Applied Vegetation Science 13: 498–509, 2010
DOI: 10.1111/j.1654-109X.2010.01089.x

Radial growth responses to gap creation in large, old *Sequoiadendron giganteum*

Robert A. York, Danielle Fuchs, John J. Battles & Scott L. Stephens

Abstract

Questions: Do large, old *Sequoiadondron giganteum* trees respond to the creation of adjacent canopy gaps? Do other co-occurring tree species and younger *S. giganteum* adjacent to gaps also respond? What are the likely factors affecting growth responses?

Location: Mixed-conifer forests of the southern Sierra Nevada, California, USA.

Methods: We measured the growth response of large, old *S. giganteum* trees (mean DBH = 164 cm; ages estimated > 1000 yr) to gap creation by coring trees and comparing growth after gap creation to growth before gap creation. We also measured young *Abies concolor*, *Pinus lambertiana*, and young *S. giganteum*. Gap-adjacent trees were compared with non-adjacent reference trees. Tree rings were analysed for carbon isotope discrimination and for longer-term growth trend correlations with climate.

Results: Following gap creation gap-adjacent old *S. giganteum* grew more than reference trees. *Abies concolor* trees also exhibited a growth response to gap creation. No response was detected for young *S. giganteum* or *P. lambertiana*, although detection power was lower for these groups. There was no difference in carbon isotope discrimination response to gap creation between gap-adjacent and reference trees for old *S. giganteum* and radial growth was positively correlated with winter precipitation, but not growing season temperature.

Conclusion: It is unclear what caused the growth release in old *S. giganteum* trees, although liberation of below-ground resources following removal of competing vegetation appears to be a significant contributor. *Sequoiadondron giganteum*, the third-longest lived and the largest of all species, remains sensitive to local environmental changes even after canopy emergence. Management activities that reduce vegetation surrounding individual specimen trees can be expected to result in increased vigor of even these very old and large trees.

Keywords: Gap-based silviculture; Sierra Nevada mixed conifer; Water-use efficiency; Growth release; Specimen old growth trees; Giant sequoia; *Sequoiadendron giganteum*.

Nomenclature: Hickman (1993).

Abbreviations: WUE = water use efficiency.

Introduction

Large, old trees are complex features that contribute to the structural make-up of old forests (Van Pelt & Sillett 2008; Bauhus et al. 2009). In western North American forests, many agents (e.g. fire suppression, exotic invasion and climate change) affect the processes that sustain large trees (Abella et al. 2007; Lutz et al. 2009). Large *Sequoiadendron giganteum* (Lindl.) Bucholz (giant sequoia), in particular, stand out as archetypal old forest structural features because of their massive size and great longevity (Stephenson & Demetry 1995). Declines in *S. giganteum* regeneration over the past century (Stephenson 1994) have led to efforts to initiate young cohorts (Demetry et al. 1995; York et al. in press). The success of these efforts depends on the persistence of mature *S. giganteum*, which hold huge banks of seeds stored in serotinous cones in their crowns (Harvey et al. 1980), providing a source of seed for recovering populations. Large trees such as *S. giganteum* that persist through moderate or severe disturbances can influence post disturbance vegetation dynamics via seed dispersal and microclimate alteration (Keeton & Franklin 2005).

Disturbances that result in distinct canopy gaps alter community composition and structure by initiating within-gap regeneration, but they can also influence adjacent mature trees (Runkle 1982; York & Battles 2008). In Sierra Nevada mixed

York, R.A. (Corresponding author, ryork@berkeley.edu) & **Battles, J.J.** (jbattles@berkeley.edu): Center for Forestry, University of California Berkeley, 4501 Blodgett Forest Road, Georgetown CA 95634 University of California Berkeley, Environmental Science, Policy, and Management, 137 Mulford Hall, UC Berkeley 94720-3114.
Fuchs, D. (dffuchs@gmail.com) & **Stephens, S.L.** (sstephens@berkeley.edu): University of California Berkeley, Environmental Science, Policy, and Management, 137 Mulford Hall, UC Berkeley 94720-3114.

conifer forests, *S. giganteum* regeneration is linked with distinct canopy gap formation (Stephenson 1994; Stephens et al. 1999; York et al. in press), but gap creation effects on adjacent large *S. giganteum* trees have not been studied; and effects of gap creation on adjacent large trees are generally not predictable from existing physiological information. Tree growth rates in most species are generally expected to decline as upper size or age limits are approached (Weiner & Thomas 2001). Moreover, large *S. giganteum* often already have emergent crowns mostly exposed to full sunlight before gap creation so a disturbance will not necessarily increase the amount of available light. In addition, they may tap deep water sources (Anderson et al. 1995) that are insensitive to changes in nearby vegetation. These arguments suggest that adjacent trees would not respond to gap creation. Conversely, *S. giganteum* may be similar to old trees of some other species that maintain the capacity to respond to increases in resource availability (Phillips et al. 2008). Large trees in western USA forests in particular may be experiencing heavy competition for resources (especially below-ground resources) with surrounding lower-canopy trees as forests have become denser following a century of fire suppression (Ansley & Battles 1998). Their response to gap creation is important, as treatments designed to build resilience and promote *S. giganteum* regeneration at the stand scale are considered as management options (Stephens et al. 1999; Piirto & Rogers 2002). For individual specimen trees, status and response to changes in surrounding vegetation (caused, for example, by fire suppression, prescribed fires or fire hazard vegetation removal) are of particular interest to managers and visitors.

In this study, we ask whether large *S. giganteum* respond to gap creation and, if so, what are the likely drivers of the response. We measured radial growth responses of large *S. giganteum* and co-occurring species to experimental gap creation within a native grove in the southern Sierra Nevada of California. We use patterns of growth ring thickness as an indicator of the vigor of individual trees and a quantitative measure of their response to gap creation. As growth is often sensitive to water availability in dry western forests (Law et al. 2001; Royce & Barbour 2001), we looked for changes in intrinsic water-use efficiency (WUE), as estimated from carbon isotope ratios, in individual *S. giganteum* trees following gap creation as a possible explanation of treatment effects. We also looked for correlations between radial growth and climate over a 30-yr period in order to explain longer-term trends in *S. giganteum* radial growth.

Methods

Study area

Experimental gaps were created at California Department of Forestry Mt Home Demonstration Forest on the western slope of the southern Sierra Nevada, California, USA. The study area is within the Mt Home grove, which is near the southern end of the range of *S. giganteum* and is one of the largest of about 75 groves that make up the native population (Willard 2000). Gaps were created at two locations: the Fraser Mill site (36°14′N, 118°41′W) at an elevation of approximately 1950 m and the nearby Rockcrusher site (36°13′,N, 118°40′,W) at an elevation of approximately 2070 m. Precipitation at Mt Home averaged 92 cm yr^{-1} and ranged between 34 and 170 cm yr^{-1} between 1976 and 2005. Average annual temperature was 6.7°C with a range from 5.8 to 8.7°C.

Forests at Mt Home are primarily Sierra Nevada mixed conifer forest type (Fites-Kaufman et al. 2007) with the addition of *S. giganteum*. Other canopy species include *Calocedrus decurrens* Torr., *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr., *Pinus lambertiana* Dougl., *Pinus ponderosa* Dougl. ex. Laws., and *Quercus kelloggii* Newb. Before fire suppression policies and grazing introduced in the 1860s, fires within *S. giganteum* groves occurred at intervals of approximately 2–13 yr (Swetnam 1993).

Experimental design

In a separate study focusing on regeneration response of *S. giganteum* to gap formation (Stephens et al. 1999), 36 canopy gaps were created in 1993, distributed evenly among sizes ranging from 0.01 to 0.3 ha. This size range is consistent with gap-based silviculture regimes in mixed conifer forests and with pre-settlement era gap-size ranges estimated by reconstruction studies (Bonnicksen & Stone 1982; Demetry et al. 1995; Piirto & Rogers 2002). We consider this gap-size range to be representative of what would occur under management or restoration scenarios; gap size is not an experimental treatment but contributes to variation in measurements.

Gaps were located on similar aspects (generally west facing) and slopes (10–40%). Along the perimeter of each gap, there were two to five very large, old *S. giganteum*. ‘Old’ *S. giganteum* were distinguished from younger trees using characteristic features of fire scars, trunk reiterations and a lack of lower branches (including dead branches). The old trees used in this study averaged 164-cm DBH with a maximum of 444 cm.

Sampling was designed to assess radial growth response of old *S. giganteum* to gap creation. Because growth increases or decreases following gap creation can be caused by forces not related to gap creation (e.g. drought, insect attack), the sample of gap-adjacent trees was compared against a reference sample of trees from the intact forest surrounding the gaps. This created two treatment groups: gap-adjacent and non-adjacent reference trees. The intact forest surrounding the reference trees was subject to diffuse canopy disturbances from individual tree deaths, but did not have any distinct canopy gaps similar in size to the harvested gaps. Young *S. giganteum* (trees without the distinguishing old-tree features listed above) were measured and analysed separately from old trees. *Pinus lambertiana* and *A. concolor* are common along gap perimeters and were also measured, but we did not distinguish between young and old trees because this classification is much more subjective with these species. Sampling took place after the 2005 growing season, 13 yr following the gap-creation treatment. The gap-adjacent sample of trees was selected by visiting each gap and coring all old *S. giganteum* along gap edges. In addition to the old *S. giganteum*, alternating trees along all gap perimeters were cored to build samples for young *S. giganteum*, *P. lambertiana* and *A. concolor* (sample sizes are therefore proportional to density). Trees that were overtopped by neighboring trees or that were smaller than 30-cm DBH were excluded.

The reference sample was compiled by selecting trees from points located 20 m away from the north and south edges of each gap. At each 20-m distant point, the closest tree directly to the north and south of the point, regardless of species, was cored. Previous work in the central Sierra Nevada found that the influence of gap creation on the growth of surrounding trees did not extend beyond 10 m from gap boundaries (York & Battles 2008). Therefore, we were confident that reference trees were sufficiently far away from gaps to not be influenced by gap creation. As with gap-adjacent trees, reference sample trees could not be overtopped by neighboring trees and were at least 30-cm dbh. At every reference sampling point, the closest old *S. giganteum* tree was also sampled in order to ensure a sufficient sample size since these trees were our primary interest.

Stemwood material for carbon isotope analysis was collected with a large-diameter (10-mm) increment borer. Two old trees adjacent to each gap at the Fraser Mill site were selected randomly for sampling. All old trees from the reference population (from 20-m distant points to the north and south of gaps) were sampled. Three reference points did not have an old *S. giganteum* available that was at least 20 m away from a gap. A total of 32 gap-adjacent trees and 29 reference were trees sampled for carbon isotope analysis. All cores were stored in paper sheaths for transport to the lab.

Sample processing and data analysis

For growth analysis, we used small-diameter cores from 114 old *S. giganteum*, 48 young *S. giganteum*, 55 *P. lambertiana*, and 277 *A. concolor*. Cores were dried, mounted and sanded to increase ring visibility. Annual radial increments from 1976 to 2005 were measured to the nearest 0.01 mm using a dissecting microscope and a sliding stage micrometer.

Analyses were done separately for old and young *S. giganteum*, *P. lambertiana*, and *A. concolor* to detect effects of gap creation on growth of gap-adjacent trees, compared to reference trees. Pre-gap-creation growth was averaged over 5-yr (1989–1993) and 10-yr (1984–1993) periods. Post-gap-creation growth was averaged over equivalent periods following the harvest (1994–1998 and 1994–2003). A profile analysis using multivariate ANOVA of repeated measures (MANOVAR) was used to test for non-parallel trends in growth between gap-adjacent and reference trees. The response variables in the MANOVAR model were pre-gap-creation and post-gap-creation growth, analysed separately for 5- and 10-yr periods. The within-subject effects were time, which tested whether the trends were flat, and a time×treatment interaction, which tested whether the trends were parallel between gap-adjacent and reference trees. The time×treatment interaction is the main effect of interest because it detects differences in growth trends between gap-adjacent and reference trees. Tree location was the between-subject effect, which tested whether overall growth increments were different between gap-adjacent and reference trees, regardless of time. Statistical conclusions were based on *F*-test statistics with the determination of significance at $P<0.05$. When growth trends were different between gap-adjacent and reference trees for a given species or size class, yearly growth patterns were displayed by graphing radial growth trends across the 20-year study period.

Large-diameter cores were used to obtain carbon isotope ratios ($\delta^{13}C$) of growth rings in old *S. giganteum*. Rings were first dated, then separated, using a razor blade, into two sections representing the 5 yr before and after gap creation. For each core, the late wood from the 5 yr before gap creation (1989–1993) was separated from the early wood and pooled into one sample, and the latewood from the 5 yr after gap creation (1994–1998) was pooled for a second sample. Early wood material was not used. The latewood was isolated because soils in this region are more depleted of soil moisture late in the growing season (Royce & Barbour 2001) and water status differences should therefore be more easily detected (Schulze et al. 2004). Using latewood also helps to avoid carry-over effects of carbon from the previous year (Livingston & Spittlehouse 1996). After drying at 60°C, the isotope samples were ground to a fine powder with a Wig-L-Bug ball mill (Dentsply Rinn, Elgin, IL, US). Approximately 5 mg of each ground sample was weighed into a tin capsule and combusted in a continuous-flow isotope-ratio mass spectrometer at the Center for Stable Isotope Biogeochemistry at the University of California at Berkeley, USA.

Isotope ratios (δ^{13}C) within the growth rings reflect crown-level intrinsic WUE by recording photosynthetic activity per unit of stomatal conductance (Farquhar & Richards 1984). Carbon within cell walls is immobile once deposited in stemwood (Tans et al. 1978), and can therefore be used to reconstruct past WUE changes. Because the isotope ratio of the atmosphere changes over time (Keeling et al. 1989), time-series of isotope ratios may need to be corrected. Between 1989 and 1998, the isotope ratio of atmospheric CO_2 changed by about 0.12 (Keeling et al. 2005). This difference was not large enough to influence the analysis, so no atmospheric correction was made. We interpret changes in δ^{13}C following gap creation among gap-adjacent trees compared with reference trees as an indication of a physiological adjustment in WUE to changes in water availability. δ^{13}C data were analyzed with MANOVAR. The response variables were δ^{13}C prior to and following gap creation. Within-subject effects were time and a time × treatment interaction, testing for trends in δ^{13}C over time and for non-parallel trends between gap-adjacent and reference trees. The between-subject effect was tree location. As with the growth data, the time × treatment interaction was the main effect of interest, indicating a significant physiological adjustment to gap creation.

Climate effects on growth

Diameter growth in Sierra Nevada conifers is positively correlated with winter precipitation and, to a lesser extent, summer air temperature (Battles et al. 2009; Robards 2009). Although year-to-year variation in these factors was large at our study site, trends in both of these variables coincided with the timing of harvest (Fig. 1; Climate data are available at http://www.fire.ca.gov/resource_mgt/resource_mgt_stateforests_data.php). For the 5 yr before harvest, winter precipitation was, on average, 15 cm lower than the 30-yr mean (1976–2005) and reached a minimum in 1990. In the 5 yr following harvest, winter precipitation was 16.3 cm more than the long-term average and reached a maximum in 1997 (Fig. 1). The trend in summer air temperature was less extreme but in general, summers were warmer in the 10 yr after the harvest than before the harvest (Fig. 1).

Because the observed trends in climate coincided with the timing of our experimental treatment and because *S. giganteum* was not included in the climate-sensitive growth model developed by Robards (2009), we analysed the sensitivity of *S. giganteum* diameter growth to winter precipitation and summer air temperature. To examine these climatic factors on *S. giganteum* growth, we removed endogenous neighborhood influences in the growth record by standardizing (linear fit) and detrending (second-order autoregressive process) the raw ring widths. We applied robust mean estimation procedures to obtain a chronology [option 'resid' in the ARSTAN computer program (Holmes & Cook 1986)], which highlights the common climate signal in tree growth while removing any autocorrelation. For this analysis, all *S. giganteum* samples were included regardless of location or size. An independent test on the resulting chronology detected no time lags or other autocorrelation in the time series. To quantify correspondence between climate and growth, we used the Pearson-product moment correlation coefficient. Statistical significance was evaluated with two-tailed, *t*-tests. Statistical analyses were done with JMP statistical software (version 8.0; SAS Institute, Cary, NC, US).

Results

In general, trees grew more rapidly following gap creation compared with before gap creation, regardless of proximity to gap. This was the case for both old trees (5-yr interval, $P < 0.01$; 10-yr interval, $P = 0.04$) and young trees (5-yr interval, $P < 0.01$; 10-yr interval, $P = 0.01$) of *S. giganteum*. *A. concolor* also grew more following gap creation ($P < 0.01$ for both 5- and 10-yr intervals). *Pinus lambertiana* grew

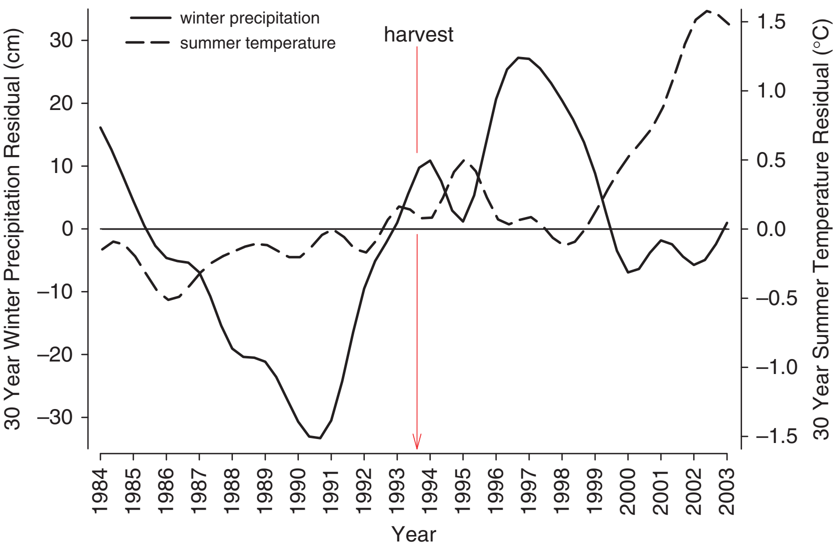

Fig. 1. Precipitation and temperature trends at Mt Home State Demonstration Forest, California, USA. Residual values are displayed for average air temperature in the summer (Jun–Sep) and total precipitation in the winter (Oct–Feb). Trends in climate parameters are presented in relation to the timing of the harvest. Lines represent cubic splines fit through 3-yr moving averages of the 30-yr residuals (1976–2005).

Table 1. Radial stem growth of gap-adjacent and reference trees prior to and following gap creation within a native giant sequoia grove at Mt Home Demonstration Forest, California, USA. Annual radial growth (mm) is averaged over 5- and 10-yr periods before and following gap creation. *P*-values are from a repeated measures MANOVA testing for an interaction between growth and time (i.e. testing for non-parallel trends between gap-adjacent trees and reference trees).

	MANOVAR *P*-value	Gap-adjacent trees		Reference trees		Gap-adjacent trees		Reference trees	
		5-yr pre-gap	5-yr post-gap	5-yr pre-gap	5-yr post-gap	10-yr pre-gap	10-yr post-gap	10-yr pre-gap	10-yr post-gap
Old *Sequoiadondron giganteum*	0.02	1.32	1.64	1.09	1.18	1.49	1.85	1.24	1.23
Young *Sequoiadondron giganteum*	0.72	2.47	3.11	2.29	2.8	2.71	3.59	2.52	2.93
Abies concolor	<0.01	1.75	2.22	1.84	1.99	1.87	2.26	1.96	1.89
Pinus lambertiana	0.93	1.88	2.33	1.92	2.23	2.02	2.34	2.21	2.08

more following gap creation at the 5-yr interval ($P<0.01$), but not the 10-yr interval ($P=0.52$). However, growth response in gap-adjacent old *S. giganteum* was greater than in reference trees over both 5-yr ($P=0.02$) and 10-yr ($P=0.02$) intervals (Table 1). Old *S. giganteum* adjacent to gaps increased 24% during the 5 yr following gap creation, compared with an 8% increase in reference trees. For the 10 yr following gap creation, gap-adjacent trees grew 24% more while reference trees grew 0.8% less than the period before gap creation. In contrast, there was no difference in growth detected between gap-adjacent and reference trees for young *S. giganteum* for either the 5-yr ($P=0.72$) or 10-yr ($P=0.34$) intervals.

Following gap creation, *A. concolor* trees along gap borders grew more than reference trees for both the 5-yr (27% increase in gap-adjacent trees versus an 8% increase in reference trees; $P<0.01$) and 10-yr intervals (21% increase in gap-adjacent trees versus a 4% decrease in reference trees $P<0.01$). *Pinus lambertiana* trees adjacent to gaps showed greater growth response than reference trees (Table 1), but the difference was not significant (5-year interval $P=0.56$; 10-year interval $P=0.13$).

For *A. concolor* and old *S. giganteum* along gap edges, the positive growth response was evident by the fourth year following gap creation (Fig. 2). The magnitude of the treatment effect increased with time, as gap-adjacent trees continued to grow more than reference trees for 10 yr following gap creation. Before gap creation, old *S. giganteum* adjacent to gaps were growing slightly more than reference trees, but this difference was not significant

($P = 0.20$ from a t-test comparing pre-gap growth means between gap-adjacent and reference trees).

For all old *S. giganteum* trees combined, $\delta^{13}C$ was lower (more negative, i.e. lower WUE) during the 5-yr period following gap creation compared with the 5-yr period before gap creation ($P < 0.001$; Fig. 3). However, there was no detected effect of gap-adjacency on the change in $\delta^{13}C$ following gap creation ($P = 0.98$), as $\delta^{13}C$ changed similarly for both gap-adjacent and reference trees.

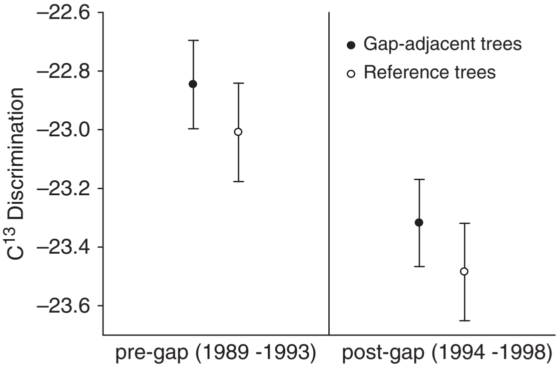

Fig. 3. Means and standard errors of carbon isotope discrimination from growth rings of old *Sequoiadendron giganteum* trees adjacent to canopy gaps and approximately 20 m distant from gaps (reference trees). More positive values on the y-axis indicate greater crown-level intrinsic water use efficiency.

Sequoiadondron giganteum growth was positively correlated with winter precipitation ($r = 0.52$, $P < 0.001$, df = 160). Radial growth during the relatively dry 5 years prior to harvest was lower than average (Fig. 4). Both winter precipitation and radial growth increased in the years immediately following the harvest (Fig. 4). In contrast, there was no detectable correlation between *S. giganteum* growth and summer air temperature ($r = -0.081$, $P = 0.31$, df = 160).

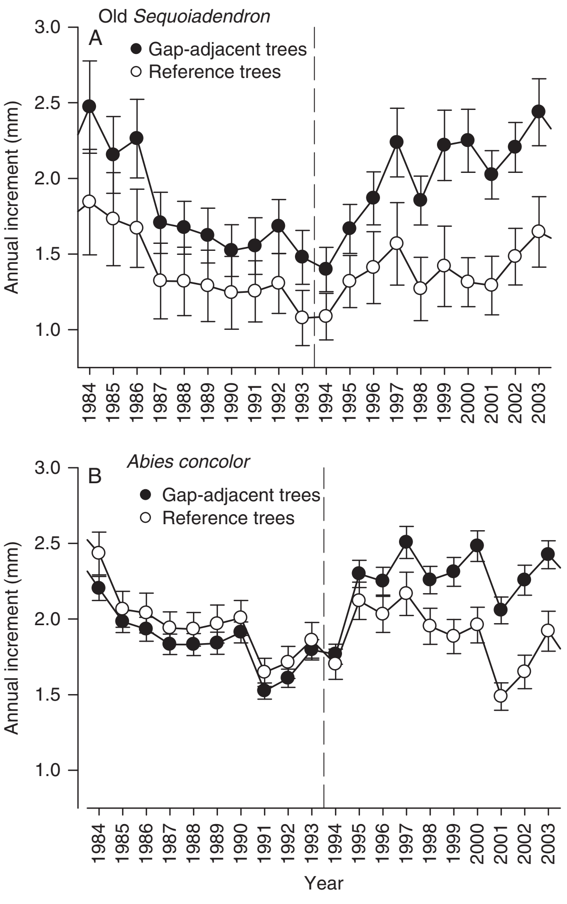

Fig. 2. Yearly variation in radial growth (means and standard errors) for old *Sequoiadendron giganteum* (**a**) and *Abies concolor* (**b**) gap-adjacent and reference trees. The dashed vertical line indicates the time of a gap-creation harvest.

Discussion

Sequoiadondron giganteum ranks third among tree species in longevity and first in total volume (Hartesveldt et al. 1975). Despite their great age and massive size, old *S. giganteum* responded positively and with surprising sensitivity to the creation of adjacent canopy gaps. The response occurred quickly and was sustained for the decade following gap creation (Fig. 2). While suppression–release cycles are more typically thought of as occurring during the sapling stage (Wright et al. 2000), many species do maintain growth sensitivity to changing environmental conditions late in life. Increased vigor in old trees responding to thinning has been observed in *Pseudotsuga menziesii* (Mirb.) Franco (Newton & Cole 1987), *Pinus strobus* L. (Bebber et al. 2004), *Pinus contorta* Dougl. ex. Loud. (Waring & Pitman 1985), *P. ponderosa* (McDowell et al. 2003), and *Pinus sylvestris* L. (Martinez-Vilalta et al. 2007; DeSoto et al. 2010). While none of these species approach the longevity of *S. giganteum*, there are long-lived counterparts in forest types the world over that present researchers with potential opportunities to use individual trees as long-term bioindicators of changing environmental conditions (Phillips et al. 2008). Even the longest-lived species, *Pinus longaeva* D.K. Bailey, has recently been shown to be sensitive to changing environments late in life (Salzer et al. 2009).

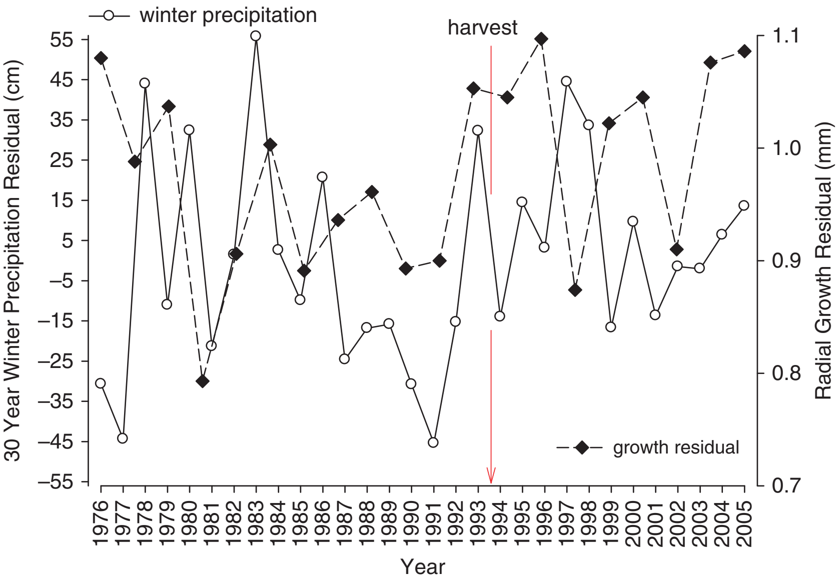

Fig. 4. Relationship between winter precipitation residuals and *Sequoiadendron giganteum* growth residuals. Residual values (annual–mean) are displayed for total precipitation in the winter (Oct–Feb) at Mountain Home State Forest, California, based on the 30-yr mean (1976–2005). Radial growth residuals were standardized and detrended for 162 *S. giganteum* growth chronologies from 1976 to 2005.

The disturbances used in the studies cited above were partial thinnings and not distinct canopy gaps as were used in this study. We do not know how old *S. giganteum* trees would respond to more uniform thinnings or other disturbances, but our results suggest that they respond when enough growing space is liberated. We refer to 'growing space' as the collective of resources (light, water, nutrients and physical space) necessary for growth (*sensu* Oliver & Larson 1996). Hence the same silvicultural principles applied to thinning around developing trees (Smith et al. 1997) apply to old *S. giganteum*. As demonstrated by our results, however, trees of different species and size classes should be expected to have different degrees of response, or they may have no detectable response at all, as was the case with young *S. giganteum* and *P. lambertiana* in this study. In addition to inherent differences in physiological capacity to release, there are a number of explanations why some trees may not respond with radial growth to increases in growing space. One explanation is that the no-response trees do indeed use the increased growing space, but resources are allocated to functions other than radial growth such as height growth or reproduction. Alternatively, no-response trees may not be using the resources because they are not necessary for growth (i.e., they are non-limiting). A third alternative is that the no-response trees are simply out-competed for the increased growing space by neighboring vegetation. The older *S. giganteum* trees in this study, for example, likely have much more established root systems that penetrate further, both vertically and horizontally, into adjacent areas at the time of gap creation compared with younger *S. giganteum*. The older trees may therefore be in a better position to 'capture' the additional growing space made available.

The response of *A. concolor* is similar to other results from the central Sierra Nevada beyond the range of *S. giganteum* (York & Battles 2008). The lack of a detected treatment effect in *P. lambertiana* demonstrates the potential for high between-species variability in radial growth response to changes in growing space. It should be noted that for both young *S. giganteum* and *P. lambertiana*, however, there was less power of detection in our analysis compared with old *S. giganteum* and *A. concolor* because of smaller sample sizes. For all groupings of trees, trends in growth were the same (more growth response in gap-adjacent trees compared with reference trees), even though magnitude and statistical significance varied.

Factors of growth response in old S. giganteum

Because we did not measure crown-level changes in light availability, we cannot rule out increases in light as a contributing factor to the growth response. We consider this unlikely as a major reason for the growth increase, however, because the crowns of emergent old trees are mostly above the surrounding canopy. The canopies of *S. giganteum* groves are often distinctly two-tiered. There is a main canopy of dense co-dominant and dominant trees, with old *S. giganteum* emerging above the main canopy forming a sparse upper canopy. At Whitaker's Forest Research Station within the Redwood Mountain grove, for example, the average height to crown base of old *S. giganteum* is 35.6 m, while the average total height of adjacent co-dominant and dominant trees is 1 m less in stature than the crown bases of emergent *S. giganteum* (R.A. York, unpublished). While we do not have measurements to quantify this canopy stratification within the grove studied, personal observations indicate a similar structure. Even if old *S. giganteum* adjacent to study gaps had canopies that overlapped partially with the main canopy before gaps were created, the exposed branches of the old *S. giganteum* would be from lower portions of crowns, where photosynthetic capacity is diminished because of self- and neighbor- shading (Bond et al. 1999). Eventually, the old trees adjacent to gaps may capture the increased light made available by gap creation by making physiological adjustments to lower branches or by producing epicormic sprouts on lower portions of stems (O'Hara et al. 2008).

As Phillips et al. (2008) noted, the experimental understanding of old-tree physiological responses to environmental changes remains speculative because of sampling challenges and the lack of a true control for changes in atmospheric CO_2. While we do have controls for the gap-creation treatment in this experiment, our interpretation of water relations in study trees is also speculative because of potentially contributing factors that we did not measure. If gap creation increased the water available to old *S. giganteum*, then WUE should have decreased relative to reference trees. WUE decreases with increased water availability because stomatal conductance increases more rapidly than carbon assimilation (Meinzer et al. 1997). However, there was no difference in the change in WUE (as indicated by a change in $\delta^{13}C$) between gap-adjacent and reference trees. Increases in water availability were therefore not supported by the isotope analysis as the main reason for the growth response to gap creation. Old *S. giganteum* can tap into deep water sources (Anderson et al. 1995) and may therefore be insensitive to changes in water availability near soil surfaces, particularly if deep water is the primary source of water.

Another possible scenario is that changes in nitrogen availability influenced the WUE response. As has been found elsewhere (Denslow et al. 1990; Walters et al. 2006), a 'below-ground gap' of increased nitrogen availability directly beneath the above-ground canopy gap often develops following gap creation. This is especially likely in our study area given the dry Mediterranean climate of the Sierra Nevada. Changes in nitrogen availability can alter WUE, thus leading to a possible overwhelming of water availability (Warren et al. 2001) as a detectable factor, even though an increase in water may have been an important factor in the growth increase.

Increased nitrogen availability may have influenced growth directly if nitrogen was more available to gap-adjacent trees than reference trees because of reduced competition. However, we did not measure light or nitrogen and therefore cannot isolate nitrogen as the primary cause of growth responses. It does appear likely, however, that below-ground resources contributed to the growth response.

Growth trends during the study period

A persistent trend in our results was that tree growth increased during the 5 yr after harvest compared with the 5 yr before harvest, regardless of species and location relative to gaps. This growth trend coincided with a climatic pattern in which parameters shown to be favorable to diameter growth were lower just before harvest and increased just after harvest. In particular, there was a very strong shift in winter precipitation (Fig. 1). Based on Robards' (2009) climate-sensitive growth and yield model, annual diameter increment for *A. concolor* and *P. lambertiana* should be positively correlated to winter precipitation – an expectation consistent with our results. *Sequoiadondron giganteum* was not included in Robards' (2009) model. However, our analysis documented a significant and positive correlation between diameter growth and winter precipitation (Fig. 4). This correlation held for all subsets of the *S. giganteum* sample regardless of canopy status (dominant or codominant) or location (gap adjacent or reference). Conifer growth in the Sierra Nevada is also sensitive to summer temperature but the relationship is weak compared with winter precipitation (Battles et al. 2009; Robards 2009). For *S. giganteum* in this study, we found no correlation with summer temperature. Given these climate trends and the dependence of tree growth on the availability of water and energy, it is not surprising that diameter growth generally increased after 1993. Soil moisture is a primary factor in the restriction of grove boundaries to their present locations (Rundel 1972). The link between *S. gigan-*

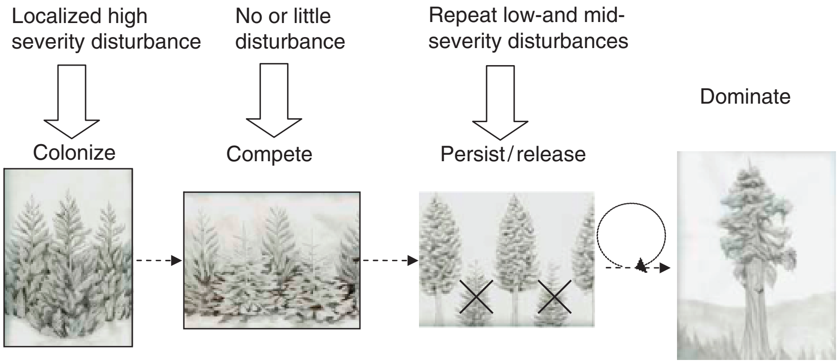

Fig. 5. A simplified conceptual model of how *Sequoiadendron giganteum* life history interacts with a low to moderate mixed severity disturbance regime. The *S. giganteum* competitiveness, longevity, persistence and release mechanisms allow for eventual dominance. Actual development is likely to be non-linear and complex.

teum growth and precipitation found here further contributes to the importance of water as a factor of population dynamics.

Another possible contributor to the overall growth trend is that nitrogen availability increased across the entire study area. The study area is upslope of the southern central valley of California, where agricultural and urban activities are sources of nitrogen that is deposited in mixed conifer forests primarily via precipitation (Bytnerowicz et al. 2001). Unlike Pacific Northwest forests to the north of the study area (Holland et al. 1999), mixed conifer forests of the southern Sierra Nevada are experiencing increases in nitrogen deposition, with our study area having particularly high deposition rates (Fenn et al. 2003).

In addition to climate trends and anthropogenic nitrogen deposition, atmospheric CO_2 concentrations or stand dynamics-related trends may also contribute to the observed general increases in tree growth. The fact that there was a significant gap-creation effect even under favorable environmental conditions reinforces the notion that these old trees have a high degree of sensitivity to changes in growing conditions. Silvicultural treatments that either reduce densities or create distinct canopy gaps are likely to result in increased growth of individual old *S. giganteum*, even while exogenous processes drive region-wide changes in Sierra Nevada forests (van Mantgem et al. 2009).

The response mechanism in long-lived pioneers

We use these results to refine the conceptual model of how *S. giganteum* life history is adapted to a mixed-severity disturbance regime (Fig. 5). Regeneration occurs following a disturbance that is severe enough to kill multiple overstory trees (Stephenson 1994). A colonization phase then occurs immediately following such a disturbance, facilitated by cone serotiny and bare soils. Huge pulses of light seeds are dispersed following fires intense enough to scorch the lower crowns of the largest trees (Harvey et al. 1980; Stephens et al. 1999). Assuming adequate soil moisture conditions (Schubert 1962), subsequent seedling establishment leads to a phase of competition with other species. In disturbed areas where canopy openings are greater than 0.1 ha, *S. giganteum* can outgrow all associated conifer species for at least the first 7 yr following disturbance (York et al. 2007). In mixed conifer forests of the Sierra Nevada, pre-settlement fires occurred at intervals from approximately 8 to 20 yr (Stephens et al. 2007). Rapid early growth could therefore confer a competitive advantage in surviving through high-frequency, low-severity disturbances.

At longer intervals, moderate and local high-intensity fires inevitably occur. While other species may perish, individual *S. giganteum* can survive higher-intensity fires because of their ability to withstand very high levels of crown scorch (Stephens & Finney 2002), thick and non-resinous bark, and high crown base (Weatherspoon 1990). Young *S. giganteum* are also able to reconstruct damaged crowns with epicormic sprouts (O'Hara et al. 2008). Our results suggest that in addition to these persistence mechanisms that are already well-known for *S. giganteum* and other long-lived pioneer species, there is an additional response mechanism that may facilitate eventual emergence and persistence of a dominant canopy position following moderate or local high-severity disturbances that are confined to the immediate neighborhood of individual, large

S. giganteum (Fig. 5). Those individuals that do persist through these disturbances quickly capture resources made available by the disturbance and establish a dominant position in the canopy (and may also dominate the below-ground growing space). This persistence/release mechanism may occur numerous times over the life span of long-lived species (perhaps hundreds of times over the 3000+yr life span of a *S. giganteum*). While *S. giganteum* may be the most conspicuous example of this long-lived pioneer life-history strategy, there are numerous other species that potentially have the same nuanced interaction with a mixed-severity disturbance regime (York et al. in press). It is unknown, however, if many of these other species also remain sensitive to environmental changes even as emergent, long-lived dominants in forest communities. If so, the response mechanism could be one of the defining life-history traits of long-lived pioneers.

Acknowledgements. Save the Redwoods League, UC California Agricultural Experiment Station and UC Center for Forestry provided support. David Dulitz provided assistance during setup. Jose Medina and California Department of Forestry and Fire Protection offered assistance during field work. Amy Sprague, Travis Freed, Lia Marroquin, Lacy Jane and Matthew Brown provided field assistance. Stefania Mambelli and the Center for Stable Isotope Biogeochemistry assisted with laboratory work. Helge Eng reviewed an earlier version of the manuscript.

References

Abella, S.R., Covington, W.W., Fule, P.Z., Lentile, L.B., Meador, A.J.S. & Morgan, P. 2007. Past, present, and future old growth in frequent-fire conifer forests of the Western United States. *Ecology and Society* 12(2), article 16.

Anderson, M.A., Graham, R.C., Alyanakian, G.J. & Martynn, D.Z. 1995. Late summer water status of soils and weathered bedrock in a giant sequoia grove. *Soil Science* 160: 415–422.

Ansley, J.S. & Battles, J.J. 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. *Journal of the Torrey Botanical Society* 125: 297–308.

Battles, J.J., Robards, T., Das, A. & Stewart, W. 2009. *Projecting climate change impacts on forest growth and yield for California's sierran mixed conifer forests – Final Report*. Public Interest Energy Research, California Energy Commission, Sacramento, CA, US. CEC-500-2009-047-F.

Bauhus, J., Puettmann, K. & Messier, C. 2009. Silviculture for old-growth attributes. *Forest Ecology and Management* 258: 525–537.

Bebber, D.P., Thomas, S.C., Cole, W.G. & Balsillie, D. 2004. Diameter increment in mature eastern white pine *Pinus strobus* L. following partial harvest of old-growth stands in Ontario, Canada. *Trees* 18: 29–34.

Bond, B.J., Farnsworth, B.T., Coulumbe, R.A. & Winner, W.E. 1999. Foliage physiology and biochemistry in response to light gradients in conifers with varying shade tolerance. *Oecologia* 120: 183–192.

Bonnicksen, T. & Stone, E.C. 1982. Reconstruction of a presettlement giant sequoia mixed conifer forest community using the aggregation approach. *Ecology* 63: 1134–1148.

Bytnerowicz, A., Padgett, P.E., Parry, S.D., Fenn, M.E. & Arbaugh, M.J. 2001. Concentrations, deposition, and effects of nitrogenous pollutants in selected California ecosystems. *Scientific World Journal* 1: 304–311.

Demetry, A., Covington, W.W. & Duriscoe, D.M. 1995. Regeneration patterns within canopy gaps in a giant sequoia-mixed conifer forest: implications for forest restoration. *Bulletin of the Ecological Society of America* 76(2 Suppl. Part 2): 62–63.

Denslow, J.S., Schultz, J.C., Vitousek, P.M. & Strain, B.R. 1990. Growth responses of tropical shrubs to treefall gap environments. *Ecology* 71: 165–179.

DeSoto, L., Olano, J.M., Rozas, V. & De la Cruz, M. 2010. Release of *Juniperus thurifera* woodlands from herbivore-mediated arrested succession in Spain. *Applied Vegetation Science* 13: 15–25.

Farquhar, G.D. & Richards, R.A. 1984. Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. *Australian Journal of Plant Physiology* 11: 539–552.

Fenn, M.E., Baron, J.S., Allen, E.B., Rueth, H.M., Nydick, K.R., Geiser, L., Bowman, W.D., Sickman, J.O., Meixner, T., Johnson, D.W. & Neitlich, P. 2003. Ecological effects of nitrogen deposition in the western United States. *Bioscience* 53: 404–420.

Fites-Kaufman, J., Rundel, J.P., Stephenson, N. & Weixelman, D.A. 2007. Montane and subalpine vegetation of the Sierra Nevada and Cascade Ranges. In: Barbour, M., Keeler-Wolf, T. & Schoenherr, A.A. (eds.) *Terrestrial vegetation of California*. pp. 456–501. University of California Press, Berkeley, CA, US.

Hartesveldt, R.J., Harvey, H.T., Shellhammer, H.S. & Stecker, R.E. 1975. *The giant sequoia of the Sierra Nevada*. U.S. Department of the Interior, National Park Service, Washington, DC, US.

Harvey, H.T., Shellhammer, H.S. & Stecker, R.E. 1980. *Giant sequoia ecology*. 182, U.S. Department of the Interior, National Park Service, Scientific Monograph Series 12, Washington, DC, US.

Hickman, J.C. 1993. *The Jepson Manual: higher plants of California*. University of California Press, Berkeley, CA, US.

Holland, E.A., Dentener, F.J., Braswell, B.H. & Sulzman, J.M. 1999. Contemporary and pre-industrial global reactive nitrogen budgets. *Biogeochemistry* 46: 7–43.

Holmes, R.L. & Cook, E.R. 1986. Guide for computer program ARSTAN. In: Holmes, R.L., Adams, R.K. & Fritts, H.C. (eds.) *Users manual for program ARSTAN, tree-ring chronologies of Western North America: California, eastern Oregon and northern Great basin*. pp. 50–65. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, US.

Keeling, C.D., Bacastow, R.B., Carter, R.F., Piper, S.C., Whorf, T.P., Heimann, M., Mook, W.G. & Roeloffzen, H. 1989. A three dimensional model of atmospheric CO2 transport based on observed winds. 1. Analysis of observational data. In: Peterson, D.G. (ed.) *Geophysical monograph*. volume 55, pp. 165–236. American Geophysical Union, Washington, DC, US.

Keeling, C.D., Bollenbacher, A.F. & Whorf, T.P. 2005. Monthly atmospheric $^{13}C/^{12}C$ isotopic ratios for 10 SIO stations. In: *Trends: a compendium of data on global change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, TE, US.

Keeton, W.S. & Franklin, J.F. 2005. Do remnant old-growth trees accelerate rates of succession in mature Douglas-fir forests? *Ecological Monographs* 75: 103–118.

Law, B.E., Goldstein, A.H., Anthoni, P.M., Unsworth, M.H., Panek, J.A., Bauer, M.R., Fracheboud, J.M. & Hultman, N. 2001. Carbon dioxide and water vapor exchange by young and old ponderosa pine ecosystems during a dry summer. *Tree Physiology* 21: 229–308.

Livingston, J.J. & Spittlehouse, D.L. 1996. Carbon isotope fractionation in tree ring early and late wood in relation to intra-growing season water balance. *Plant, Cell & Environment* 19: 768–774.

Lutz, J.A., van Wagtendonk, J.W. & Franklin, J.F. 2009. Twentieth-century decline of large-diameter trees in Yosemite National Park, California, USA. *Forest Ecology and Management* 257: 2296–2307.

Martinez-Vilalta, J., Vanderklein, D. & Mencuccini, M. 2007. Tree height and age-related *Pinus sylvestris* L. *Oecologia* 150: 529–544.

McDowell, N., Brooks, J.R., Fitzgerals, S.A. & Bond, B.J. 2003. Carbon isotope discrimination and growth response of old Pinus ponderosa trees to stand density reductions. *Plant, Cell & Environment* 26: 631–644.

Meinzer, F.C., Hinkley, T.M. & Ceulemans, R. 1997. Apparent responses of stomata to transpiration and humidity in a hybrid poplar canopy. *Plant, Cell and Environment* 23: 1109–1118.

Newton, M. & Cole, E.C. 1987. A sustained-yield scheme for oldgrowth Douglas-fir. *Western Journal of Applied Forestry* 2: 22–25.

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

Oliver, C.D. & Larson, B.C. 1996. *Forest stand dynamics*. John Wiley & Sons, New York, NY, US.

Phillips, N.G., Buckley, T.N. & Tissue, D.T. 2008. Capacity of old trees to respond to environmental change. *Journal of Integrative Plant Biology* 50: 1355–1364.

Piirto, D.D. & Rogers, R.R. 2002. An ecological basis for managing giant sequoia ecosystems. *Environmental Management* 30(1): 110–128.

Robards, T.A. 2009. *Empirical forest growth model evaluations and development of climate-sensitive hybrid models*. PhD dissertation. University of California, Berkeley, Berkeley, p. 234.

Royce, E.B. & Barbour, M.G. 2001. Mediterranean climate effects. I. Conifer water use across a Sierra Nevada ecotone. *American Journal of Botany* 88: 911–918.

Rundel, P.W. 1972. Habitat restriction in giant sequoia: the environmental controls of grove boundaries. *American Midland Naturalist* 87: 81–89.

Runkle, J.R. 1982. Patterns of disturbance in some old growth mesic forests of Eastern North America. *Ecology* 63: 1533–1546.

Salzer, M.W., Hughes, M.K., Bunn, A.G. & Kipfmueller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of National Academy of Sciences, USA* 106(48): 20348–20353.

Schubert, G.G. 1962. Silvical characteristics of giant sequoia. USDA For. Serv. Tech. Paper 20. Pacific Southwest Forest and Range Experiment Station, Berkeley, CA, 16pp.

Schulze, B., Wirth, C., Linke, P., Brand, W.A., Kuhlmann, I., Horna, V. & Schulze, E. 2004. Laser ablation-combustion-GC-IRMS – a new method for online analysis of intra-annual variation of delta C-13 in tree rings. *Tree Physiology* 24: 1193–1201.

Smith, D.M., Larson, B.C., Kelty, M.J. & Ashton, P.M.S. 1997. *The practice of silviculture, applied forest ecology*. John Wiley & Sons, New York, NY, US.

Stephens, S.L. & Finney, M.A. 2002. Prescribed fire mortality of Sierra Nevada mixed conifer tree species: effects of crown damage and forest floor combustion. *Forest Ecology & Management* 162: 261–271.

Stephens, S.L., Dulitz, D.J. & Martin, R.E. 1999. Giant sequoia regeneration in group selection openings in the southern Sierra Nevada. *Forest Ecology & Management* 120: 89–95.

Stephens, S.L., Martin, R.E. & Clinton, N.E. 2007. Prehistoric fire area and emissions from California's shrublands, and grasslands. *Forest Ecology & Management* 251: 205–216.

Stephenson, N.L. 1994. Long-term dynamics of giant sequoia populations: implications for managing a pioneer species. *USDA Forest Services General Technical Report* PSW-GTR-151: 56–63.

Stephenson, N.L. & Demetry, A. 1995. Estimating ages of giant sequoias. *Canadian Journal of Forest Research* 25: 223–233.

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

Tans, P.P., deJohn, A.F.M. & Mook, W.G. 1978. Chemical pretreatment and radial flow of 14C in tree rings. *Nature* 271: 234–235.

van Mantgem, P.J., Stephenson, N.L., Byrne, J.C., Daniels, L.D., Franklin, J.F., Fulé, P.Z., Harmon, M.E., Larson, A.J., Smith, J.M., Taylor, A.H. & Veblen, T.T. 2009. Widespread increase of tree mortality rates in the western United States. *Science* 323: 521–524.

Van Pelt, R. & Sillett, S.C. 2008. Crown development of coastal *Pseudotsuga menziesii*, including a conceptual model for tall conifers. *Ecological Monographs* 78: 283–311.

Walters, M.B., Lajzerowicz, C.C. & Coates, K.D. 2006. Soil resources and the growth and nutrition of tree seedlings near harvest gap – forest edges in interior cedar–hemlock forests of British Columbia. *Canadian Journal of Forest Research* 36: 62–76.

Waring, R.H. & Pitman, G.B. 1985. Modifying lodgepole pine stands to change susceptibility to mountain pine beetle attack. *Ecology* 66: 889–897.

Warren, C.R., McGrath, J.F. & Adams, M.A. 2001. Water availability and carbon isotope discrimination in conifers. *Oecologia* 127: 476–486.

Weatherspoon, C.P. 1990. *Sequoiadendron giganteum* (Lindl.) Buchholz Giant Sequoia. In: Burns, R.M. & Honkala, B.G. (eds.) *Silvics of North America*. pp. 552–562. USDA Forest Service Agricultural Handbook 654, Washington, DC, US.

Weiner, J. & Thomas, S.C. 2001. The nature of tree growth and the "age-related decline in forest productivity". *Oikos* 94: 374–376.

Willard, D. 2000. *A guide to the sequoia groves of California*. Yosemite Association, Yosemite National Park, CA, US.

Wright, E.F., Canham, C.D. & Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern British Columbia. *Canadian Journal of Forest Research*. 30: 1571–1580.

York, R.A & Battles, J.J. 2008. Growth response of mature trees versus seedlings to gaps associated with group selection management in the Sierra Nevada, California. *Western Journal of Applied Forestry* 23: 94–98.

York, R.A., Battles, J.J., Eschtruth, A.E. & Schurr, F.G. Giant sequoia (*Sequoiadendron giganteum*) regeneration in experimental canopy gaps. *Restoration Ecology*, in press.

York, R.A., Battles, J.J. & Heald, R.C. 2007. Gap-based silviculture in a sierran mixed-conifer forest: effects of gap size on early survival and 7-year seedling growth. *USDA Forest Services General Technical Report* PSW-GTR-203: 181–191.

Supporting Information

Additional supporting information may be found in the online version of this article:

Figure S1. Artistic representation of a large, old giant sequoia (*Sequoiadendron giganteum*) from native grove in the mixed conifer forest of California, USA.

Figure S2. Coring a large, old giant sequoia (*Sequoiadendron giganteum*) in the Mt Home grove, California, USA.

Figure S3. Measuring diameter at breast height of a large, old giant sequoia (*Sequoiadendron giganteum*) in the Redwood Mountain Grove, California, USA.

Received 27 April 2009;
Accepted 14 March 2010.
Co-ordinating Editor: Dr Kerry Woods