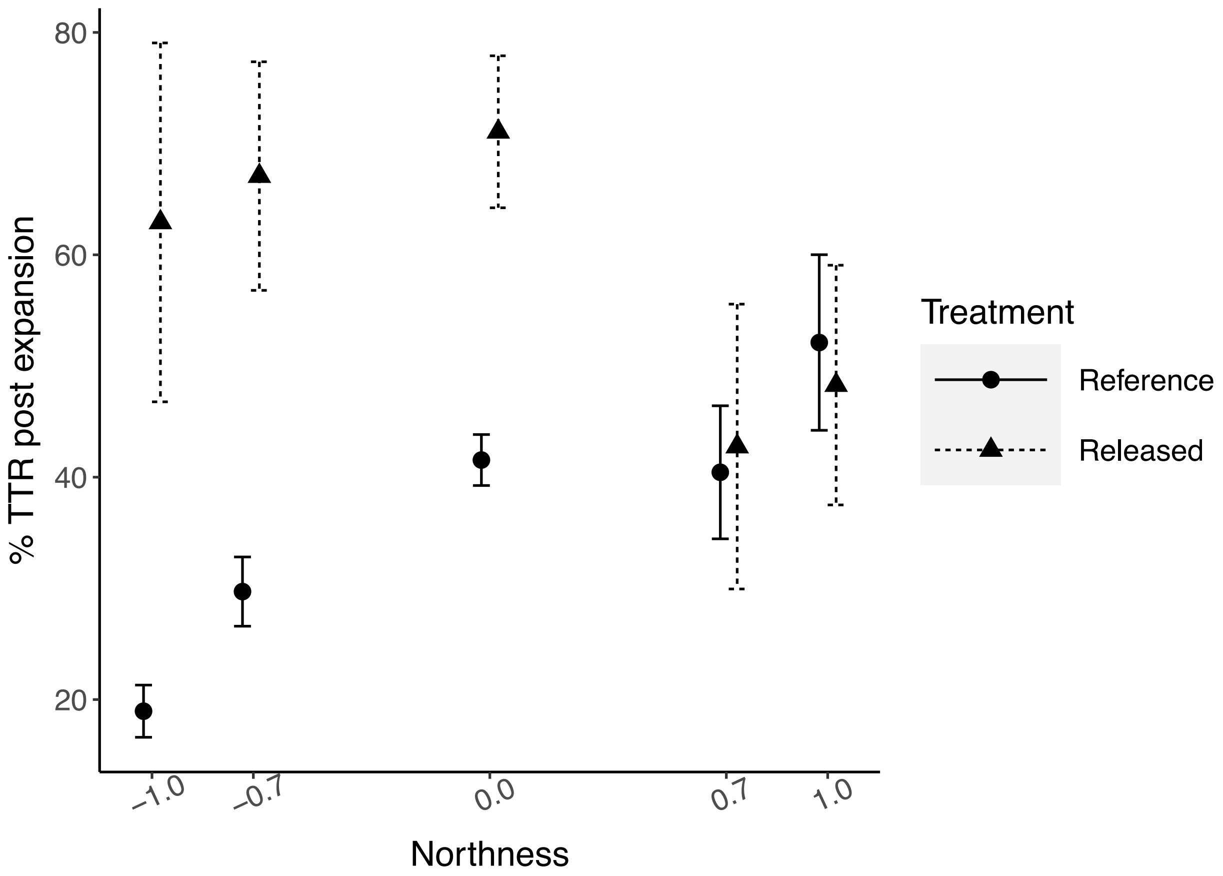

Figure 4. Percent Total Transmitted Radiation (%TRR) after experimental gap expansions at Blodgett Forest in the central Sierra Nevada. Bars represent standard error. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

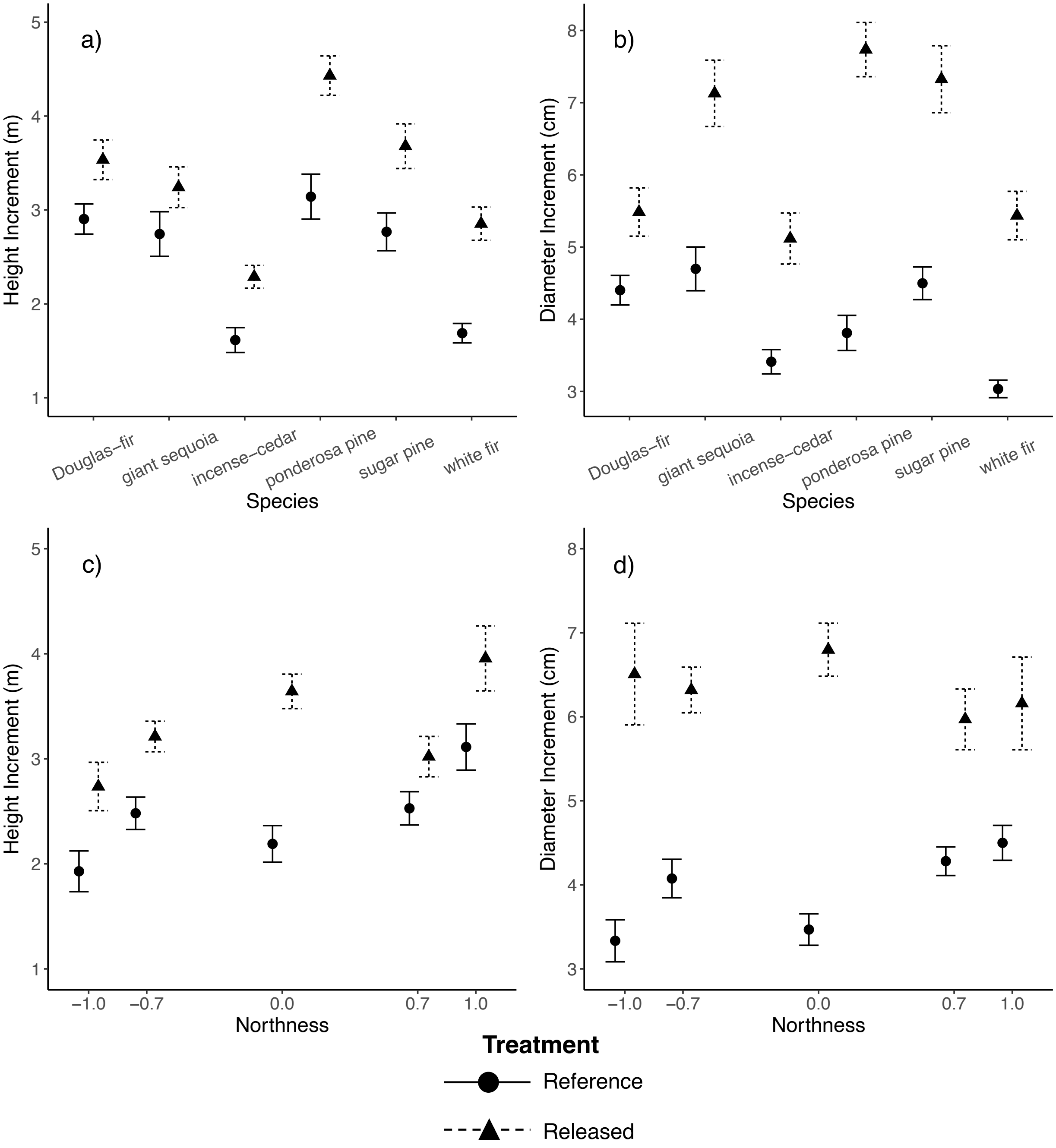

Figure 5. Mean height increment (m) and diameter increment (cm) of edge trees planted in experimental groups at Blodgett Forest between the 15th and 21st growing seasons. A femelschlag harvest was implemented in the 13th growing season. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix. Bars represent standard error.

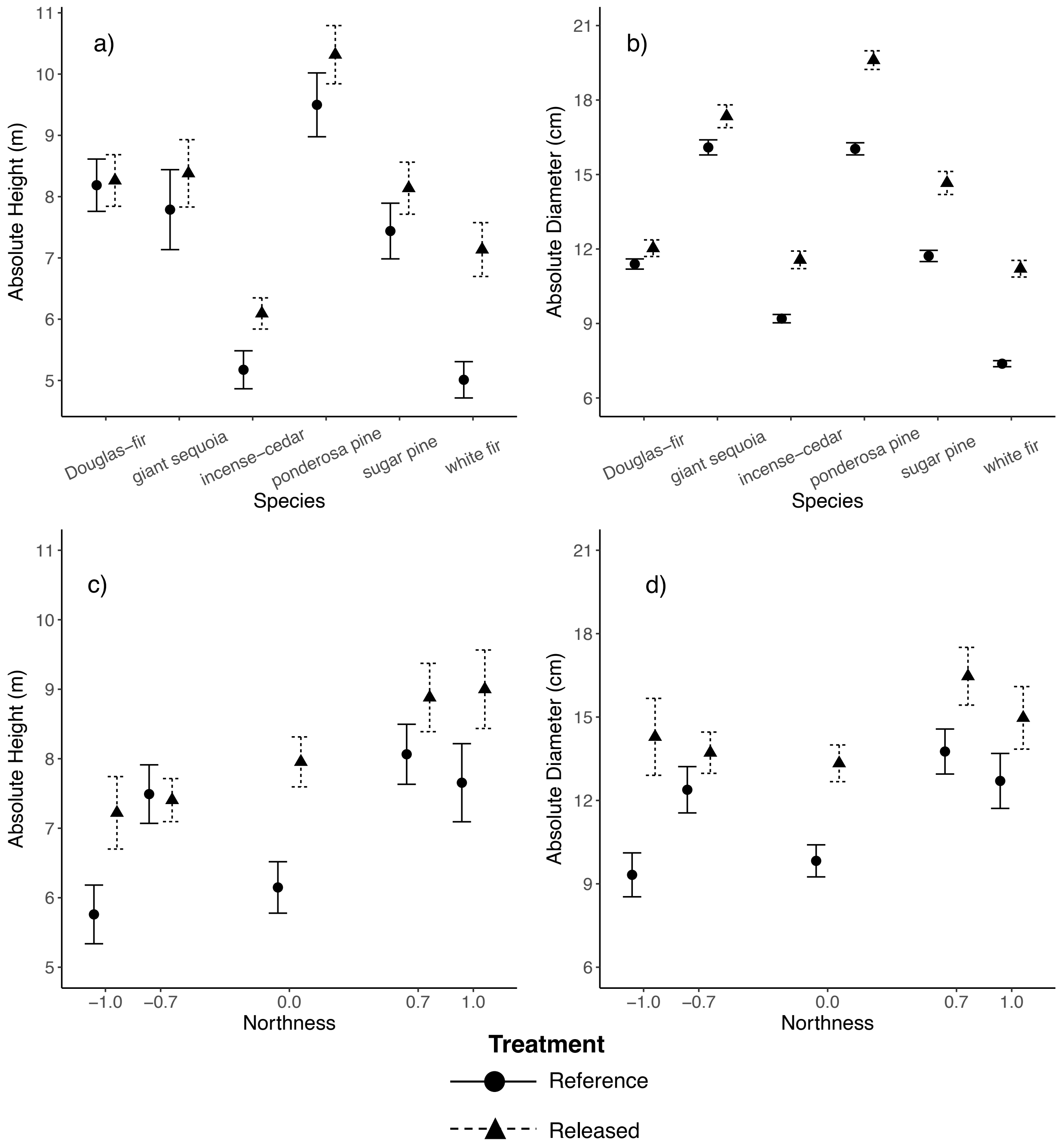

Figure 6. Mean height (m) and diameter at breast height (cm) of edge trees planted in experimental groups at Blodgett Forest after 21 growing seasons. Bars represent standard error. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

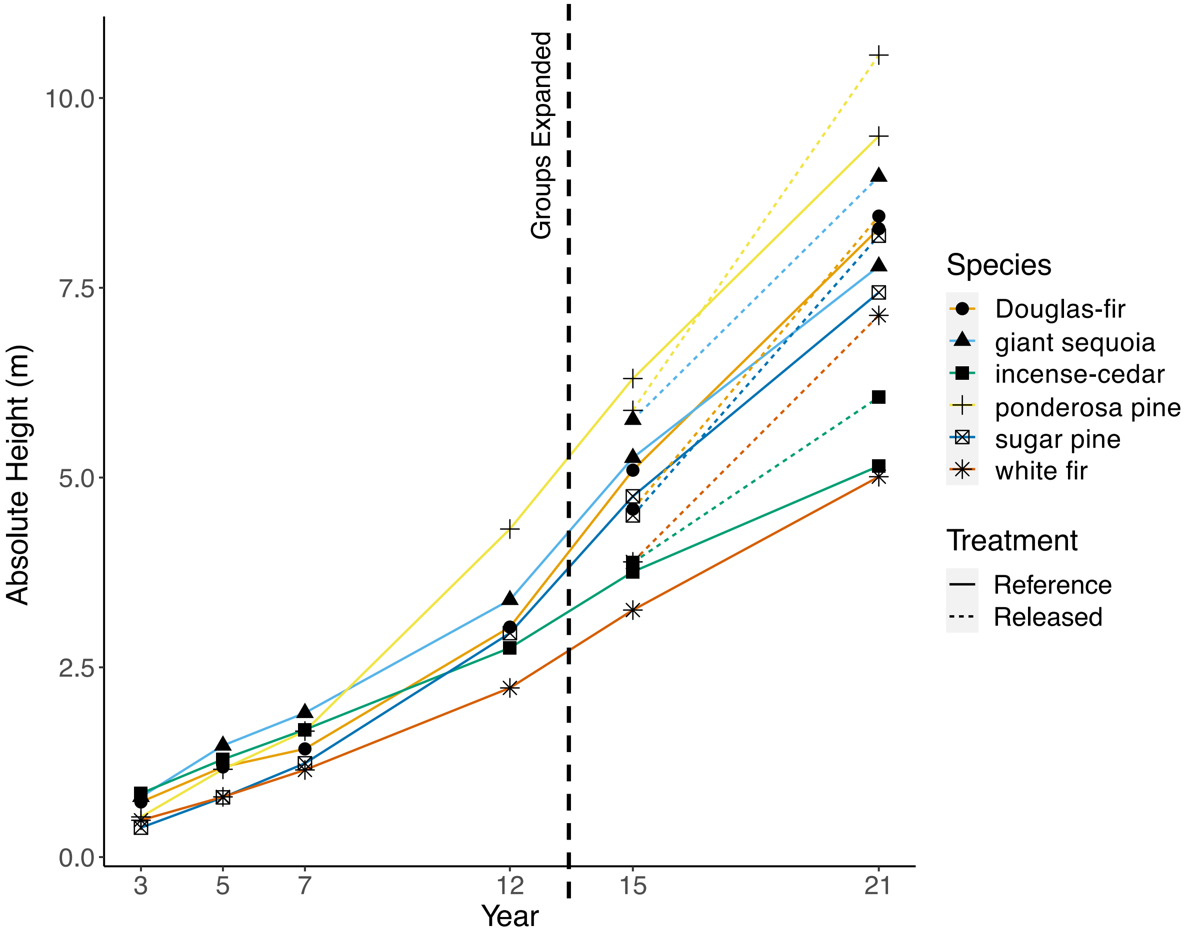

Figure 7. Mean height (m) of edge trees planted in experimental groups at Blodgett Forest in the central Sierra Nevada over 21 years. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

CONCLUSION

In this dissertation, I investigated the growth dynamics of species native to the Sierra Nevada mixed conifer forest to inform future management decisions. I used repeated measures data from both experimental density manipulations and silvicultural regeneration harvests to evaluate the long-term effects of specific management decisions. As future droughts and fires threaten western forests, conserving at-risk species, managing for climate resilient species, and implementing silvicultural treatments that increase the structural heterogeneity are effective strategies for promoting resilient future forests.

Giant sequoias are understudied compared to other commercial species of Sierra Nevada mixed conifer forests. Results from Chapter 1 provide valuable information on density-growth relationships for giant sequoia that are necessary to inform early stand management decisions. I showed that giant sequoias are able to produce merchantable timber at a young age and are also able to sequester large amount of carbon over a relatively short period of time. Incorporating giant sequoia into young, managed stands is one method for meeting a variety of management objectives while ensuring the species persists on the landscape.

Relative to other commercial species in the Sierra Nevada mixed conifer forest, there is a paucity of information on the growth and yield of incense-cedar. Incense-cedar is drought resistant and host to few lethal pests and pathogens, exhibiting promise as a climate resilient species for future forests. As climate change threatens future forest functioning, prioritizing native species that are adapted to hotter, drier climates is one approach to managing for resiliency. Chapter 2 provides an understanding of the species young stand dynamics that may be used to inform management. By analyzing early survival and growth through 18 years, I found that herbivore protection used during survival strongly influences the survival of incense-cedar. Chapter 2 results show that incense-cedar generally follows expectations for individual tree growth and stand production. The trajectory of individual incense-cedars and their stand-level production indicates the potential for both timber production and carbon sequestration.

A century of fire suppression in the Sierra Nevada has resulted in high-density, homogenous forest structures. Gap-based silviculture is a promising method to restore heterogenous forest structures, regenerate a diversity of tree species, and increase ecosystem resilience. In Chapter 3, I investigate the effects of group selection harvests and subsequent femelschlag harvests on trees planted along original group edges. The results from this study indicate that all mixed conifer species may be grown along the edges of original groups, including 0.1 ha groups, and that most species will show increased diameter and height growth after release. One concern of managers to implement a gap-based approach is the ability to grow shade intolerant species in gap openings. Chapter 3 demonstrates that ponderosa pine, a shade intolerant species, not only performed best among all species along gap edges prior to the femelschlag harvest, but also responded positively to release. These results provide long-term insight for implementing a gap-based silvicultural system in the Sierra Nevada.

As climate change and altered disturbance regimes continue to threaten mixed conifer forests, an adaptive management approach is essential for maintaining forests into the future. More research is needed on the long-term growth dynamics of giant sequoia and incense-cedar (i.e. full rotation length), as well as information about inter-specific competition with associated species. Although Chapter 3 provides insight to an operational gap-based silvicultural system, it is important to acknowledge the complexity of the silvicultural design. The trees that were released during the femelschlag harvests are also the matrix trees for the new gap expansion and future management activities will continue to impact their growth. Long-term monitoring is necessary to understand such impacts and an iterative approach to future planning is essential. Throughout three chapters, I have explored a variety of management options aimed towards created more resilient forests for the future. Long-term experimental datasets provided a unique opportunity to investigate the lasting impacts of a suite of silvicultural operations. Together, these chapters provide a basis to evaluate future management decisions in the Sierra Nevada mixed conifer forest.

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CHAPTER 1 APPENDIX A

Tables and Figures for all Spacing Treatments

Table S1. Ranking of DBH models for a giant sequoia spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Models are ranked by AIC values.

Rank	Model	Random Effect	Correlation Structure	AIC	ΔAIC	df	w_i	R_m^2	R_c^2
1	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corARMA	-10741.9	0	13	0.73	0.843227	0.8451719
2	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corARMA	-10739.9	2	14	0.27	0.843227	0.845172
3	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corAR1	-9755	986.9	12	<0.001	0.8498744	0.9675549
4	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	NONE	-8868.5	1873.5	11	<0.001	0.8422126	0.972762
5	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corAR1	-8813.1	1928.9	11	<0.001	0.8515329	0.8536914
6	log(DBH) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-2150.4	8591.6	11	<0.001	0.835439	0.9407993
7	log(DBH) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	NONE	-1975	8766.9	8	<0.001	0.830071	0.9444468
8	log(DBH) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-1973.1	8768.9	9	<0.001	0.830118	0.9444561
9	log(DBH) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-1747	8995	10	<0.001	0.8344209	0.9372426
10	log(DBH) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-1522.9	9219.1	8	<0.001	0.829542	0.9386756
11	log(DBH) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	NONE	-1413	9328.9	7	<0.001	0.8262932	0.9416574
12	log(DBH) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corARMA	-1213.9	9528	10	<0.001	0.8359948	0.8372896
13	log(DBH) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corAR1	-848.1	9893.9	8	<0.001	0.8359154	0.8371601
14	log(DBH) ~ log(YEAR) * SPACING	1|BLOCK/TREE	NONE	1048.6	11790.5	7	<0.001	0.8186648	0.9237438
15	log(DBH) ~ SPACING * YEAR * YEAR^2	1|BLOCK	NONE	3036.6	13778.6	10	<0.001	0.8546753	0.8565219
16	log(DBH) ~ SPACING * YEAR	1|BLOCK/TREE	corARMA	9962.6	20704.5	10	<0.001	0.6929855	0.6938841
17	log(DBH) ~ SPACING + YEAR	1|BLOCK/TREE	corARMA	10127.3	20869.2	9	<0.001	0.6896491	0.6905368
18	log(DBH) ~ SPACING * YEAR	1|BLOCK/TREE	corAR1	10176.5	20918.4	8	<0.001	0.693973	0.6948643
19	log(DBH) ~ SPACING + YEAR	1|BLOCK/TREE	corAR1	10343.1	21085.1	7	<0.001	0.6906636	0.6915437
20	log(DBH) ~ SPACING * YEAR	1|BLOCK/TREE	NONE	11667	22408.9	7	<0.001	0.7109615	0.7497479
21	log(DBH) ~ SPACING + YEAR	1|BLOCK/TREE	NONE	11956.6	22698.6	6	<0.001	0.7046769	0.7439631

Table S2. Ranking of height models for a giant sequoia spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Models are ranked by AIC values.

Rank	Model	Random Effect	Correlation Structure	AIC	ΔAIC	df	w_i	R_m^2	R_c^2
1	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corARMA	-18531.4	0	14	1	0.8243034	0.9394847
2	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corARMA	-18480.3	51.1	13	<0.001	0.8269186	0.8283029
3	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corAR1	-18380.9	150.5	12	<0.001	0.8250494	0.9431464
4	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corAR1	-18268.9	262.5	11	<0.001	0.8286992	0.8300434
5	log(HT) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corARMA	-15885.8	2645.6	10	<0.001	0.8252112	0.9370711
6	log(HT) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corAR1	-15625.1	2906.3	8	<0.001	0.8290602	0.9225284
7	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	NONE	-15041.8	3489.6	11	<0.001	0.8233219	0.9737921
8	log(HT) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-13395.9	5135.6	11	<0.001	0.8268706	0.9462971
9	log(HT) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-12926.3	5605.2	9	<0.001	0.8268696	0.9450412
10	log(HT) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-12905.2	5626.2	10	<0.001	0.8259	0.9369587
11	log(HT) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-12456.8	6074.6	8	<0.001	0.8260163	0.9339844
12	log(HT) ~ log(YEAR) * SPACING	1|BLOCK/TREE	NONE	-12268.2	6263.2	7	<0.001	0.8208935	0.9650972
13	log(HT) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	NONE	-11116.5	7415	8	<0.001	0.8195263	0.9606615
14	log(HT) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	NONE	-10127	8404.4	7	<0.001	0.8148407	0.9569612
15	log(HT) ~ SPACING * YEAR	1|BLOCK/TREE	corARMA	-4289.8	14241.6	10	<0.001	0.7608081	0.7617118
16	log(HT) ~ SPACING + YEAR	1|BLOCK/TREE	corARMA	-4066.8	14464.6	9	<0.001	0.7554297	0.7563116
17	log(HT) ~ SPACING * YEAR	1|BLOCK/TREE	corAR1	-3385	15146.4	8	<0.001	0.7627262	0.763545
18	log(HT) ~ SPACING + YEAR	1|BLOCK/TREE	corAR1	-3160.4	15371	7	<0.001	0.7575532	0.7583506
19	log(HT) ~ SPACING * YEAR * YEAR^2	1|BLOCK	NONE	-2121.4	16410	10	<0.001	0.8435309	0.8450684
20	log(HT) ~ SPACING * YEAR	1|BLOCK/TREE	NONE	257.1	18788.5	7	<0.001	0.7733891	0.8671465
21	log(HT) ~ SPACING + YEAR	1|BLOCK/TREE	NONE	763	19294.4	6	<0.001	0.7667284	0.8613113

Table S3. Ranking of models for individual bole volume for a giant sequoia spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Models are ranked by AIC values.

Rank	Model	Random Effect	Correlation Structure	AIC	ΔAIC	df	w_i	R_m^2	R_c^2
1	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corARMA	6446.3	0	13	0.71	0.8372124	0.8388942
2	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corARMA	6448.2	1.8	14	0.29	0.837166	0.8582859
3	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corAR1	6970	523.6	12	<0.001	0.8386298	0.9494475
4	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corAR1	7054.8	608.4	11	<0.001	0.8402856	0.8419487
5	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	NONE	10507	4060.6	11	<0.001	0.8348511	0.979419
6	log(VOL) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corARMA	12019.1	5572.8	10	<0.001	0.8479944	0.862912
7	log(VOL) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corAR1	12500.2	6053.8	8	<0.001	0.8484909	0.8497327
8	log(VOL) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corARMA	14860.7	8414.4	11	<0.001	0.8386409	0.9519781
9	log(VOL) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corAR1	15327.5	8881.2	9	<0.001	0.8367882	0.95279
10	log(VOL) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corARMA	15385.1	8938.8	10	<0.001	0.8377979	0.94507
11	log(VOL) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corAR1	15851.3	9405	8	<0.001	0.8360413	0.9455918
12	log(VOL) ~ log(YEAR) * SPACING	1|BLOCK/TREE	NONE	16254.6	9808.3	7	<0.001	0.8294352	0.9629825
13	log(VOL) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	NONE	16413	9966.6	8	<0.001	0.8294286	0.9623599
14	log(VOL) ~ SPACING + YEAR + YEAR2	1|BLOCK/TREE	NONE	17382.3	10935.9	7	<0.001	0.8249823	0.9588983
15	log(VOL) ~ SPACING * YEAR * YEAR^2	1|BLOCK	NONE	25046.2	18599.8	10	<0.001	0.8548597	0.8564865
16	log(VOL) ~ SPACING * YEAR	1|BLOCK/TREE	corARMA	26085.6	19639.3	10	<0.001	0.7491709	0.7501119
17	log(VOL) ~ SPACING + YEAR	1|BLOCK/TREE	corARMA	26296.6	19850.3	9	<0.001	0.7442522	0.7451742
18	log(VOL) ~ SPACING * YEAR	1|BLOCK/TREE	corAR1	26803.6	20357.3	8	<0.001	0.751574	0.7524423
19	log(VOL) ~ SPACING + YEAR	1|BLOCK/TREE	corAR1	27016.4	20570	7	<0.001	0.7468084	0.7476575
20	log(VOL) ~ SPACING * YEAR	1|BLOCK/TREE	NONE	29817.9	23371.6	7	<0.001	0.7656622	0.8411201
21	log(VOL) ~ SPACING + YEAR	1|BLOCK/TREE	NONE	30255.6	23809.3	6	<0.001	0.7590034	0.8352425

Table S4. Ranking of relative growth rate models for a giant sequoia spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Models are ranked by AIC values.

Rank	Model	Random Effect	Correlation Structure	AIC	ΔAIC	df	w_i	R_m^2	R_c^2
1	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corARMA	-525.8	0	13	0.399	0.8224856	0.823794
2	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK	NONE	-524.8	1	10	0.243	0.8227165	0.8238787
3	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corARMA	-523.8	2	14	0.147	0.8224856	0.823794
4	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	NONE	-522.8	3	11	0.089	0.8227165	0.8238787
5	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corAR1	-522.8	3	11	0.089	0.8227165	0.8238787
6	log(RGR) ~ SPACING * YEAR * YEAR^2	1|BLOCK/TREE	corAR1	-520.8	5	12	0.033	0.8227165	0.8238787
7	log(RGR) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-444.7	81	11	<0.001	0.8176188	0.8189634
8	log(RGR) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	NONE	-436.5	89.3	8	<0.001	0.8173012	0.8184357
9	log(RGR) ~ SPACING * YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-434.5	91.3	9	<0.001	0.8173012	0.8184357
10	log(RGR) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corARMA	-261.7	264	10	<0.001	0.8068765	0.8081656
11	log(RGR) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corARMA	-260.2	265.6	10	<0.001	0.8063797	0.8077264
12	log(RGR) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	NONE	-259.9	265.9	7	<0.001	0.8062387	0.8074446
13	log(RGR) ~ SPACING + YEAR + YEAR^2	1|BLOCK/TREE	corAR1	-257.9	267.9	8	<0.001	0.8062387	0.8074446
14	log(RGR) ~ log(YEAR) * SPACING	1|BLOCK/TREE	NONE	-257.5	268.3	7	<0.001	0.8061651	0.807272
15	log(RGR) ~ log(YEAR) * SPACING	1|BLOCK/TREE	corAR1	-255.5	270.3	8	<0.001	0.8061651	0.807272
16	log(RGR) ~ SPACING * YEAR	1|BLOCK/TREE	corARMA	1006.2	1532	10	<0.001	0.7103872	0.7115793
17	log(RGR) ~ SPACING * YEAR	1|BLOCK/TREE	NONE	1010.6	1536.4	7	<0.001	0.7063053	0.7072887
18	log(RGR) ~ SPACING * YEAR	1|BLOCK/TREE	corAR1	1012.6	1538.4	8	<0.001	0.7063053	0.7072887
19	log(RGR) ~ SPACING + YEAR	1|BLOCK/TREE	NONE	1123.2	1649	6	<0.001	0.6949937	0.6960457
20	log(RGR) ~ SPACING + YEAR	1|BLOCK/TREE	corARMA	1124.1	1649.9	9	<0.001	0.6979798	0.6991785
21	log(RGR) ~ SPACING + YEAR	1|BLOCK/TREE	corAR1	1125.2	1651	7	<0.001	0.6949937	0.6960457

Table S5. Ranking of stand volume models for a giant sequoia spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Models are ranked by AIC values.

Rank	Model	Random Effect	Correlation Structure	AIC	ΔAIC	df	w_i	R_m^2	R_c^2
1	log(VOL.HA) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corARMA	-171.4	0	13	0.9925	0.9901235	0.9915236
2	log(VOL.HA) ~ SPACING * YEAR * YEAR^2	1|BLOCK	corAR1	-161.6	9.8	11	0.0075	0.9896859	0.9910483
3	log(VOL.HA) ~ SPACING * YEAR * YEAR^2	1|BLOCK	NONE	-46	125.4	10	<0.001	0.988134	0.9899663
4	log(VOL.HA) ~ SPACING + YEAR + YEAR^2	1|BLOCK	corARMA	30.4	201.8	9	<0.001	0.9761313	0.9770247
5	log(VOL.HA) ~ SPACING * YEAR + YEAR^2	1|BLOCK	corARMA	32	203.4	10	<0.001	0.9762907	0.9771959
6	log(VOL.HA) ~ log(YEAR) * SPACING	1|BLOCK	corARMA	36.8	208.1	9	<0.001	0.9660227	0.9662058
7	log(VOL.HA) ~ SPACING + YEAR + YEAR^2	1|BLOCK	corAR1	52.8	224.2	7	<0.001	0.9762823	0.9772249
8	log(VOL.HA) ~ SPACING * YEAR + YEAR^2	1|BLOCK	corAR1	54	225.4	8	<0.001	0.976518	0.9774798
9	log(VOL.HA) ~ log(YEAR) * SPACING	1|BLOCK	corAR1	60.9	232.3	7	<0.001	0.9668149	0.9669665
10	log(VOL.HA) ~ SPACING * YEAR + YEAR^2	1|BLOCK	NONE	100.1	271.5	7	<0.001	0.9756411	0.9772721
11	log(VOL.HA) ~ SPACING + YEAR + YEAR^2	1|BLOCK	NONE	101	272.3	6	<0.001	0.9752934	0.9769188
12	log(VOL.HA) ~ log(YEAR) * SPACING	1|BLOCK	NONE	147.2	318.6	6	<0.001	0.9688818	0.9704038
13	log(VOL.HA) ~ SPACING + YEAR	1|BLOCK	corARMA	355	526.4	8	<0.001	0.8171366	0.8171366
14	log(VOL.HA) ~ SPACING * YEAR	1|BLOCK	corARMA	357	528.4	9	<0.001	0.8171337	0.8171337
15	log(VOL.HA) ~ SPACING + YEAR	1|BLOCK	corAR1	388.8	560.1	6	<0.001	0.8260424	0.8260424
16	log(VOL.HA) ~ SPACING * YEAR	1|BLOCK	corAR1	390.7	562.1	7	<0.001	0.8262807	0.8262807
17	log(VOL.HA) ~ SPACING + YEAR	1|BLOCK	NONE	450.8	622.2	5	<0.001	0.8473139	0.8473139
18	log(VOL.HA) ~ SPACING * YEAR	1|BLOCK	NONE	452.4	623.8	6	<0.001	0.847662	0.847662

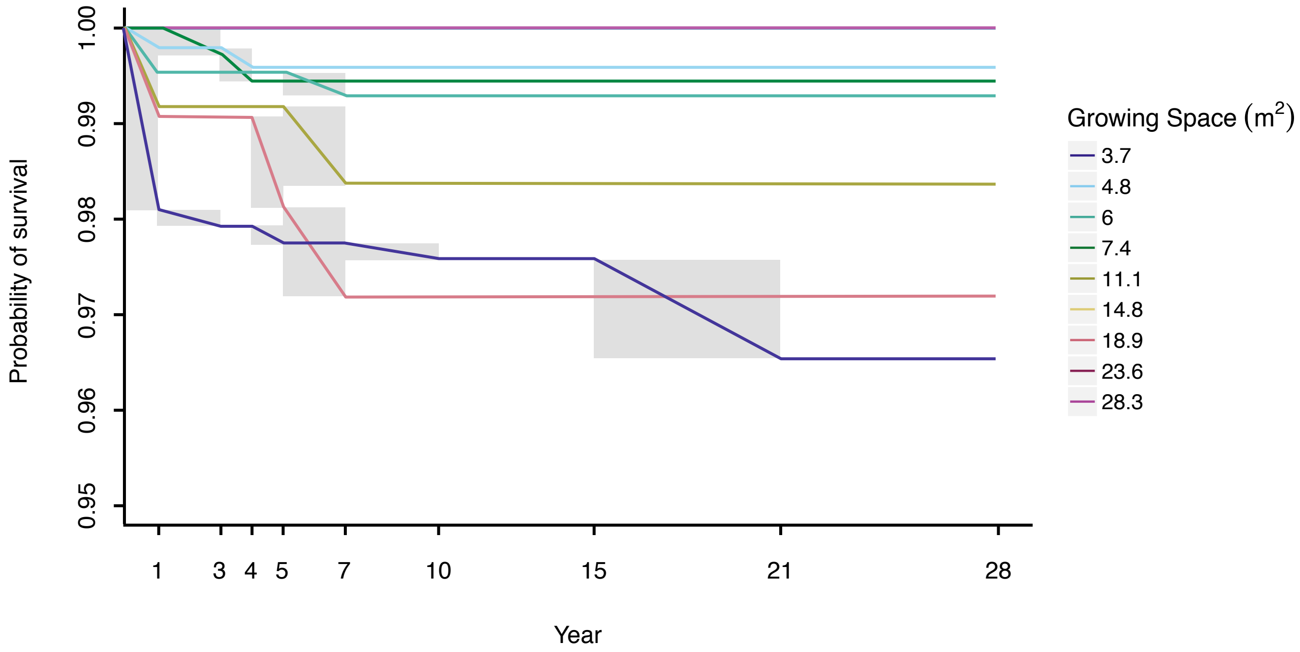

Figure S1. Probability of survival of giant sequoia across different initial planting density treatments in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

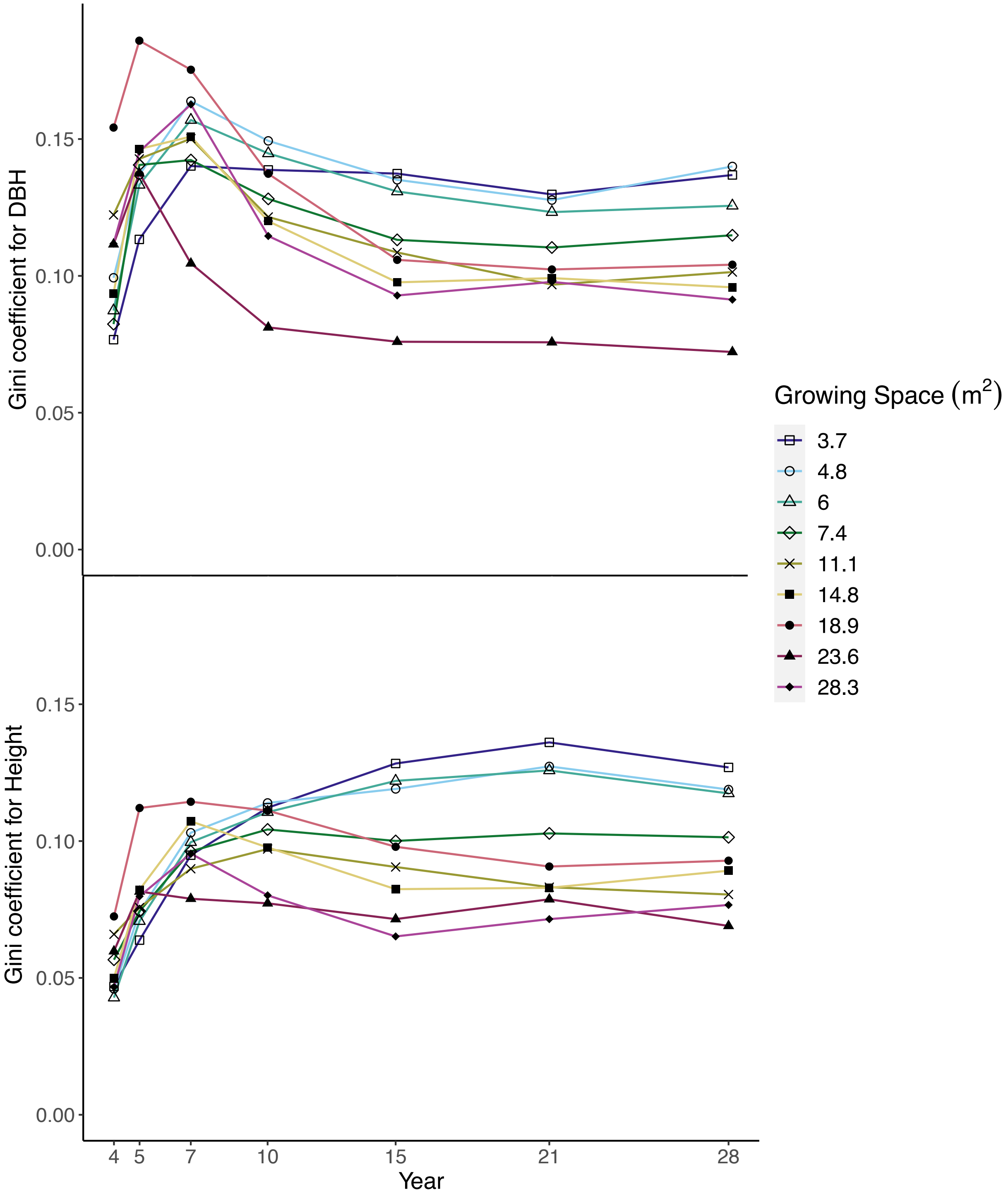

Figure S2. Gini coefficients based on diameter at breast height (cm, DBH) and height (m) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

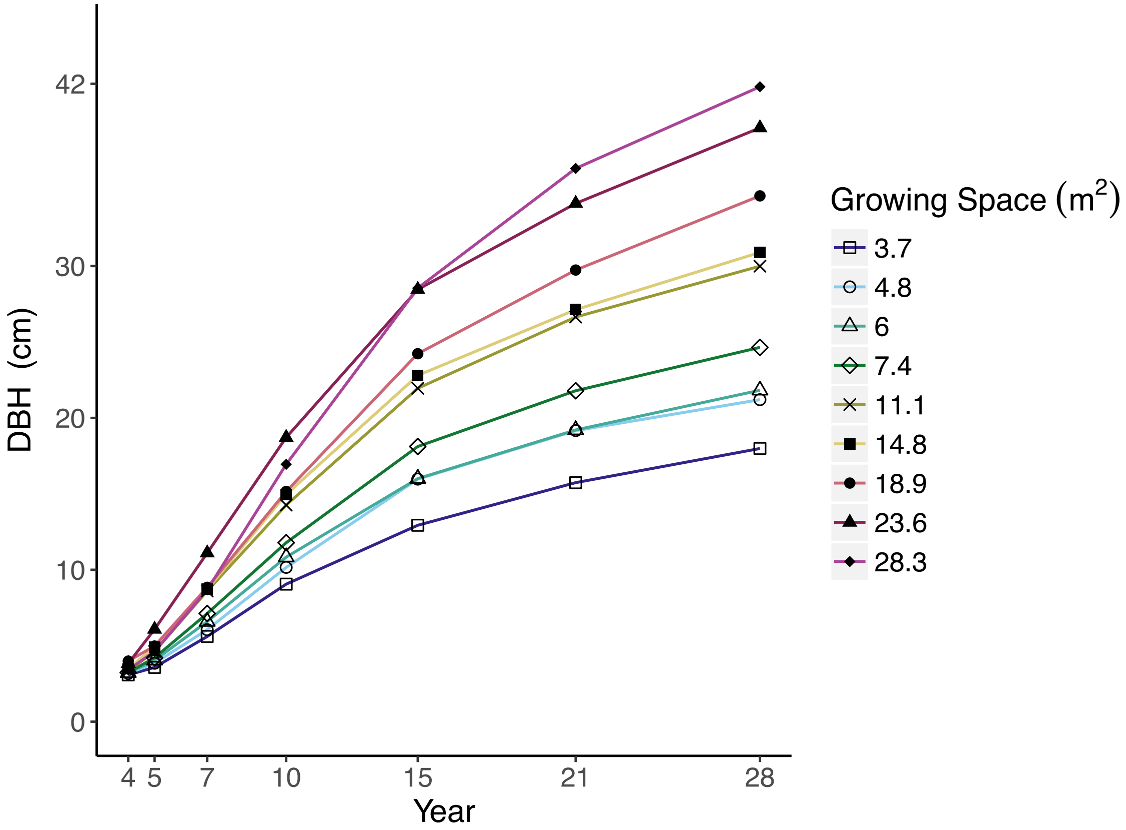

Figure S3. Diameter at breast height (cm, DBH) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

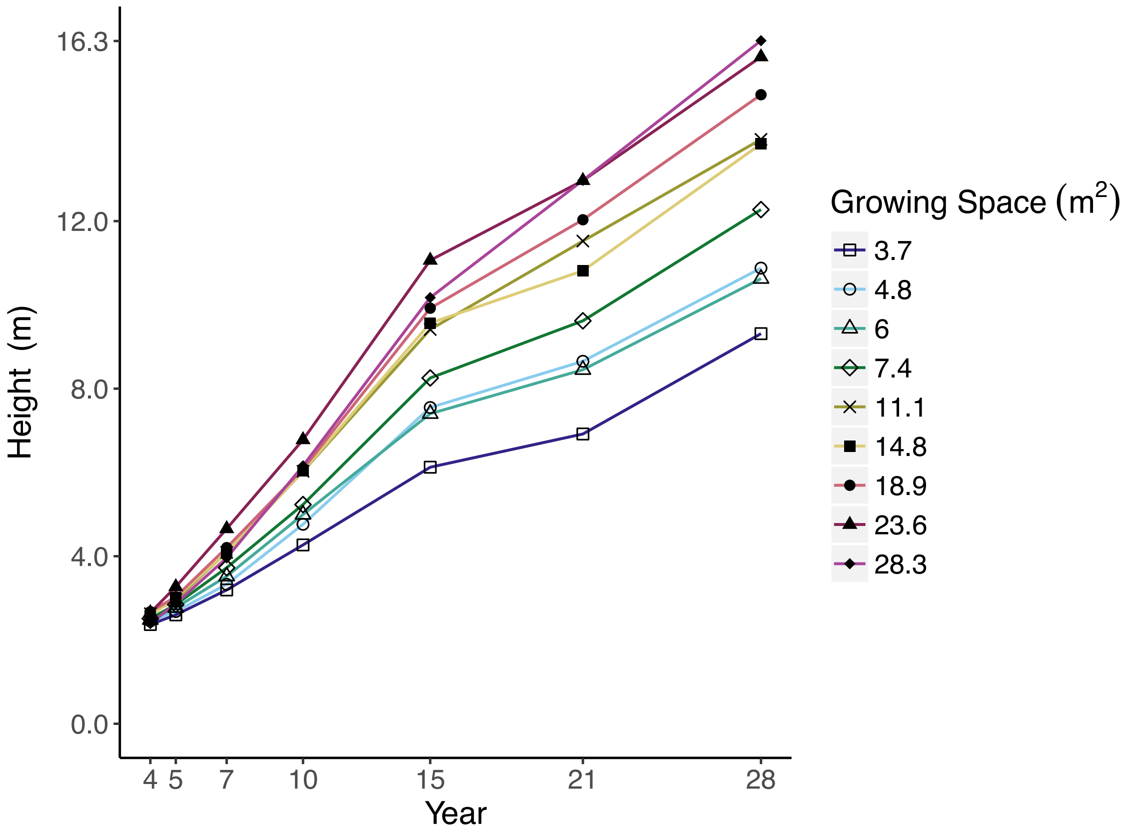

Figure S4. Mean height (m) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

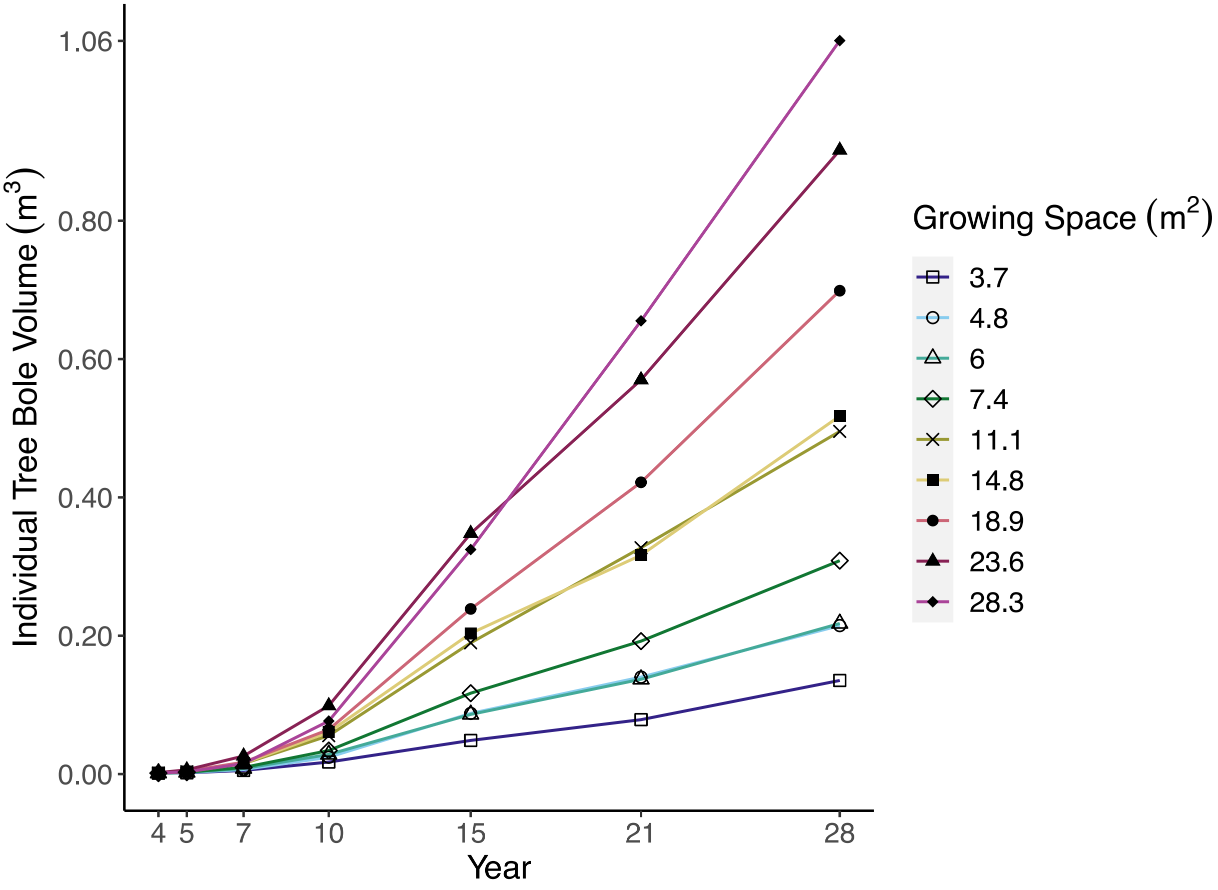

Figure S5. Mean bole volume (m^3) of trees in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

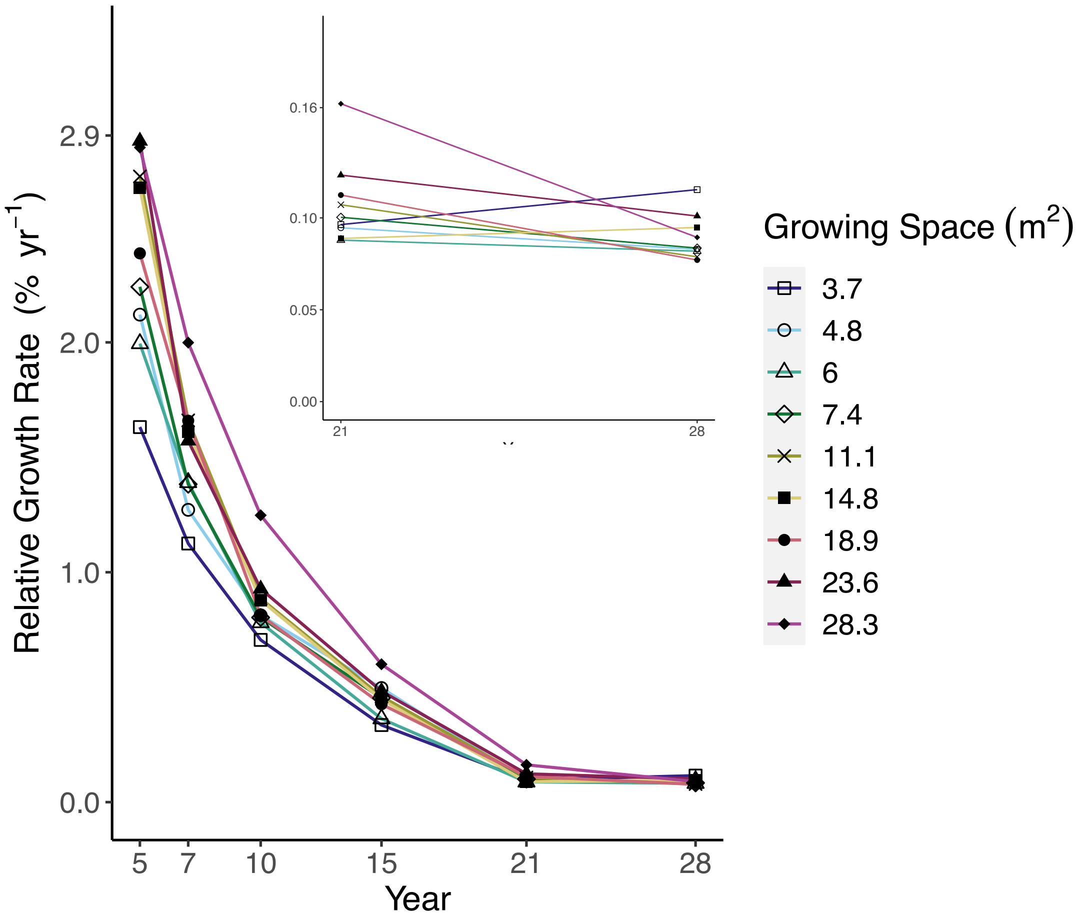

Figure S6. Relative growth rate (% yr^{-1}) based on bole volume of trees in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments. The inset shows relative growth rates based on bole volume during the most recent sampling period.

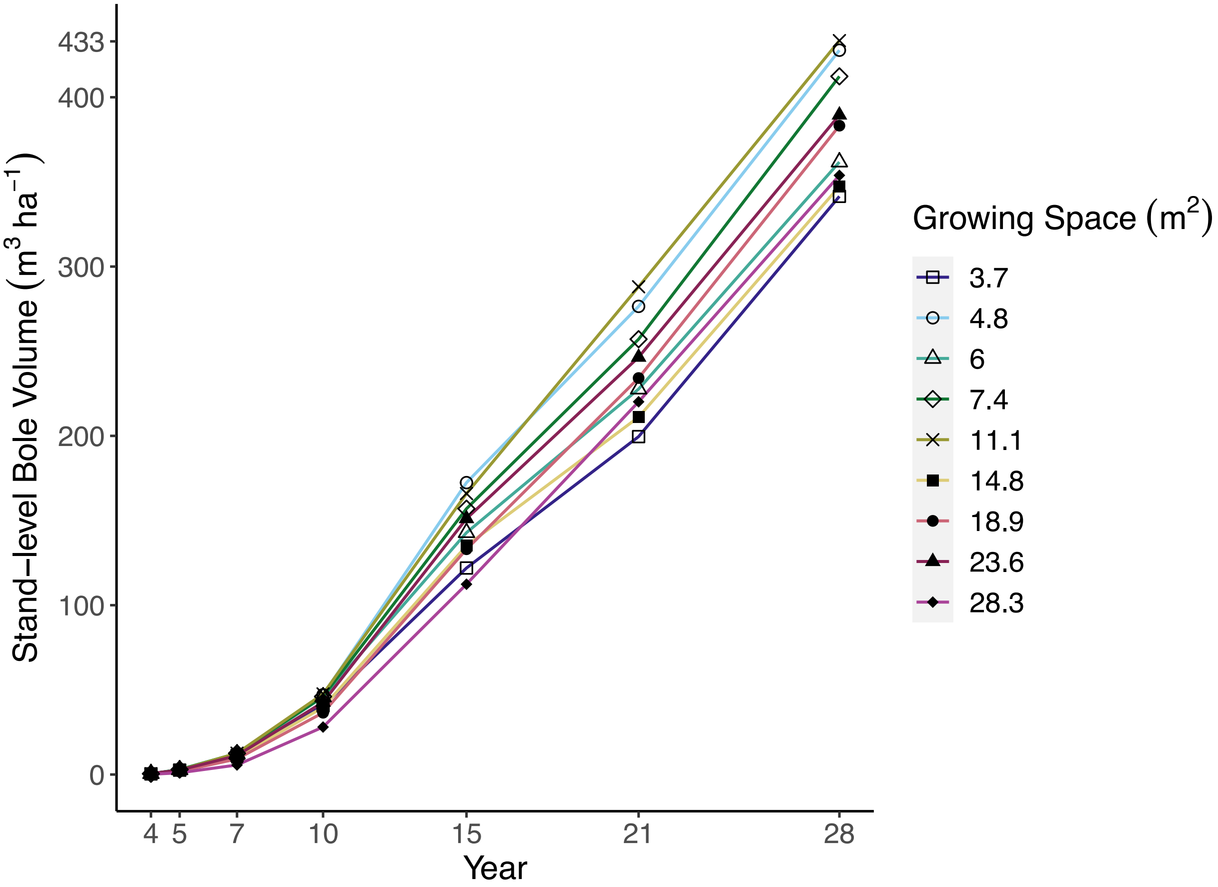

Figure S7. Mean stand bole volume (m^3 ha^{-1}) in giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

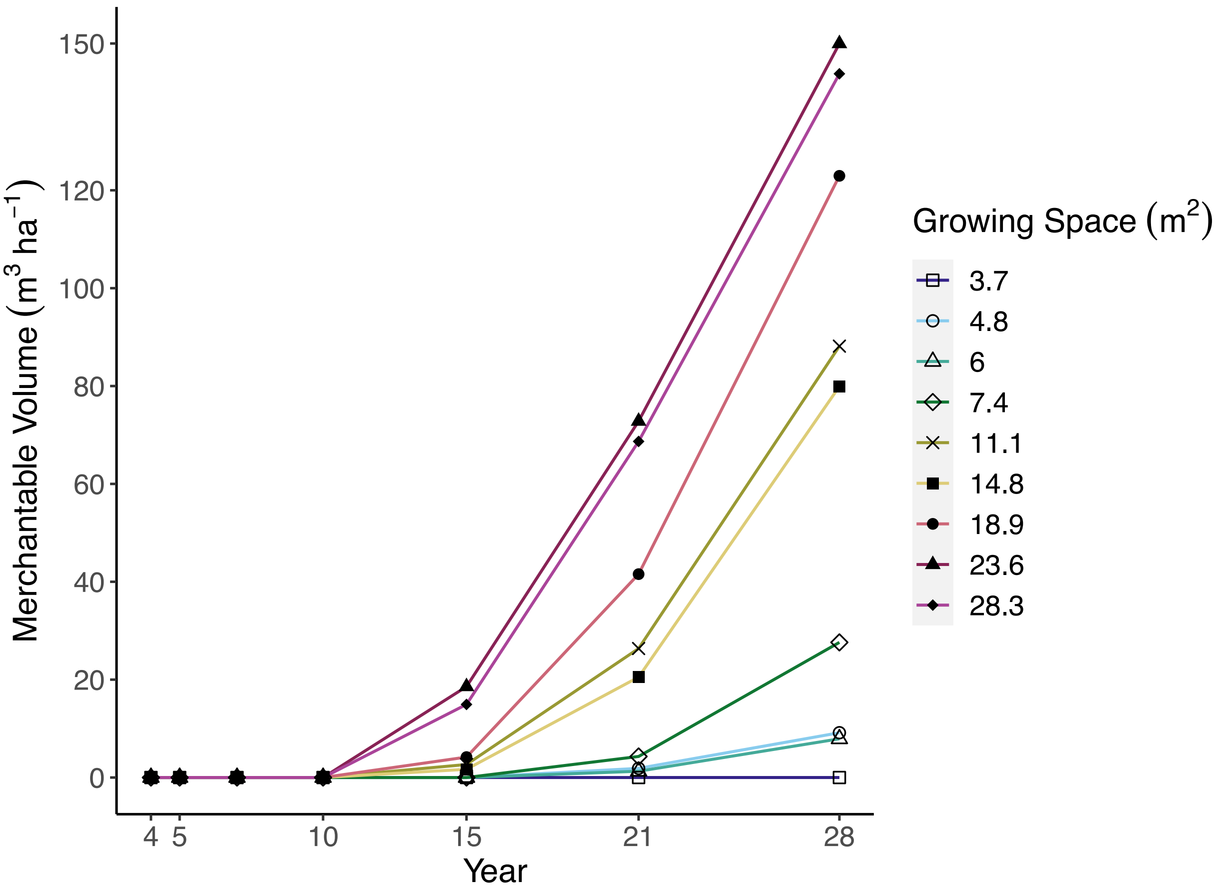

Figure S8. Merchantable volume (m^3 ha^{-1}) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

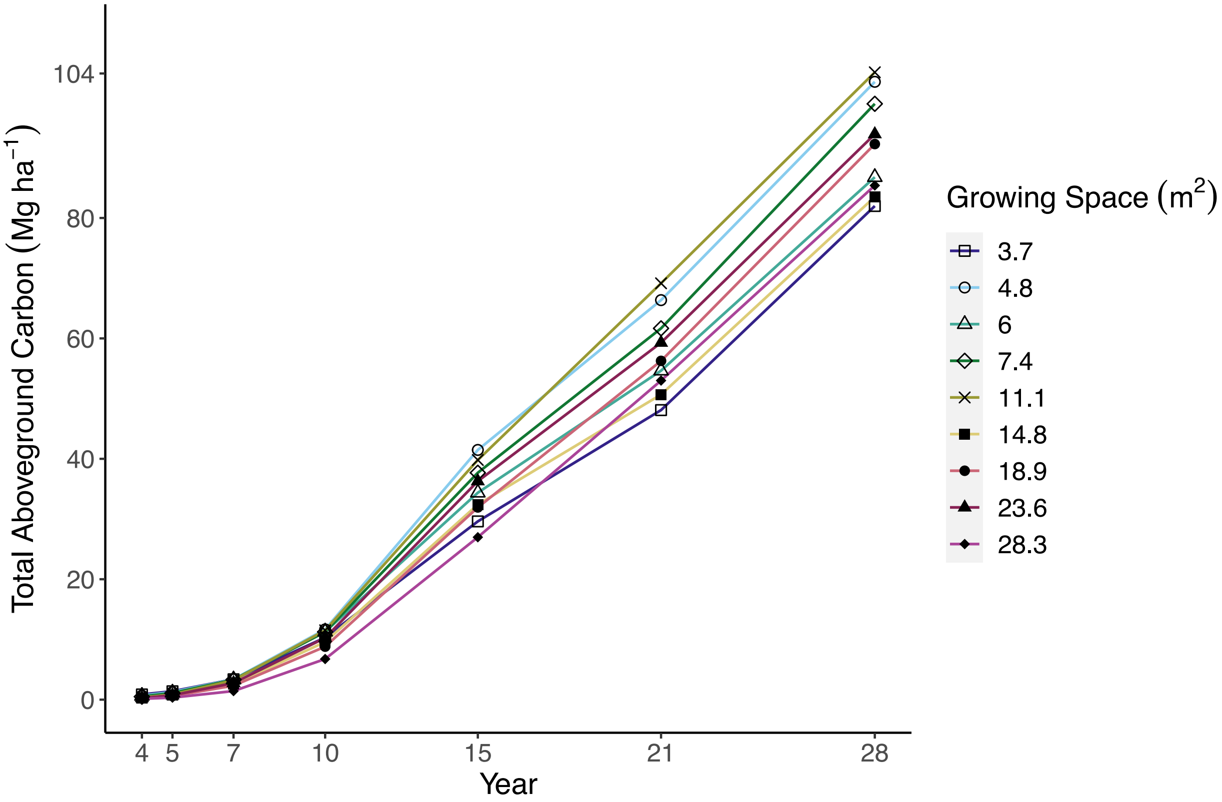

Figure S9. Aboveground carbon (Mg ha^{-1}) of giant sequoia in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada. Growing space indicates different initial planting density treatments.

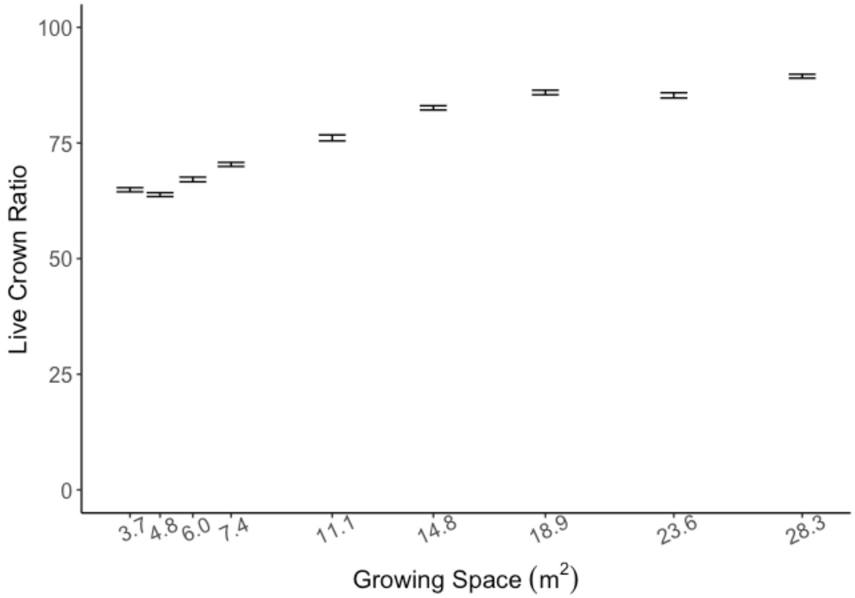

Figure S10. Live crown ratio of giant sequoia in a spacing trial after 28 years at Blodgett Forest Research Station in the central Sierra Nevada. Bars indicate standard error. Growing space indicates different initial planting density treatments.

CHAPTER 1 APPENDIX B

Development of volume equations for planted giant sequoia (*Sequioadendron giganteum).*

INTRODUCTION

We developed site-specific allometric equations to estimate stem volume as a function of diameter at breast height (DBH, breast height = 1.37 m) and tree height. The equations were based on direct determinations of volume from sample trees. We calculated estimators for total stem volume as defined by the USDA Forest Inventory and Analysis program (FIA 2020) and for merchantable volume as defined by a local scaling agreement. Coefficients for both metric and English units are included. Our description of these equations follow best practices outlined in Henry et al. (2013).

STUDY SITE

The tree data for the development of the giant sequoia (*Sequoiadendron giganteum)* volume equations were obtained at the Blodgett Forest Research Station during July of 1997. Trees were sampled in Compartment 200, a 6.5 ha unit managed as an even-aged stand. The unit has a west-southwesterly aspect with an average slope of 25%; the elevation ranges from 1,189 m to 1,280 m. The soils are characterized by Holland and Bighill series with deeply weathered horizons of granodiorite parent materials extending one to two meters deep. The unit was clear-felled in 1980 and planted in 1981 with a species mix that included incense-cedar (*Calocedrus decurrens)*, ponderosa Pine (*Pinus ponderosa)*, Douglas-fir (*Psuedotsuga menziesii)*, giant sequoia (*Sequoiadendron giganteum)*, sugar pine (*Pinus lambertiana),* and white Fir (*Abies lowiana)*. California black oak (*Quercus kelloggii)* was regenerated through coppice and natural seeding. Pre-commercial thinning was conducted throughout the stand during the summer of 1989 to reduce the shrub component and maintain optimal stocking levels.

Table S6. Dimensions of the giant sequoia trees selected for volume determination. DBH is the stem diameter at breast height (1.37 m); height is total tree height; and volume is total tree volume. Sample size is 34 trees.

	DBH cm	Height m	Volume m^3
Mean	29.2	12.4	0.35
Standard deviation	5.0	1.5	0.16
Minimum	21.2	8.1	0.15
Maximum	41.7	15.0	0.81

VOLUME ESTIMATION

We felled a representative sample of 34 trees (Table S6). We used steel tapes to take all diameter and height measures. Trees ranged from a minimum of 8.1 m tall to a maximum of 15.0 m tall. The mean height was 12.4 m with a standard deviation of 1.5 m. The stump diameter was taken at the standard height above the soil surface on the uphill side of the tree (FIA 2020, 30.5 cm). Subsequent diameter measurements were taken at the following heights (Fig. S10): breast height (1.37 m above the ground), 5.0 m (the height of trim allowance for sawlog merchantability), and where the stem diameter inside the bark equaled 15.2 cm (the height where the "top" of the tree begins). The total height (i.e., length) of the stem was also measured. To calculate the stem volume, we considered the giant sequoia stems to be composites of geometrical solids (Fig. S10). Our designations and the formulae used to calculate these pieces follow Kershaw et al. (2016).

As noted above, we defined two stem volumes. Total stem volume includes all the stem pieces in Fig. 1 and is equivalent to the FIA definition of CVTS (total volume including tops and stumps, FIA 2020). The other is the merchantable volume defined by local convention as all the stem pieces except the cone (Fig. S10). It varies from the standard sawlog definition by including the stump section of the stem. This revised definition reflects the local operational practice where trees this size are harvested via a feller-buncher that cuts stems flush to the ground (i.e., leaves little to no stump).

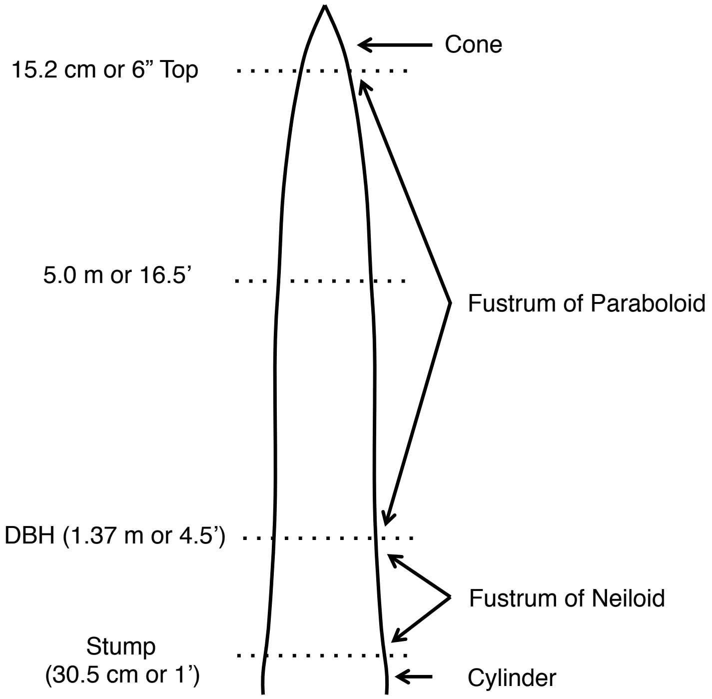

Figure S10. Diagram describing how stem volume was calculated by matching segments of the stems to the appropriate geometrical solid.

ALLOMETRIC ANALYSIS

Following the recommendation in Picard et al. (2015), we used measures of both diameter and height to estimate stem volume. Specifically, we fit a power law equation:

$$Stem\ volume = aDBH^{b}Height^{c} \qquad \text{Equation 1}$$

where DBH = diameter at breast height and Height = total tree height. Parameters were estimated using non-linear least squares regression. All analyses were conducted in R version 3.4 (R Core Team 2017).

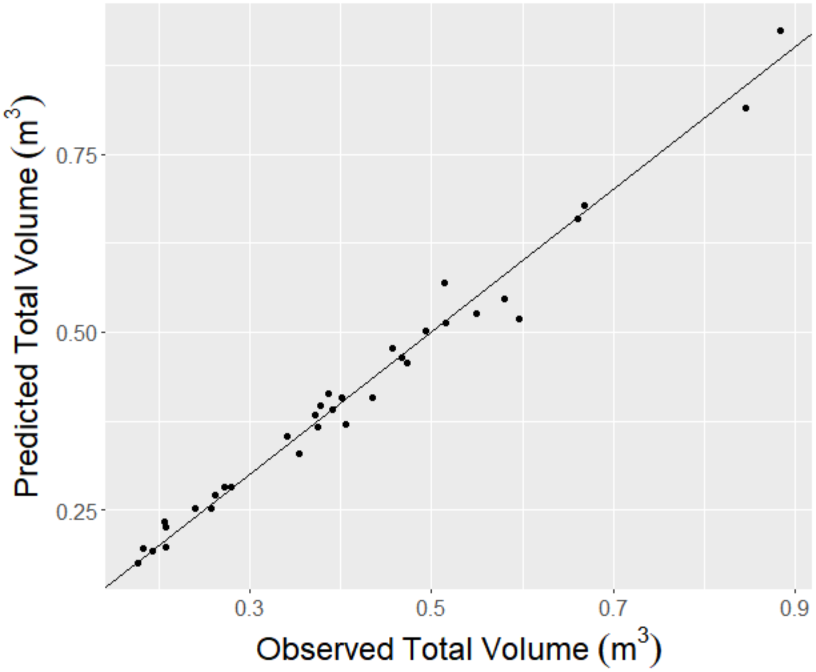

Figure S11. A comparison of the observed total stem volume to the predicted total stem volume volume for 34 giant sequoia trees sampled at Blodgett Forest Research Station.

RESULTS

The two factor power law equation (Equation 1) provided an exceptional fit to the data (Fig. S11). For total stem volume, the residual standard error was 2.54E-02 m^3, an error rate equivalent to about 7% of the mean total stem volume. The estimates of the coefficients were significantly different from 0 (Table S7) and the assumption of a random distribution of residuals was met. The performance of the two parameter power model was similar for the estimates of merchantable volume (Table S8). Only the intercept changes for the volume equations calculated in English units (Table S9).

Table S7. Allometric equation predicting total stem volume as a function of DBH and Height. DBH in cm, Height in m, Volume in m^3: Volume = $a*DBH^b*Height^c$. The residual standard error = 2.54E-02; degrees of freedom = 31.

Coefficient	Estimate	Standard error	P value
a	5.84E-05	1.4E-05	3.0E-04
b	1.89E+00	9.3E-02	2.0E-19
c	9.64E-01	1.4E-01	1.3E-07

Table S8. Allometric equation predicting merchantable volume as a function of DBH and Height. DBH in cm, Height in m, Volume in m^3: Volume = $a*DBH^b*Height^c$. The residual standard error = 2.99E-02; degrees of freedom = 31.

Coefficient	Estimate	Standard error	P value
a	2.32E-05	7.41E-06	3.83E-03
b	2.11E+00	1.21E-01	1.39E-17
c	9.97E-01	1.84E-01	6.51E-06

Table S9. Estimates of the coefficients for the allometric equations predicting total stem volume and merchantable volume as a function of DBH and Height. DBH in inches, Height in ft, Volume in ft^3: Volume = $a*DBH^b*Height^c$. Note: only the intercept term (a) changes from the metric versions.

Coefficient	Total volume	Merchantable volume
a	3.83E-03	1.79E-03
b	1.89E+00	2.11E+00
c	9.64E-01	9.97E-01

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CHAPTER 2 APPENDIX

Table S1. Model rankings for incense-cedar survival three growing seasons after planting in a spacing trial at Blodgett Forest Research Station in the central Sierra Nevada.

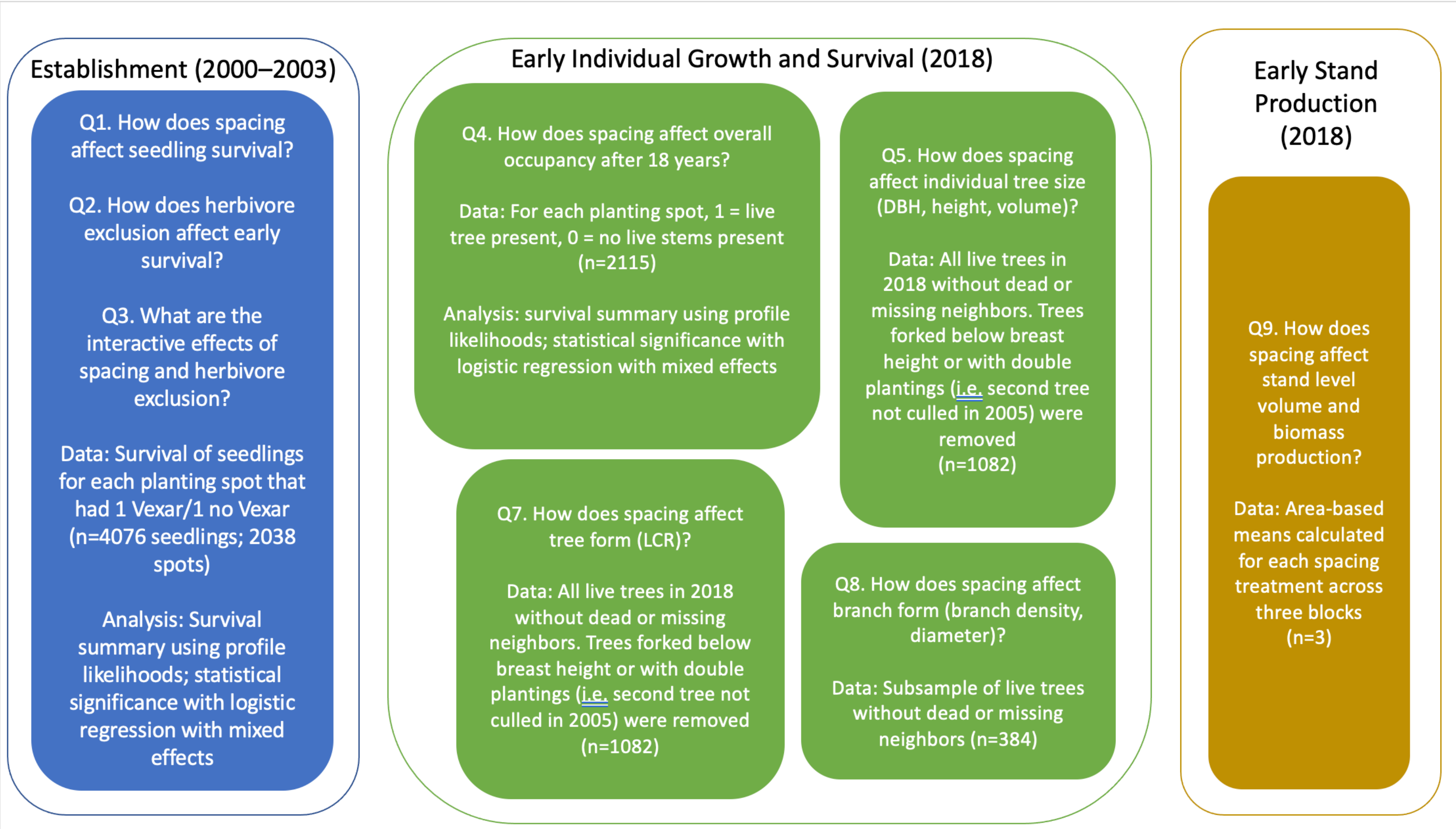
ID	Model	AIC	ΔAIC	df	Weight
Additive	Survival ~ Spacing + Vexar + (1|Block)	3402.1	0	4	0.639
Full	Survival ~ Spacing * Vexar + (1|Block)	3403.7	1.5	5	0.295
Vexar	Survival ~ Vexar + (1|Block)	3406.7	4.5	3	0.066
Spacing	Survival ~ Spacing + (1|Block)	3511.3	109.1	3	<0.001

Table S2. Statistical results from planting space occupancy model after 18 years for incense cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada.

Fixed Effects	**Estimate**	**Std. Error**	***p***
Intercept	2.59	0.38	<0.001
Spacing	-0.03	0.01	<0.001
Random Effect	**Variance**	**Std. Dev.**	
Block	0.40	0.63	

Table S3. Model rankings for individual tree and stand-level characteristics for an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada.

	Response	Model	AIC	ΔAIC	df	Weight
Question 5	**Diameter**	Log-linear	6368.7	0	4	0.9727
		Quadratic	6376.7	8	5	0.0176
		Asymptotic	6377.9	9.2	6	0.0098
		Linear	6400	31.3	4	<0.001
	Height	Asymptotic	3790.7	0	6	0.5298
		Log-linear	3791.3	0.5	4	0.4088
		Quadratic	3795.2	4.5	5	0.057
		Linear	3800.3	9.5	4	0.0045
	Individual Volume	Quadratic	-4688	0	5	0.58
		Linear	-4687.4	0.6	4	0.42
		Log-linear	-4660	28	4	<0.001
		Asymptotic	-4644.8	43.2	6	<0.001
Question 6	**Live Crown Ratio**	Asymptotic	832	0	6	1
		Log-linear	857.5	25.5	4	<0.001
		Quadratic	869	37	5	<0.001
		Linear	901.5	69.5	4	<0.001
Question 7	**Branch Density**	Quadratic	1476.9	0	4	0.674
		Log-linear	1478.7	1.8	3	0.27
		Linear	1481.8	5	3	0.056
		Asymptotic	2558.2	1081.3	3	<0.001
	Branch Diameter	Asymptotic	2522.4	0	3	0.754
		Log-linear	2525.1	2.7	3	0.2
		Quadratic	2528.1	5.6	4	0.046
		Linear	2553.4	30.9	3	<0.001
Question 8	**Stand Volume**	Log-linear	213.2	0	3	0.677
		Quadratic	214.8	1.6	4	0.306
		Linear	220.7	7.4	3	0.017
		Asymptotic	285.3	72	3	<0.001
	Stand Biomass	Log-linear	208	0	3	0.5965
		Quadratic	208.9	1	4	0.3679
		Linear	213.7	5.8	3	0.0333
		Asymptotic	219.1	11.1	3	0.0023



Establishment (2000–2003)

Q1. How does spacing affect seedling survival?

Q2. How does herbivore exclusion affect early survival?

Q3. What are the interactive effects of spacing and herbivore exclusion?

Data: Survival of seedlings for each planting spot that had 1 Vexar/1 no Vexar (n=4076 seedlings; 2038 spots)

Analysis: Survival summary using profile likelihoods; statistical significance with logistic regression with mixed effects

Early Individual Growth and Survival (2018)

Q4. How does spacing affect overall occupancy after 18 years?

Data: For each planting spot, 1 = live tree present, 0 = no live stems present (n=2115)

Analysis: survival summary using profile likelihoods; statistical significance with logistic regression with mixed effects

Q5. How does spacing affect individual tree size (DBH, height, volume)?

Data: All live trees in 2018 without dead or missing neighbors. Trees forked below breast height or with double plantings (i.e. second tree not culled in 2005) were removed (n=1082)

Q7. How does spacing affect tree form (LCR)?

Data: All live trees in 2018 without dead or missing neighbors. Trees forked below breast height or with double plantings (i.e. second tree not culled in 2005) were removed (n=1082)

Q8. How does spacing affect branch form (branch density, diameter)?

Data: Subsample of live trees without dead or missing neighbors (n=384)

Early Stand Production (2018)

Q9. How does spacing affect stand level volume and biomass production?

Data: Area-based means calculated for each spacing treatment across three blocks (n=3)

Figure S1. Diagram of analytical framework for an incense-cedar spacing trial at Blodgett Forest Research Station in the central Sierra Nevada.

CHAPTER 3 APPENDIX

Table S1. Model rankings of height responses to group size after 12 years of growth at Blodgett Forest in the central Sierra Nevada. K indicates the number of parameters in each model.

			Coefficients							Cumulative
Species	**Model**		**a**	**b**	**c**	**K**	**AICc**	**ΔAICc**	**Weight**	**Weight**
Douglas-fir	Linear	Height ~ a + b*GroupSize	2.41	1.69	–	3	31.5	0.0	0.69	0.69
	Power	Height ~ a*GroupSize^b	3.89	0.19	–	3	33.9	2.4	0.20	0.89
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	2.81	-0.6	2.05	4	35.2	3.7	0.11	1.00
	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	0.43	-0.53	–	3	67.3	35.8	0.00	1.00
giant sequoia	Linear	Height ~ a + b*GroupSize	2.49	1.98	–	3	37.6	0.0	0.48	0.48
	Power	Height ~ a*GroupSize^b	4.27	0.22	–	3	38.7	1.1	0.28	0.76
	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	4.32	0.07	–	3	39.9	2.3	0.15	0.91
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	3.05	-1.28	2.91	4	41.0	3.4	0.09	1.00
incense-cedar	Linear	Height ~ a + b*GroupSize	1.91	1.54	–	3	27.6	0.0	0.38	0.38
	Power	Height ~ a*GroupSize^b	3.34	0.23	–	3	27.7	0.1	0.36	0.74
	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	3.45	0.09	–	3	28.7	1.1	0.22	0.96
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	1.98	1.19	0.32	4	32.3	4.7	0.04	1.00
ponderosa pine	Power	Height ~ a*GroupSize^b	5.07	0.25	–	3	19.1	0.0	0.61	0.61
	Linear	Height ~ a + b*GroupSize	2.81	2.41	–	3	21.2	2.1	0.22	0.83
	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	5.32	0.1	–	3	22.1	2.9	0.14	0.97
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	2.6	3.62	-1.08	4	25.2	6.1	0.03	1.00
sugar pine	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	3.33	0.08	–	3	25.3	0.0	0.43	0.43
	Power	Height ~ a*GroupSize^b	3.22	0.2	–	3	25.7	0.4	0.35	0.79
	Linear	Height ~ a + b*GroupSize	2.03	1.26	–	3	27.0	1.7	0.19	0.98
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	1.77	2.75	-1.33	4	31.1	5.7	0.02	1.00
white fir	Power	Height ~ a*GroupSize^b	2.55	0.11	–	3	29.1	0.0	0.52	0.52
	Linear	Height ~ a + b*GroupSize	2.03	0.52	–	3	29.8	0.7	0.37	0.89
	Quadratic	Height ~ a + b*GroupSize + c*GroupSize^2	1.49	3.64	-2.79	4	32.1	3.0	0.11	1.00
	Asymptotic	Height ~ (a*GroupSize)/(b+GroupSize)	0.21	-0.56	–	3	57.9	28.8	0.00	1.00

Table S2. Analysis of covariance (ANCOVA) of % total transmitted photosynthetically active radiation (%TTR) after femelschlag harvests at Blodgett Forest in the central Sierra Nevada.

	Coefficient	Df	Sum Sq	Mean Sq	F-value	p	p<0.05
Pre-treatment % TTR	0.46	1	908	908	3.072	0.08693	.
Treatment	25.7	1	7543	7543	25.533	<0.001	***
Northness	7.3	1	284	284	0.963	0.3321	
Treatment*Northness	-21.6	1	2886	2886	9.768	0.003	**
Residuals	–	42	12408	295			

Table S3. Analysis of covariance (ANCOVA) of height increment (m) of edge trees between the 15th and 21st growing seasons at Blodgett Forest in the central Sierra Nevada. A femelschlag harvest was implemented during the 13th growing season. Original group size indicates size of groups implemented prior to planting.

Response		Df	Sum Sq	Mean Sq	F-value	p	p<0.05
Height Increment (m)	Pre-treatment Height	1	286.7	286.65	266.1	<0.001	***
	Species	5	52.9	10.58	9.8	<0.001	***
	Treatment	1	44.1	44.12	41.0	<0.001	***
	Northness	1	35.8	35.77	33.2	<0.001	***
	OriginalGroupSize	1	1.3	1.31	1.2	0.27	
	Species:Treatment	5	11.9	2.39	2.2	0.05	.
	Species:Northness	5	21.1	4.23	3.9	0.00	**
	Treatment:Northness	1	1.0	1.01	0.9	0.33	
	Species:OriginalGroupSize	5	14.2	2.84	2.6	0.02	*
	Treatment:OriginalGroupSize	1	2.2	2.24	2.1	0.15	
	Northness:OriginalGroupSize	1	0.0	0.01	0.0	0.91	
	Species:Treatment:Northness	5	11.2	2.25	2.1	0.07	.
	Species:Treatment:OriginalGroupSize	5	30.3	6.07	5.6	<0.001	***
	Species:Northness:OriginalGroupSize	5	2.3	0.47	0.4	0.82	
	Treatment:Northness:OriginalGroupSize	1	5.9	5.9	5.5	0.02	*
	Species:Treatment:Northness:OriginalGroupSize	5	7.5	1.51	1.4	0.23	
	Residuals	219	235.9	1.08			

Table S4. Analysis of covariance (ANCOVA) of diameter increment (cm) of edge trees between the 15th and 21st growing seasons at Blodgett Forest in the central Sierra Nevada. A femelschlag harvest was implemented during the 13th growing season. Original group size indicates size of groups implemented prior to planting.

Response		**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**p**	**p<0.05**
Diameter Increment (cm)	Pre-treatment Diameter	1	203.9	203.90	70.6	<0.001	***
	Species	5	103.7	20.70	7.2	<0.001	***
	Treatment	1	382.0	382.00	132.2	<0.001	***
	Northness	1	6.8	6.80	2.3	0.13	
	OriginalGroupSize	1	6.5	6.50	2.3	0.14	
	Species:Treatment	5	98.6	19.70	6.8	<0.001	***
	Species:Northness	5	111.7	22.30	7.7	<0.001	***
	Treatment:Northness	1	3.6	3.60	1.2	0.27	
	Species:OriginalGroupSize	5	24.4	4.9	1.7	0.14	
	Treatment:OriginalGroupSize	1	1.6	1.6	0.5	0.46	
	Northness:OriginalGroupSize	1	0.4	0.4	0.1	0.70	
	Species:Treatment:Northness	5	98.8	19.8	6.8	<0.001	***
	Species:Treatment:OriginalGroupSize	5	46.0	9.2	3.2	0.01	**
	Species:Northness:OriginalGroupSize	5	10.0	2	0.7	0.63	
	Treatment:Northness:OriginalGroupSize	1	34.2	34.2	11.8	<0.001	***
	Species:Treatment:Northness:OriginalGroupSize	5	34.1	6.8	2.4	0.04	*
	Residuals	172	497.0	2.9			

Table S5. Analysis of covariance (ANCOVA) of height (m) of edge trees between the 15th and 21st growing seasons at Blodgett Forest in the central Sierra Nevada. A femelschlag harvest was implemented during the 13th growing season. Original group size indicates size of groups implemented prior to planting.

Response		Df	Sum Sq	Mean Sq	F-value	p	p<0.05
Absolute Height (m)	Pre-treatment Height	1	3233.0	3233.0	1522.1	<0.001	***
	Species	5	99.0	20.0	9.3	<0.001	***
	Treatment	1	45.0	45.0	21.3	<0.001	***
	Northness	1	47.0	47.0	22.2	<0.001	***
	OriginalGroupSize	1	1.0	1.0	0.6	0.46	
	Species:Treatment	5	10.0	2.0	0.9	0.48	
	Species:Northness	5	13.0	3.0	1.2	0.30	
	Treatment:Northness	1	1.0	1.0	0.5	0.48	
	Species:OriginalGroupSize	5	11.0	2.0	1.0	0.42	
	Treatment:OriginalGroupSize	1	5.0	5.0	2.5	0.11	
	Northness:OriginalGroupSize	1	0.0	0.0	0.1	0.71	
	Species:Treatment:Northness	5	32.0	6.0	3.0	0.01	*
	Species:Treatment:OriginalGroupSize	5	12.0	2.0	1.1	0.35	
	Species:Northness:OriginalGroupSize	5	3.0	1.0	0.3	0.90	
	Treatment:Northness:OriginalGroupSize	1	10.0	10.0	4.9	0.03	*
	Species:Treatment:Northness:OriginalGroupSize	5	14.0	3.0	1.3	0.26	
	Residuals	270	574.0	2.0			

Table S6. Analysis of covariance (ANCOVA) of diameter (cm) of edge trees between the 15th and 21st growing seasons at Blodgett Forest in the central Sierra Nevada. A femelschlag harvest was implemented during the 13th growing season. Original group size indicates size of groups implemented prior to planting.

Response		**Df**	**Sum Sq**	**Mean Sq**	**F-value**	**p**	**p<0.05**
Absolute Diameter (cm)	Pre-treatment Diameter	1	8146	8146	1598.49	<0.001	***
	Species	5	275	55	1.08E+01	<0.001	***
	Treatment	1	478	478	9.37E+01	<0.001	***
	Northness	1	12	12	2.282	0.13	
	OriginalGroupSize	1	6	6	1.242	0.27	
	Species:Treatment	5	145	29	5.7	<0.001	***
	Species:Northness	5	99	20	3.869	0.00	**
	Treatment:Northness	1	9	9	1.736	0.19	
	Species:OriginalGroupSize	5	32	6	1.27	0.28	
	Treatment:OriginalGroupSize	1	2	2	0.474	0.49	
	Northness:OriginalGroupSize	1	12	12	2.293	0.13	
	Species:Treatment:Northness	5	93	19	3.64	0.00	**
	Species:Treatment:OriginalGroupSize	5	14	3	0.551	0.74	
	Species:Northness:OriginalGroupSize	5	2	0	0.073	1.00	
	Treatment:Northness:OriginalGroupSize	1	16	16	3.158	0.08	.
	Species:Treatment:Northness:OriginalGroupSize	5	21	4	0.818	0.54	
	Residuals	218	1111	5			

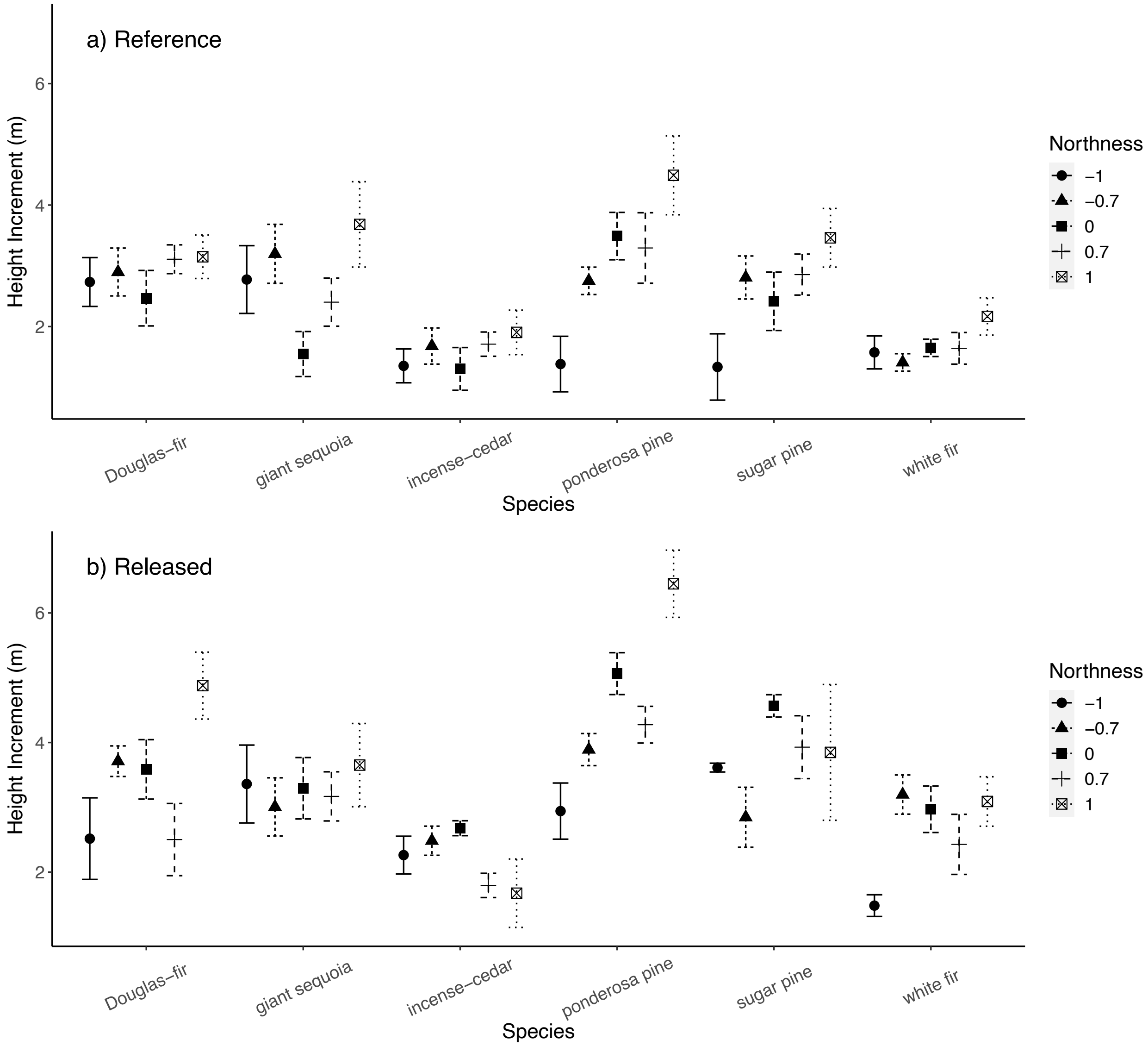


Figure S1. Mean height increment of edge trees planted in experimental groups between the 15th and 21st growing seasons at Blodgett Forest. Northness is described as cosine(aspect) of the tree location along the edge of the group. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

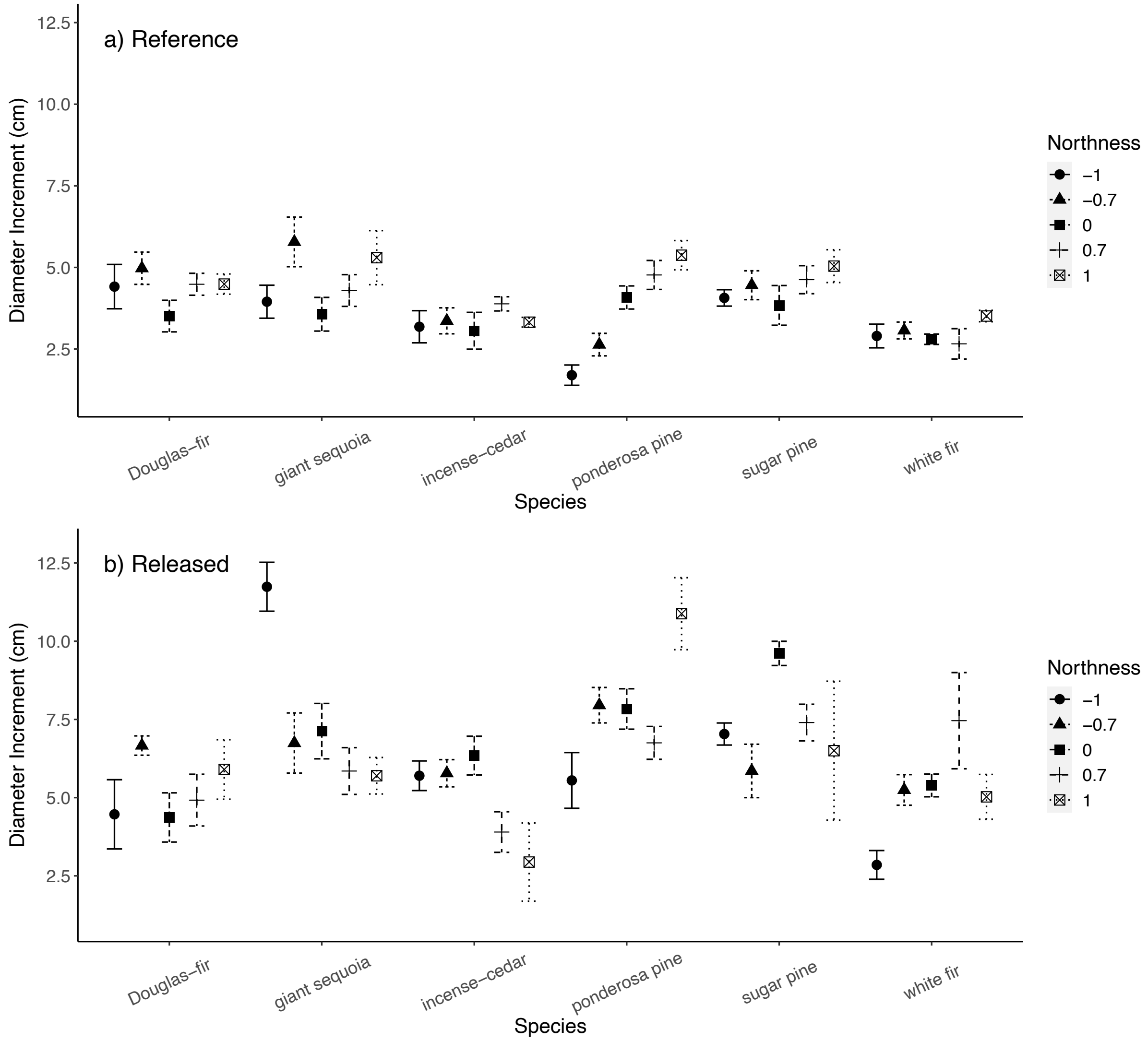


Figure S2. Mean diameter increment of edge trees planted in experimental groups between the 15th and 21st growing seasons at Blodgett Forest. Northness is described as cosine(aspect) of the tree location along the edge of the group. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

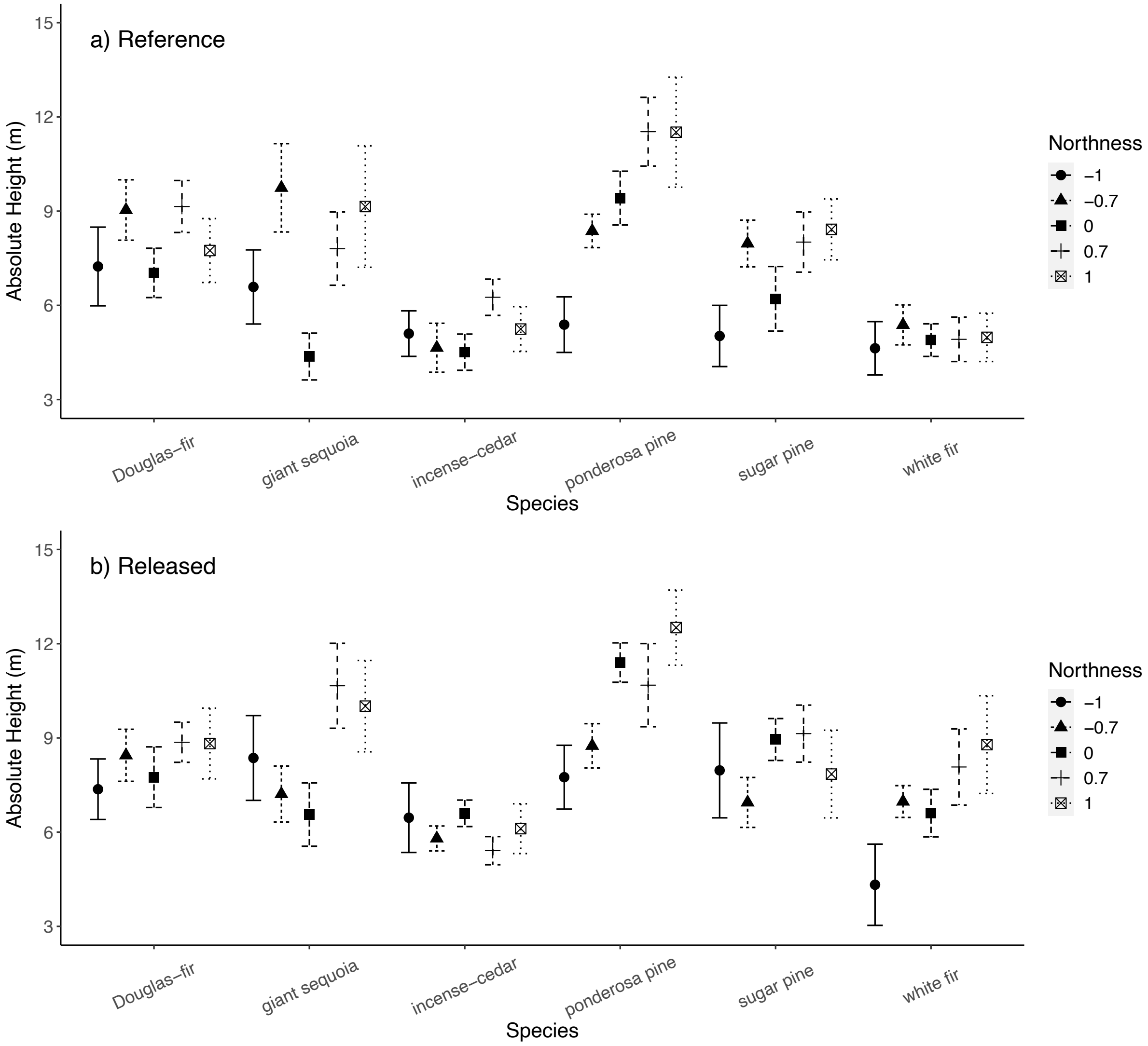


Figure S3. Mean height of edge trees planted in experimental groups after 21 growing seasons at Blodgett Forest. Northness is described as cosine(aspect) of the tree location along the edge of the group. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

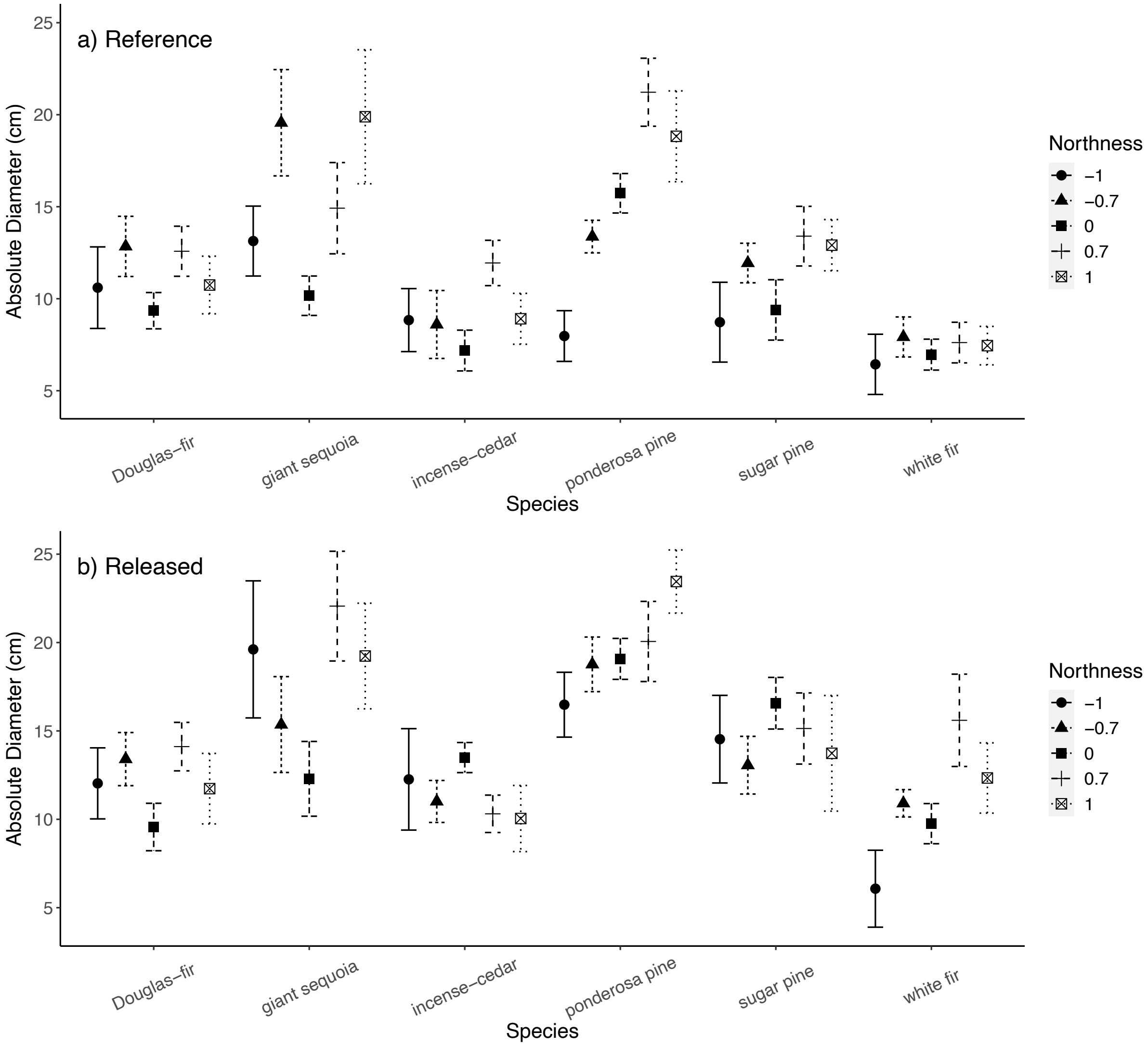


Figure S4. Mean diameter of edge trees planted in experimental groups after 21 growing seasons at Blodgett Forest. Northness is described as cosine(aspect) of the tree location along the edge of the group. Treatment refers to the implementation of the femelschlag harvest. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

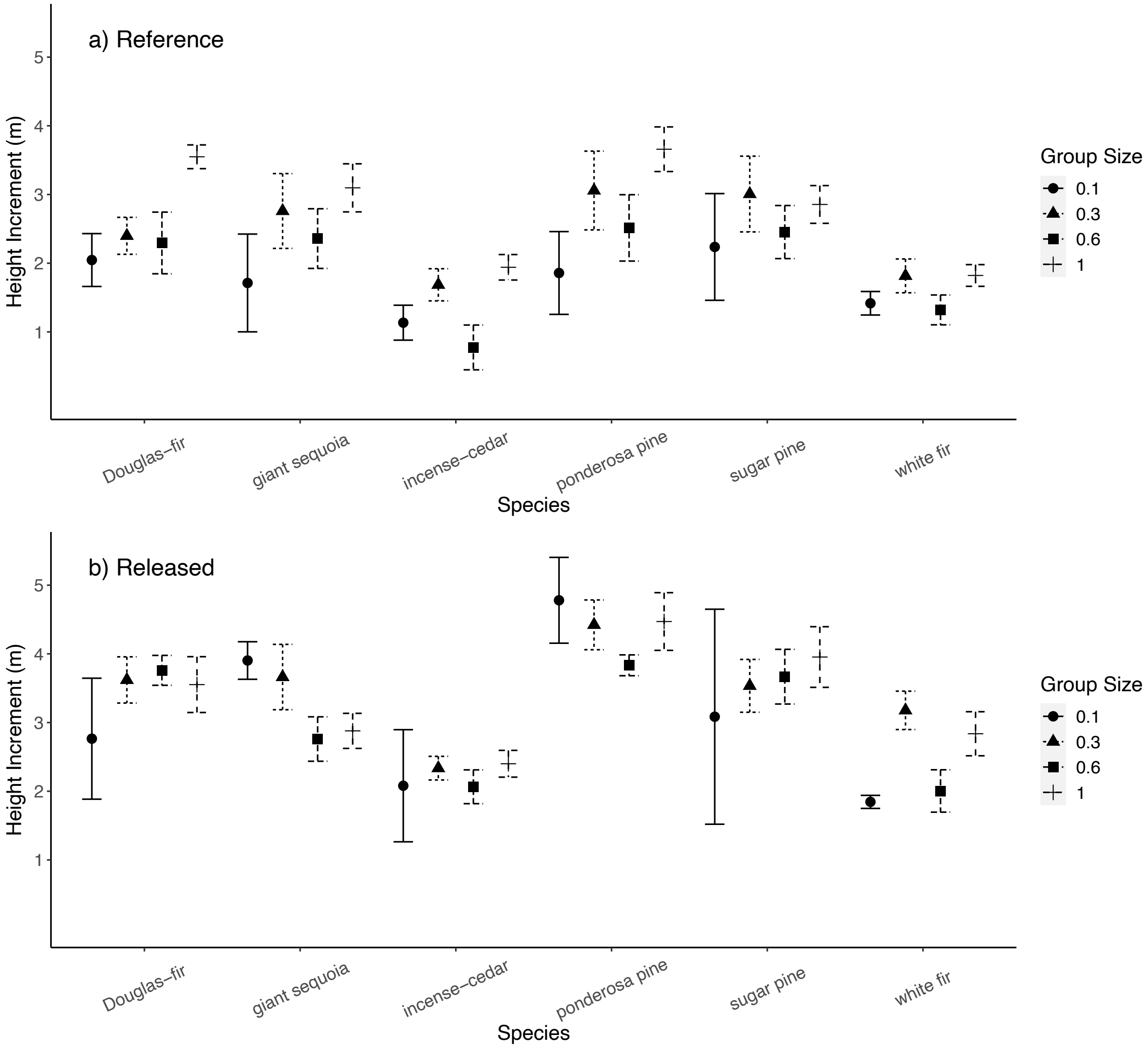


Figure S5. Mean height increment of edge trees planted in experimental groups between the 15th and 21st growing seasons at Blodgett Forest. Group size indicates the size of the original groups where the edge trees were planted. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

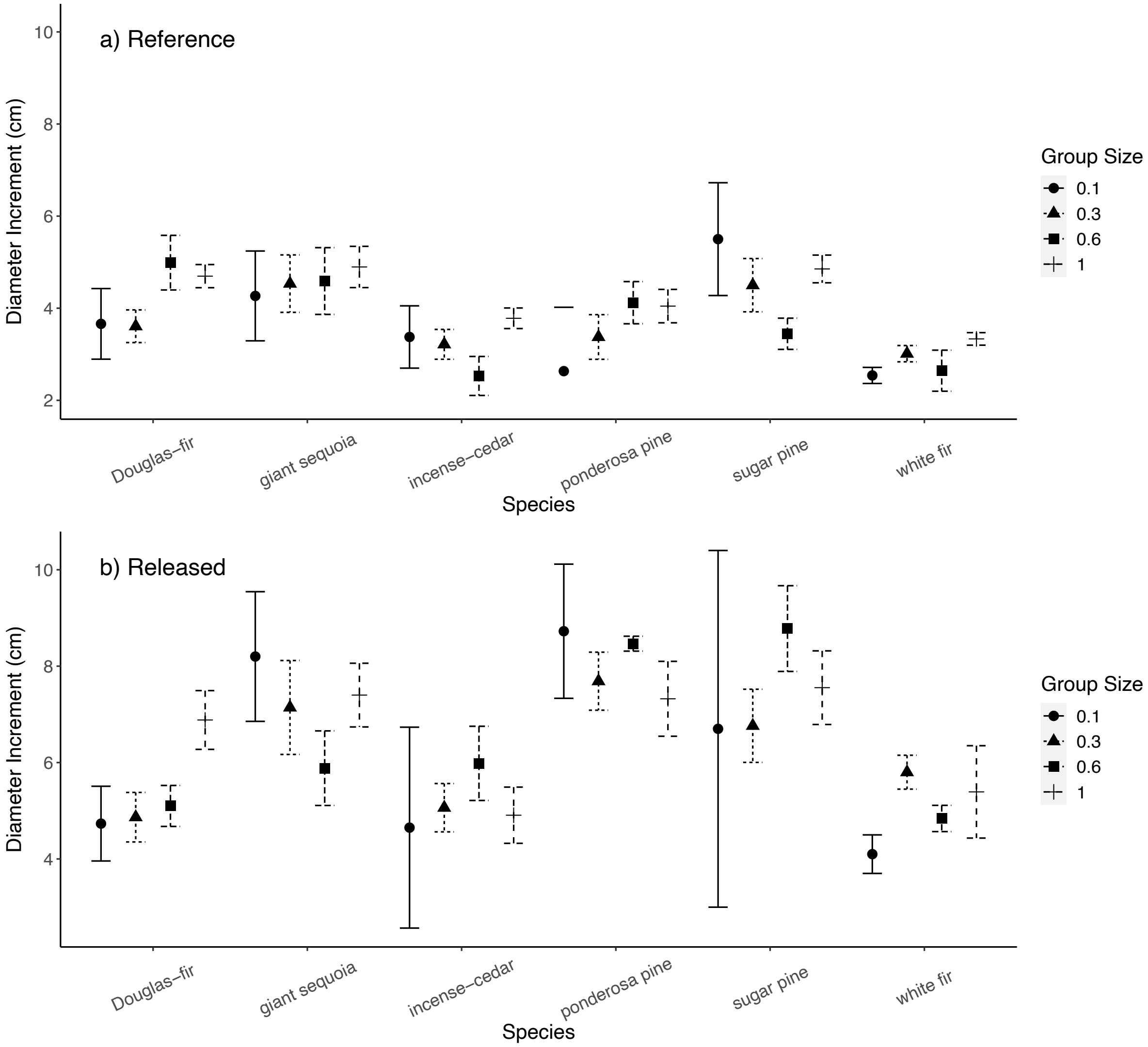


Figure S6. Mean diameter increment of edge trees planted in experimental groups between the 15th and 21st growing seasons at Blodgett Forest. Group size indicates the size of the original groups where the edge trees were planted. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

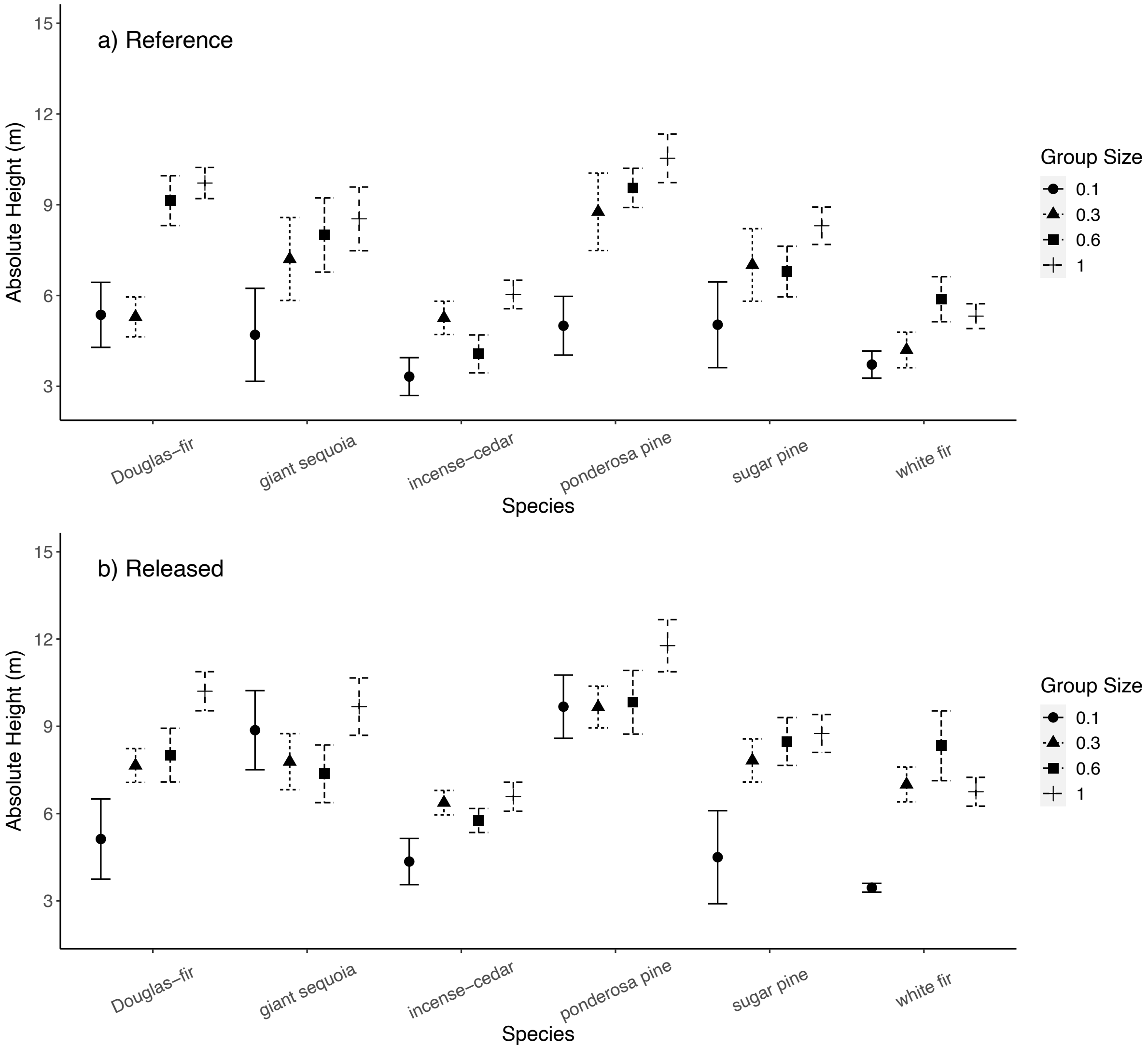


Figure S7. Mean height of edge trees planted in experimental groups after 21 growing seasons at Blodgett Forest. Group size indicates the size of the original groups where the edge trees were planted. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.

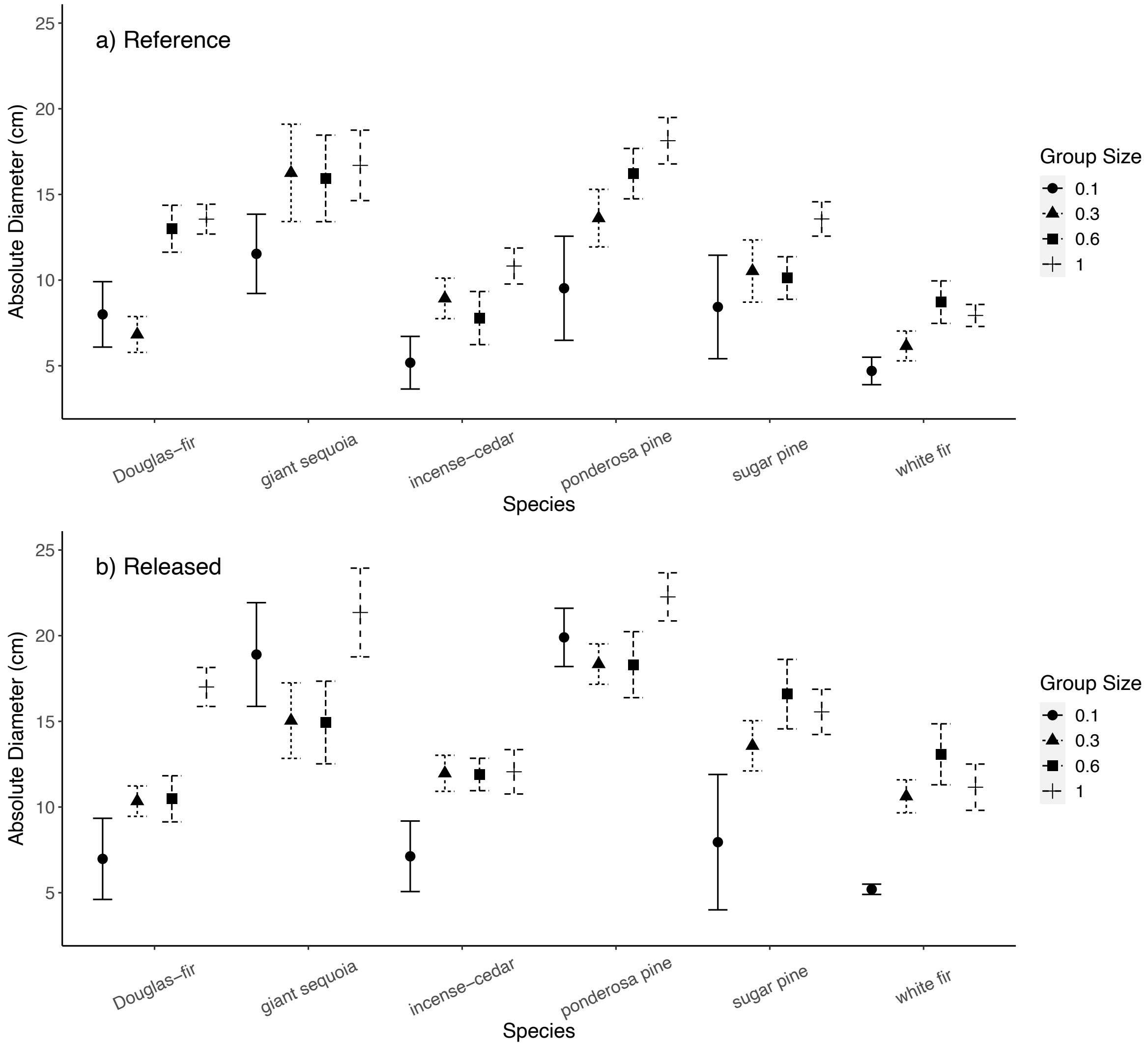


Figure S8. Mean diameter of edge trees planted in experimental groups after 21 growing seasons at Blodgett Forest. Group size indicates the size of the original groups where the edge trees were planted. Released locations are group edges adjacent to femelschlag harvests. Reference locations are group edges adjacent to the intact forest matrix.