Density Effects on Giant Sequoia (*Sequoiadendron giganteum*) Growth Through 22 Years: Implications for Restoration and Plantation Management

Robert A. York, Kevin L. O'Hara, and John J. Battles

ABSTRACT

Giant sequoia were planted at various densities and tracked for 22 years to quantify the effect of growing space on diameter, height, stem volume, branch diameter, and branch density. Beginning after just 4 years and continuing through year 22, both stem diameter and height growth were highly sensitive to initial planting density (expressed in this case as horizontal growing space per tree) within the tested range of 3.7 to 28.4 m^2. Through 22 years, treatments allocating the greatest growing space per tree had greater volume per tree with no tradeoff yet observed in stand level volume growth. Branch diameter along the stem generally increased with growing space, but branch density did not change. To meet objectives, this study demonstrates that management strategies should be tailored to species' specific growth strategies. Giant sequoia is characterized by rapid early growth coupled with exceptionally low mortality, which has relevance in both native grove restoration as well as plantation management contexts. The measurements in this study suggest either planting at low density or thinning giant sequoia very early in dense stands if the objective is to increase individual tree growth rates without a corresponding reduction in stand volume. Young stands developing following high-severity fires may benefit from low-severity prescribed burns if objectives are to increase average stem growth or the rate of canopy recruitment.

Keywords: spacing study, density management, intraspecific competition

Understanding the nature of competition between plants for finite resources is fundamental to the study of vegetation dynamics (Hutchings and Budd 1981). In young forest stands, it is essential for meeting objectives of management. The onset of competition and its influence on long-term management objectives inform decisions throughout stand development. The ability to predict competitive effects provides a practical guide for the timing and design of planting, thinning, pruning, or burning treatments to eventually meet objectives of growth, recruitment, vigor, or composition (Drew and Flewelling 1979). While outcomes can vary due to site-specific factors, the accuracy of predicting general treatment effects at the stand level improves greatly when informed by field experiments that control levels of competition via density manipulations and then track growth over time scales long enough to be relevant for planning (e.g., McClian et al. 1994, Harms et al. 2000).

Because of its rapid growth, decay resistance, great longevity, incomparable size, and resistance to fire, giant sequoia (*Sequoiadendron giganteum*) has exceptional potential to provide economic and ecological assets well beyond its native range (Knigge 1992, Stewart et al. 1994, Peracca and O'Hara 2008, Kitzmiller and Lunak 2012). In native groves, management objectives revolve around cohort establishment and canopy recruitment following regeneration failures related to fire suppression (York et al. 2012). Controlled density experiments have provided both basic biological insight and guidance for designing management prescriptions for most commercial tree species, including all of those co-occurring with giant sequoia (e.g., Speechly and Helms 1985, O'Hara 1988, Cochran and Barrett 1999, Zhang and Oliver 2006). Because it is not widely managed as a commercial species, however, such insights for giant sequoia are limited despite the relevance for both commercial and restoration applications.

In this study, we present the effects of initial planting density on giant sequoia growth through 22 years in a controlled field setting near its current native range. Using a classically designed density experiment, we track with high plot-level and temporal precision the trends in competitive effects over time. Stem diameter, height, branch diameter, branch density, and stem volume are the measurements of interest. We analyze this suite of growth parameters since each could be of interest from either a plantation management context or from a restoration context for giant sequoia. Further, the precise nature of the relationship between density and growth can

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This article uses metric units; the applicable conversion factors are: meters (m): 1 m = 3.3 ft; square meters (m^2): 1 m^2 = 10.8 ft^2; cubic meters (m^3): 1 m^3 = 35.3 ft^3; centimeters (cm): 1 cm = 0.39 in; kilometers (km): 1 km = 0.6 mi; hectares (ha): 1 ha = 2.47 ac.

vary distinctly between species and growth parameters, providing specific insights for predictions of competitive effects and corresponding management implications. We, therefore, focus on measuring the nature of the development of the density-growth relationships over time, an approach possible in this case because of the frequency and precision of measurements at regular intervals during stand development.

Methods

Study Site

Blodgett Forest Research Station (BFRS) is located on the western slope of the Sierra Nevada mountain range in California (38°52′N; 120°40′W). The study is within BFRS at an elevation of 1,320 m. The climate is Mediterranean with dry, warm summers (14–17° C) and mild winters (0–9° C). Annual precipitation averages 166 cm, most of it coming from rainfall during fall and spring months, while snowfall (~35% of total precipitation) typically occurs between December and March. Before fire suppression (ca. 1890), the median point fire interval in the area was 9–15 years (Stephens and Collins 2004). The soil developed from andesitic lahar parent material. Soils are productive, with heights of mature codominant trees at BFRS typically reaching 31 m in 50 years.

Vegetation at BFRS is dominated by a mixed conifer forest type, composed of variable proportions of five coniferous and one hardwood tree species (Tappeiner 1980). Giant sequoia is not among the five native conifer species present. BFRS is, however, approximately 16 km south of the northernmost native grove. The topography, soils, and climate of the study area are similar to the conditions found in native groves, although total precipitation at BFRS tends to be greater than in the southern Sierra Nevada where the majority of native groves occur. As within native groves, giant sequoia grows well in the study area, outgrowing all associated species through at least year 7 in planted canopy openings (Peracca and O'Hara 2008, York et al. 2004, 2011). In plantation settings throughout the Sierra Nevada, giant sequoias outgrow other conifer species through 3 decades after planting where soil productivity is high (Kitzmiller and Lunak 2012). Where it has been planted in Europe, it also typically outgrows other conifers (Knigge 1992).

Study Design and Analysis for Height and Stem Diameter

Seedlings were planted in 1989 at nine levels of density ranging from 2.1- to 6.1-m hexagonal spacing between seedlings. To ensure that a tree was growing at each planting location, seedlings were initially double-planted, with the less vigorous seedling of the pair removed after 2 years. Treatments were applied across 0.08- to 0.2-ha plots, depending on planting density (i.e., wider spacings required larger plots). Competing vegetation was removed periodically to control for any variation in resource availability not due to gradients in giant sequoia density (e.g., West and Osler 1995). Treatments were installed with a randomized block design (Figure 1), with each treatment randomly assigned once within three adjacent blocks (i.e., $n = 3$ plot replications for each level of density).

Measurements of height and dbh (1.37 m) for all trees following the 4th, 10th, 16th, and 22nd growing seasons are reported. For analysis, trees along the edges of the treated areas (i.e., "guard trees") were removed to avoid interactions between treatments. Trees that had a dead or missing neighbor on any side after 22 years were also removed from the analysis (32 planting spots had dead or missing trees). The final dataset was made up of 2,303 trees. Results through the 7th year were presented by Heald and Barrett (1999). Here, detailed analysis of density effects is done for the most recent measurement (year 22), and all of the diameter and height measurements from 6-year intervals are used to reconstruct the trend in density-related competitive effects over time. Measurements are analyzed with the plot as the experimental unit and density as a continuous variable ($n = 3$ replicates for each of 9 density levels = 27 total sample units).

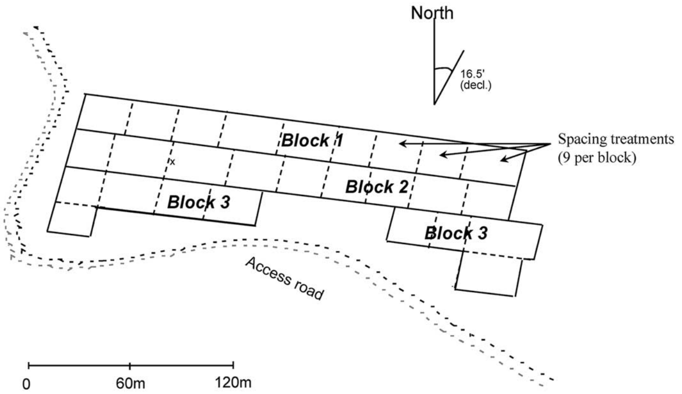

Figure 1. Overhead view of randomized block design from the giant sequoia density study at Blodgett Forest, CA.

The first step in the analysis of height and diameter growth was to fit the 22nd-year measurements with an appropriate equation that best described the relationship between density and tree size. We then used the selected 22nd-year equation to fit data from previous measurement years to reconstruct how the density effect developed. This approach has the drawback of assuming that the density-tree size relationship is similar over time because separate fits are not selected for each measurement period. It has the advantage, however, of providing the same slope parameter over time so that the trend of the density-size relationship can be quantified. Tracking the change in slope allowed us to profile the changing nature of competitive effects on the given growth parameter over time. For each level of planting density, the amount of horizontal growing space partitioned equally between each tree (m^2) was used as the predictor variable. Growing space was calculated by dividing the total space of each treatment area by the number of trees planted in the area with hexagonal spacing. The boundaries of the growing space for each treatment were defined to extend out beyond the stems of the perimeter trees, halfway to adjacent neighbor trees. Hence, growing space is here defined simply as the amount of horizontal space partitioned to each seedling at the time of planting and is related to linear distance between trees and inversely to tree density. From this point on, we use the term growing space to indicate stem density, but note that growing space is inversely related to density. The treatment gradient ranged from a minimum growing space of 3.7 m^2/stem (2,702 stems/ha) to a maximum of 28.4 m^2/stem (353 stems/ha).

We used the 22nd-year measurements to select the best model from a set of bona fide candidate models (*sensu* Johnson and Omland 2004) to describe the effect of growing space on average individual tree growth in terms of height and stem diameter. We then used the selected model to fit measurements from previous years, comparing the models' slope parameters and corresponding 95%-confidence intervals between years to track the change in competitive effects over time. Candidate models had to be simple (i.e., few parameters) quantifications of plausible growing space-size relationships that each represented separate biological mechanisms at work. The candidate set included four relationships. The first was a simple linear equation, reflecting an additive relationship between growing space and tree size (i.e., more space equals more growth without any diminishing or increasing returns):

$$Tree\ size = a + b^{*}growing\ space$$

where a is the y-intercept and b is linear coefficient (i.e., the slope). The management application of such a relationship is that individual tree growth is maximized at the widest spacing.

The second model was a log-linear fit, reflecting a multiplicative effect of growing space on tree size:

$$Tree\ size = a + b(log^{*}growing\ space)$$

A log-linear fit occurs when tree size increases monotonically across the range of growing space considered. Growth is maximized at the widest spacing, but unlike with a linear fit, the returns in terms of tree size diminish with the widest spacings.

The third model was a quadratic fit, reflecting an eventual negative effect of growing space on tree size:

$$Tree\ size = a + b^{*}growing\ space + c^{*}growing\ space^{2}$$

where c is the quadratic coefficient. A quadratic fit occurs when there is an eventual negative effect of increased growing space on tree size. This has been known to occur when, for example, trees grow taller as a response to near-neighbor shading (Gilbert et al. 2001).

The final model was a Michaelis–Menten fit, which is an asymptotic curve reflecting a saturating effect:

$$Tree\ size = d^{*}growing\ space\ /\ e + growing\ space$$

where d is the asymptote of the curve (the maximum tree size predicted) and e is the growing space at which tree size is half of maximum. This relationship implies a maximum growing space where further increases cause neither greater nor less in terms of tree size. It is worth noting that these mathematical relationships, when expressed in graphical form and when used for making inferences to management, are constricted by the limits of the data. For example, if a quadratic form were to be chosen, we obviously do not expect tree size to trend to zero. Nor would we expect a linear relationship to continue indefinitely. While differences between these curves can be subtle when correlations are variable, the high precision of this particular data set allowed us to distinguish between them. Akaike's information criteria weights (AIC_w), with a small sample correction (Sugiura 1978), were used to rank and choose the best models. AIC weights are likelihood transformations of raw AIC values, and are, therefore, more meaningful than raw values when comparing how well each model performed. An AIC_w of 0.80, for example, implies an 80% likelihood of that model being the best model when compared with the other candidate models and given the data (Burnham and Anderson 2002). While raw AIC values are typically interpreted as the lowest value being the best model, AIC weights are the opposite. We also report the evidence ratio, which is the ratio between the best model's AIC_w and each other model. The evidence ratio essentially measures *how much better* the best model was.

Measurements and Analysis for Branch Diameter, Branch Density, and Stem Volume

Branch diameter and branch density data were collected following the 16th year only (timed to coincide with a logical age for conducting artificial pruning). The branch closest to 1.37-m stem height on the west side of each tree was measured with digital calipers where the branch attached to the stem (while avoiding the swollen branch collar). To measure branch density, the total number of branches on the stem between 1.37 m and 1.67 m stem height were counted. The few epicormic sprouts encountered were not counted. As with height and stem diameter, branch diameter is generally expected to increase with growing space but a flattening or even declining relationship with growing space is within reason. A similar model selection approach as described above (using the same four candidate models) was, therefore, used to describe the relationship between growing space and branch diameter at age 16. With branch density, we had no a priori reason to believe that there would be a certain set of plausible relationships between growing space and branch density, if there was any relationship at all. We, therefore, tested for the presence of any relationship between growing space and branch density with simple linear regression. A significant slope at $P < 0.05$ was used to verify a relationship between growing space and branch density.

To estimate stem volume, we used a locally derived volume equation developed from a stem analysis of 34 giant sequoia trees in a nearby planted stand at BFRS. The local equation was preferred because of its close proximity with the study area and because there are no published equations derived from the sizes of trees used in this study.

The effect of density on year 22 stem volume was analyzed at both the individual tree and stand level. To estimate stand level volumes (m^3/ha), we divided each tree volume by the amount of physical space allocated to each tree given its specific growing space treatment. Simple linear fits were then used to describe the effect of growing space on both individual tree and stand volume growth. Rather than select a model from a number of candidates as described above for the direct tree-size measurements, we fit the data with one robust model that describes very generally the contrast between growing space effects at the individual tree and stand level. Significant slope parameters of linear regressions (at $P \leq 0.05$) for both individual tree and per ha volumes are then considered together to detect the tradeoff, if any, between individual and stand level growth as influenced by growing space. In other words, a tradeoff between stem and stand growth would be confirmed by a positive slope for stem growth and a negative slope for stand growth.

Results

Within the set of four candidate models, the log-linear curve was the best way of describing the 22-year effect of growing space on stem dbh (AIC_w=0.82). The ratio of AIC weights between the superior log-linear and the second-best quadratic curve (i.e., the evidence ratio) was 7.7, indicating good support for the log-linear model. Other models had evidence ratios of greater than 12. The practical significance was that stem diameter more than doubled, increasing from 15.4 to 35.7 cm across the range of growing space (Figure 2A). Although there was a large change in diameter across the range of growing space treatments, note that only a small difference (1.6 cm) in measured mean diameter occurred between the two highest growing space treatments. This slight flattening of the relationship along with the steeper relationship in the lower growing space treatments was why the log-linear fit was a particularly good model. The magnitude of the effect of growing space on diameter growth increased steadily across the measurement period (Figure 2C), as the difference between the larger trees at greater growing

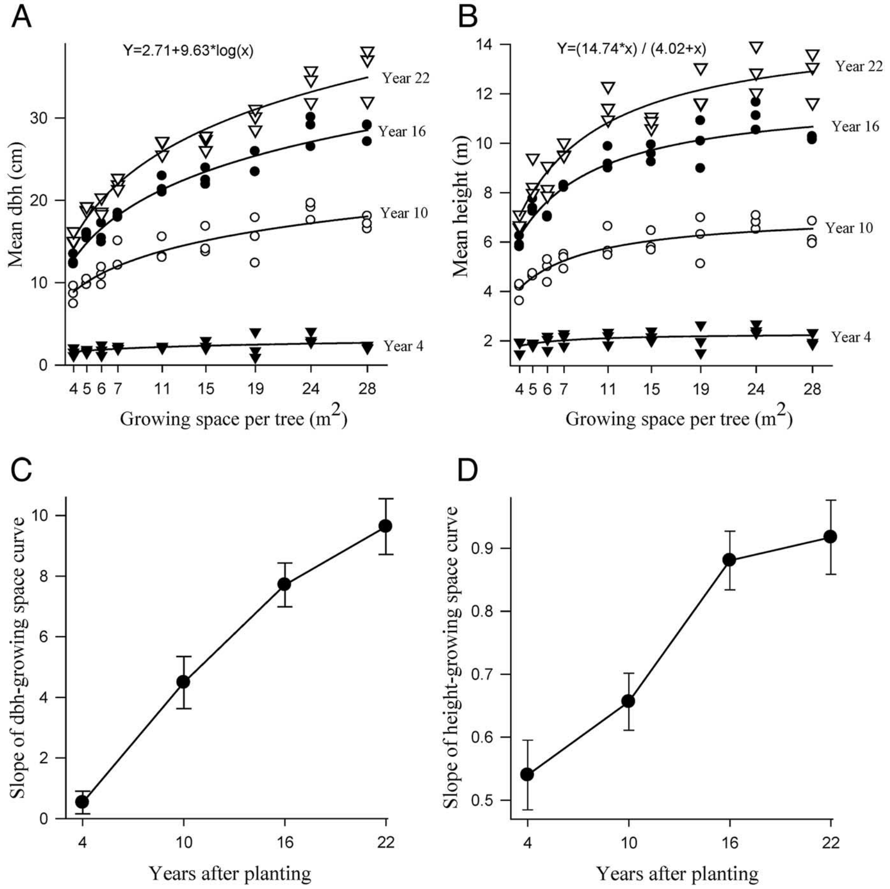

Figure 2. Effect of density on growth of planted giant sequoia through 22 years. A. and B.: mean dbh and height per treatment area against growing space (i.e., planting density); means shown are from repeated measurements following the 4th, 10th, 16th, and 22nd growing seasons; equations given are for the 22nd-year curves. C. and D.: trends in the slope parameters from the above curves; bars are 95%-confidence intervals for the parameter. The slope and confidence limits for the height curve (panel D) are calculated as the first derivative along the curve where x = 1/2 * asymptote.

space treatments and the smaller trees at lesser growing space treatments has increased over time as indicated by the increasing slope parameter.

Height was best fit with an asymptotic curve ($AIC_w=0.79$; Figure 2B). The second-ranked model (log-linear) had an AIC_w of 0.19 and evidence ratio of 4.2 (all other model evidence ratios > 37). The asymptotic curve, therefore, had strong support from the data. As with diameter, height increases rapidly with growing space at the lower levels of growing space. Instead of continuing to increase at greater amounts of growing space, however, height at year 22 is predicted to peak at 14.7 m tall. Despite the saturating relationship, the differences across the growing space range are still large—the measurements nearly doubling between the lowest and greatest growing space levels. The halfway point to the asymptote is reached at an available growing space of 4.0 m^2. This halfway point and the asymptote are the two parameters in the asymptotic curve. The slope of the tangent at this halfway point (calculated from the first derivative at x=½*asymptote) increased substantially with stand development until year 16, and then did not change between the 16th and 22nd years (Figure 2D).

The relationship between growing space and branch diameter was described well with a quadratic curve ($AIC_w=0.91$; Figure 3), which was superior to other models (all other model evidence ratios > 12). After 16 years of growth, the size of the branch closest to breast height increased with growing space up until a slight decline predicted at the greatest amount of growing space. As one might expect, this relationship was similar to the one for stem diameter at year 16 (Figure 2B), reflecting the high symmetry of crown shape in

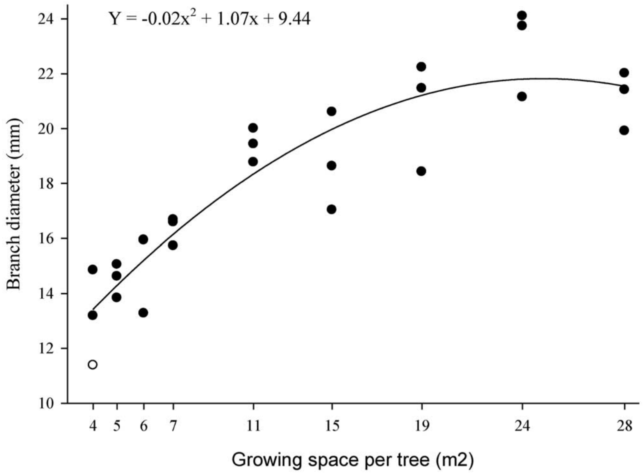

Figure 3. Effect of planted growing space on giant sequoia branch diameter growth after 16 years. The relationship is modeled with a quadratic fit (adjusted $r^2 = 0.95$).

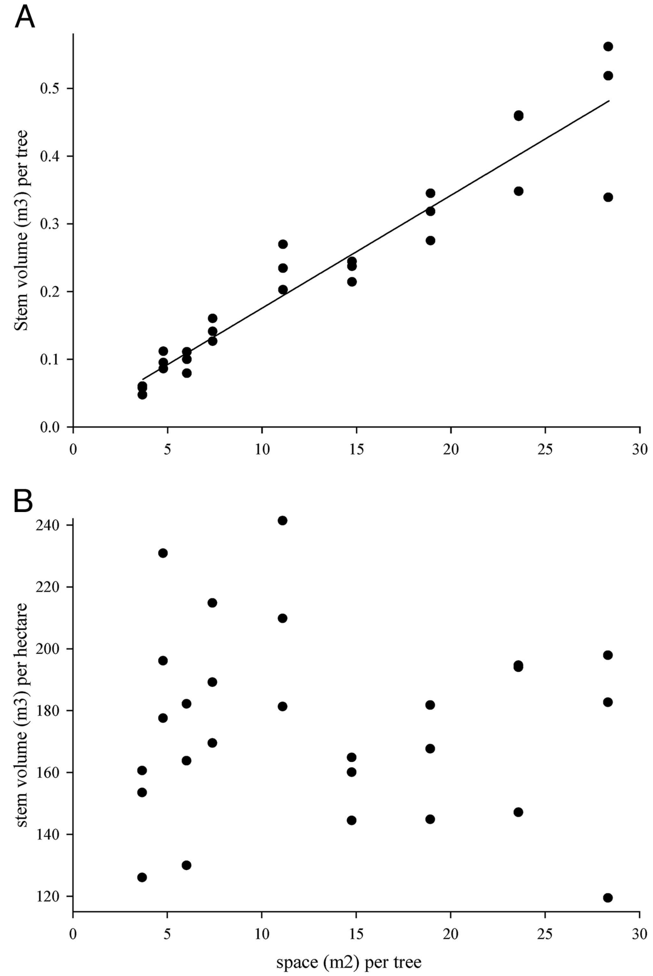

Figure 4. Density effects on stem volume (A) and stand volume (B) after 22 years for giant sequoia at Blodgett Forest, CA. A linear regression (adjusted $r^2 = 0.90$) is shown for the relationship between horizontal growing space treatment (m^2 per tree) and stem volume per tree (A). No relationship was detected between growing space treatment and total stem volume per ha (B).

young giant sequoia. Crowns were also full at year 16, most having close to 100% live-crown ratio. There was no relationship at all between growing space and branch density ($P = 0.94$). It is notable that branch density was exceptionally high in general. The average count for all trees was 10.8 branches along the stem between 1.37- and 1.67-m-height aboveground (i.e., 36 branches per meter of stem). Assuming branch density was the same along the entire length of stems and given an average tree height across all growing space treatments of 10.4 m at year 22, this represents an average of 374 branches per tree. Put another way, trees produced 17 branches per year!

Volume per tree increased with growing space (Figure 4A) with high consistency among replicates (adjusted $r^2 = 0.90$). When expanded to volume per ha, however, no relationship with growing space was detectable given the high variability (Figure 4B). A decreased number of stems per ha often results in lower total volume per ha compared to increased stem densities. In this case, however, the fewer but larger trees grew at a rate fast enough to compensate for any loss of total volume growth due to low stem density. A notable result, therefore, was that no tradeoff between stem and stand volume was detected.

Discussion

Growing Space Effects on Tree Size

In agreement with most density studies, both height and diameter growth increased with growing space but with diminishing response as growing space reached the higher extreme. As also is typical, (e.g., Harms et al. 2000, Henskens et al. 2001), diameter growth was more sensitive to growing space than height growth, indicated by the selection of a log-linear fit for diameter versus an asymptotic fit for height. The log-linear fit suggests a relationship where diameter increases across the entire range of growing space, while the asymptotic fit predicts a leveling off with increased growing space. While height growth was less sensitive to growing space compared to diameter growth, it was still surprisingly sensitive when considering the absolute change in height growth across the treatment range considered here. The range in density treatments we used is similar to those used in studies of other species, which had relatively little change in height growth with stem density (e.g., Smith 1980, McClian et al. 1994, Harms et al. 2000, Henskens et al. 2001). Because of the large change in height growth observed in this study, we consider giant sequoia to be an outlier in its relationship between height growth and density. Even after redoing the analysis with only the 10% tallest trees from each replication (i.e., those most likely to be retained as "crop trees" in a plantation management context or those most likely to "replacement trees" for very old trees in a restoration context), the asymptotic fit is still the selected model for height with large differences between low and high growing space treatments. It is clear, therefore, that significant increases in both diameter and height growth can be achieved with treatments that partition horizontal growing space to relatively few trees in young stands of giant sequoia.

The lower sensitivity of height growth to competition in most tree species can be explained physiologically by the high prioritization of carbon allocation to apical rather than cambial growth (Lanner 1985). Giant sequoia (and likely others in the *Cupressaceae* family) may not be as strictly confined to prioritizing height growth, possibly because of differences related to a sustained growth strategy that correlates growth more closely with current resource availability as opposed to the prior growing season's net resource availability (Oliver and Larson 1996). A higher priority to height growth typically leads to an asynchrony between height and diameter growth with respect to the onset of competitive effects, where diameter growth differentiation is expected to occur before height differentiation (Hutchings and Budd 1981). For giant sequoia, however, density influences on diameter and height growth were in sync, both being detectable across the range of growing space treatments at the same time in this study by year 4 (Heald and Barrett 1999). This rapid early growth is reflective of its long-lived pioneer strategy of early site colonization immediately following disturbances (York et al. 2010).

The explanation for the relationships between growing space and branch size and density are intuitively apparent. The trees were less than 2 m tall when these branches were formed. There were growing space effects on height and diameter growth at this time (Figure 2C and 2D show that confidence intervals of the slopes for both diameter and height are greater than 0 at year 4), but effect magnitudes were subtle. Trees were all growing at roughly similar rates, also producing branches at similar rates. Branch size differences then developed between growing space treatments, paralleling stem diameter differences over time as larger branches were grown on larger trees (e.g., Auty et al. 2012, Alcorn et al. 2007). A high density of persistent branches is characteristic of giant sequoia from both native and European locations (Knigge 1992), and branch removal from artificial pruning has been noted as a potential way to increase commercial value (O'Hara et al. 2008). These results suggest that pruning effort on the lower portion of the stem should be expected to increase with growing space since trees with greater amounts of growing space will have larger branches but the same number of branches to prune. This increased effort could potentially be mitigated by pruning as early as possible when branch diameter is still small.

Through age 22, no clear tradeoff between tree and stand level volume production has occurred in this study. Individual tree size was maximized at the widest spacing without a concurrent decline in stand volume (tree size may have been even greater if lower densities were used in the experimental design). Both stand and individual volume growth were achieved at low densities. Relatively wide spacing in giant sequoia is, therefore, recommended whether objectives are to achieve large individual tree size *or* total stand volume growth at a young stand age. The relationships between size and volume with density will be tracked over time to reveal longer-term trends.

A distinct lack of growth differentiation within the plots and a lack of significant competition-related mortality are likely contributing to these patterns. Strikingly, only one of the 500 trees in the lowest growing space treatment died between years 10 and 16, but an additional 19 trees died between year 16 and year 22. These plots may, therefore, be on the verge of shifting between competition primarily causing growth differences toward causing survival differences between treatments. The distinct capacity for planted giant sequoia individuals to survive (if not grow) in low-resource environments has been observed in both plantation (York et al. 2006) and native grove (York et al. 2011) settings and is likely a major explanation for these atypical patterns.

Giant sequoia can be found throughout central and western Europe, due in large part to the desire of royal landowners to have the cachet of the largest species in the world present on their arboretums after the discovery of giant sequoia in the early-1800s (Libby 1981). Although originally planted for its novelty, its potential utility as a commercial species in Europe has also been recognized (Knigge 1992). Closer to its native range and more recently in the western United States, it has been planted in industrial forestry settings but primarily as an afterthought (Kitzmiller and Lunak 2012*).* Its potential value as a plantation species is, however, becoming more apparent globally, as modern plantations are sought for uses other than just timber production alone (Paquette and Messier 2010). These results help explain quantitatively why giant sequoia is an appealing species from a modern plantation management perspective. It grows rapidly with little early mortality even in high density stands. Because it is highly sensitive to competition in both diameter and height, growth can be influenced greatly by planting and thinning treatments with little tradeoff in total stand volume production (at least early in stand development). It could be grown in high densities to produce small dimension forest products such as poles, fence boards, or residual biomass. Alternatively, large stem size can be achieved relatively quickly with low densities, producing large carbon reserves per tree (potentially the largest possible individual tree reserve on the planet) with relatively low risk of loss from fire or disease (York et al. 2012). Put simply, giant sequoia can be managed for a variety of objectives.

There are no journal-published studies of giant sequoia thinning experiments that we are aware of. Some recommendations regarding thinning can be inferred from this and other relevant studies, however. To avoid competition-related reductions in individual tree growth entirely, it is clear that thinning would be necessary very early (~ year 4 on productive sites) in dense stands because of the rapid occupancy of resources by giant sequoia (Heald and Barret 1999, York et al. 2010). To apply to plantations or natural stands where growing space is much more variable, a more practical inference would be to consider the time at which competition was limiting growth substantially across all growing space treatments. This would push back the timing of thinning to sometime between year 10 and 16, when the departure in growth between the low and high growing space treatments is accelerating (Figure 2). Given either a variable density or low density stand, a thinning treatment by year 10 would seem appropriate for maintaining rapid stem growth. If the objective is to simply avoid mortality, however, then much higher densities could be maintained. More information on competition-related mortality will be possible after further measurements in the future.

In native groves where fire is often desired for sustaining giant sequoia, the process of how young giant sequoia will recruit into dominant canopy positions during and following repeated burns is a topic needing further monitoring and studies that inform management (York et al. 2012). The intertree competitive processes occurring in the plots in this study may be similar to the processes occurring in single-cohort stands of giant sequoia that initiate following moderate or high-severity fires. This study suggests that competitive effects in dense stands of young giant sequoia will begin limiting growth relatively early, well before frequent density-dependent mortality occurs. These high densities of giant sequoia could be maintained for long periods of time (several decades), as they can persist and eventually release from competition quickly (York et al. 2006). In a native grove, it may be a fire (and not a thinning) that would be the disturbance that alters competition dynamics within young giant sequoia stands. While this study's limitations do not allow us to recommend an appropriate age for burning in young giant sequoia stands, it is interesting to note that the approximately 10 years it took for competition to influence growth across all density classes in this study is similar to the fire return interval found in native groves (Swetnam 1993). In giant sequoia groves, a frequent burning (or thinning in areas where burning is not feasible) interval may, therefore, be desirable from both a growth maximization perspective as well as the perspective of aiming to use natural disturbances as a guide for management (e.g., Drever et al. 2006). How disturbance intensity and frequency influences giant sequoia recruitment will be an interesting topic for further study.

Literature Cited

ALCORN, P.J., P. PYTTEL, J. BAUHUS, R.G.B. SMITH, D. THOMAS, R. JAMES, AND A. NICOTRA. 2007. Effects of initial planting density on branch development in 4-year-old plantation grown *Eucalyptus pilularis* and *Eucalyptus cloeziana* trees. *For. Ecol. Manage.* 252 (1/3):41–51.

AUTY, D., A.R. WEISKITTEL, A. ACHIM, J.R. MOORE, AND B.A. GARDINER. 2012. Influence of early re-spacing on Sitka spruce branch structure. *Ann. For. Sci.* 69(1):93–104.

BURNHAM, K.P., AND D.R. ANDERSON. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. Springer-Verlag, New York. 488 p.

COCHRAN, P.H., AND J.W. BARRETT. 1999. Thirty-five-year growth of ponderosa pine saplings in response to thinning and understory removal. USDA For. Serv. Pacific Northwest Research Station Research Paper. 0:1–28.

Drever, C.R., G. Peterson, C. Messier, Y. Bergeron, and M. Flannigan. 2006. Can forest management based on natural disturbances maintain ecological resilience? *Can. J. For. Res.* 36:2285–2299.

Drew, T.J., and J.W. Flewelling. 1979. Stand density management an alternative approach and its application to Douglas-fir *Pseudotsuga menziesii* plantations. *For. Sci.* 25:518–532.

Gilbert, I.R., P.G. Jarvis, and H. Smith. 2001. Proximity signal and shade avoidance differences between early and late successional trees. *Nature*. 411:792–795.

Harms, W.R., C.D. Whitesell, and D.S. DeBell. 2000. Growth and development of loblolly pine in a spacing trial planted in Hawaii. *For. Ecol. Manage.* 126:13–24.

Heald, R.C., and T.M. Barrett. 1999. Effects of planting density on early growth of giant sequoia (*Sequoiadendron giganteum*). *West. J. Appl. For.* 14:65–72.

Henskens, F.L., M. Battaglia, M.L. Cherry, and C.L. Beadle. 2001. Physiological basis of spacing effects on tree growth and form in *Eucalyptus globulus. Trees.* 15:365–377.

Hutchings, M.J., and S.J. Budd. 1981. Plant competition and its course through time. *Bioscience.* 31:640–645.

Johnson, J.B., and K.S. Omland. 2004. Model selection in ecology and evolution. *Trends Ecol. Evol.* 19(2):101–108.

Kitzmiller, J.H., and G. Lunak. 2012. Growth of giant sequoia compared to ponderosa pine and other mixed conifers in California plantations. *West. J. Appl. For.* 27(4):196–204.

Knigge, W. 1992. Giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz) in Europe. USDA For. Serv. Pacific Southwest Research Station GTR-151, Visalia, CA.

Lanner, R.M. 1985. On the insensitivity of height growth to spacing. *For. Ecol. Manage.* 13:143–148.

Libby, W.J. 1981. Some observations on Sequoiadendron and *Calocedrus* in Europe. California Forestry and Forest Products, University of California, Department of Forestry and Conservation, Forest Products Laboratory, 12 p.

McClian, K.M., D.M. Morris, S.C. Hills, and L.J. Buse. 1994. The effects of initial spacing on growth and crown development for planted northern conifers: 37-year results. *For. Chron.* 70:174–182.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. *Can. J. For. Res.* 18:859–866.

O'Hara, K.L., R.A. York, and R.C. Heald. 2008. Effect of pruning severity and timing of treatment on epicormic sprout development in giant sequoia. *Forestry.* 81:103–110.

Oliver, C.D., and B.C. Larson. 1996. *Forest stand dynamics*. John Wiley and Sons, Inc., New York. 520 p.

Paquette, A., and C. Messier. 2010. The role of plantations in managing the world's forests in the Anthropocene. *Fron. Ecol. Environ.* 8(1):27–34.

Peracca, G.G., and K.L. O'Hara. 2008. Effects of growing space on growth for 20-year-old giant sequoia, ponderosa pine, and Douglas-fir in the Sierra Nevada. *West. J. Appl. For.* 23:156–165.

Smith, J.H.G. 1980. Influences of spacing on radial growth and percentage latewood of Douglas-fir, western hemlock, and western red cedar. *Can. J. For. Res.* 10:169–175.

Speechly, H.T., and J.A. Helms. 1985. Growth and economic returns after recommercial thinning nonuniform white fir *Abies concolor* stands in California USA. *For. Ecol. Manage.* 11:111–130.

Stephens, S.L., and B.M. Collins. 2004. Fire regimes of mixed conifer forests in the North-Central Sierra Nevada at multiple spatial scales. *Northwest Sci.* 78:12–23.

Stewart, D. M., S.H. Key, B.A. Waldron, and R.R. Rogers. 1994. Giant sequoia management in the national forests of California. USDA For. Serv. Pacific Southwest Research Station Gen. Tech. Rep. 151, Visalia, CA. 7 p.

Sugiura, N. 1978. Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics, Theory and Methods* A7:13–26.

Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. *Science.* 262:885–889.

Tappeiner, J.C. 1980. Sierra Nevada mixed conifer. P. 118–119 in *Forest cover types of the United States and Canada*, Eyre, F.G. (ed.). Society of American Foresters, Washington, D.C.

West, P.W., and G.H.R. Osler. 1995. Growth response to thinning and its relation to site resources in *Eucalyptus regnans. Can. J. For. Res.* 25:69–80.

York, R.A., R.C. Heald., J.J. Battles, and J.D. York. 2004. Group selection management in conifer forests: relationships between opening size and tree growth. *Can. J. For. Res.* 34:630–641.

York, R.A., J.J. Battles, and R.C. Heald. 2006. Release potential of giant sequoia following heavy suppression: 20-year results. *For. Ecol. Manage.* 234:136–142.

York, R.A., D. Fuchs, J.J. Battles, and S.L. Stephens. 2010. Radial growth responses to gap creation in large, old *Sequoiadendron giganteum. Appl. Veget. Sci.* 13:498–509.

York, R.A., J.J. Battles., A.E. Eschtruth, and F.G. Schurr. 2011. Giant sequoia (*Sequoiadendron giganteum*) regeneration in experimental canopy gaps. *Restor. Ecol.* 19:14–23.

York, R.A., N.L. Stephenson, M. Meyer, S. Hanna, T. Moody, T. Caprio, and J.J. Battles. 2012. Giant Sequoia in *A natural resource condition assessment for Sequoia and Kings Canyon National Parks*, Panek, J.A., J.J. Battles, J.T. Austin, C.A. Sydoriak, K.R. Nydick, A.M. Esperanza, D.S. Saah (eds.). Natural Resource Report NPS/SEKI/NRR—2012/XXX. National Park Service, Fort Collins, CO. 79 p.

Zhang, J., and W.W. Oliver. 2006. Stand structure and growth of *Abies magnifica* responded to five thinning levels in northeastern California, USA. *For. Ecol. Manage.* 223:275–283.