Scientific Research Publishing

Succession in *Quercus gambelii* (Gambel's Oak) Woodlands

O. W. Van Auken[1], J. K. Bush[2]

[1]Department of Biology, University of Texas at San Antonio, San Antonio, USA
[2]College of Sciences, University of Texas at San Antonio, San Antonio, USA
Email: oscar.vanauken@utsa.edu

Abstract

Quercus gambelii (Gambel's oak) communities are found in the mountains of the western United States from Wyoming, Colorado, and Utah south into northern Mexico. Leaf gas exchange rates were measured for potential successional species in *Q. gambelii* communities. Daily average light level below the canopy was 125 $\mu mol/m^2/sec$. Light response curves indicated that *Pinus ponderosa* and *Q. gambelii* had high maximum photosynthetic rates (14.13 and 11.21 $\mu mol/m^2/sec$) and were sun species. *Abies concolor* (white fir) is a shade species with the lowest photosynthetic rate (3.71 $\mu mol/m^2/sec$). At low light levels few differences in photosynthetic rates were found between the species. *Pinus ponderosa* and *Q. gambelii* maximum photosynthetic rates were reduced 71% - 73% in shade and the shade species maximum photosynthetic rates were reduced by 50% - 57%. Comparing annual gas exchange rates for all species showed that *A. concolor* had higher gas exchange rates and could replace *Q. gambelii*. Growth in height of *Q. gambelii* was a second order quadratic function reaching a plateau of about ten meters between 80 and 95 years. Growth estimates of height of *A. concolor* in canopy shade were exponential, which would allow seedlings to reach the *Q. gambelii* canopy in approximately 35 years. *Abies concolor* wood specific gravity is 56% lower than *Q. gambelii*, which means more carbon is put into growth in height to reach the canopy at low light levels and low photosynthetic rates. The additional shading it causes would further reduce *Q. gambelii* photosynthesis rates and prevent self-replacement in these *Q. gambelii* communities, leading to an *A. concolor* dominated community.

Keywords

Gas Exchange, Growth Rates, Light Levels, Oak Replacement, Photosynthetic Rates, Population Dynamics, White Fir, Wood Specific Gravity

1. Introduction

Many *Quercus* (oak) populations in North American forests and woodlands appear to be changing and changes are widespread [1], species independent [2] and associated with a lack of replacement of mature trees [3] [4] [5]. Deviations in many *Quercus* populations appear to be related to community succession [6]-[11], more specifically to changes in light levels as succession proceeds, changes in fire frequency, and high levels of herbivory [12]-[20].

Herbivores favor *Quercus* juveniles and may cause decreases in *Quercus* populations [15] [18]. While *Quercus* produces acorns and seedlings develop, they never reach the adult population because of herbivory. In protected areas of western North America, large herbivores reduced populations of cottonwood (*Populus deltoids*), various willows (*Silax* sp.) and possibly quaking aspen (*Populus tremuloides*) [21]. With the reintroduction of the gray wolf in some areas, top-down control of these herbivores has allowed expansion and re-establishment of a number of woody species. We have not found any reports of top-down predator reintroduction effects on *Q. gambelii* Nutt. (Gambel's oak) populations or communities in western North America.

Most studies of succession and community change are not experimental where species are added or removed; but rather, consider genetic models, population models, demography and spatial observations; although there are a few direct comparisons [22] [23] [24] [25] [26]. Determining survival or mortality by marking and revisiting populations of woody plants, including various *Quercus* spp., has been infrequent. Difficulties in understanding population changes and succession of *Quercus* populations or communities relate to the potential long life of *Quercus* plants (100 - 600 years) [10] [27].

Quercus gambelii shows a lack of recruitment and populations appear to be undergoing successional changes [10]. We identified a bottleneck between juvenile *Q. gambelii* plants and adult populations with no or only a few juveniles recruited into the adult population [5] [20]. *Quercus gambelii* is a wide spread species found in the mountains of the western and southwestern United States and northern Mexico (**Figure 1**) [9]. It is xerophytic [28] and reproduces by sprouting more than by seeding, suggesting it is fire tolerant [10]. It is a sun plant or heliophyte with high photosynthetic rates in full sunlight with more than a 70% reduction in canopy shade [20]. It is probably an early successional species, but this is debated [8] [9] [10]. It has been found with *Pinus ponderosa* (Ponderosa pine), *Pseudotsuga menziesii* (Douglas fir), *Abies concolor* (white fir) and other species in many areas [29]. It forms monotypic overstories in some places [5] and may share co-dominance with, or be replaced by, *Acer grandidentatum* (bigtooth maple) in other areas [30].

We examined possible successional replacements and the mechanism controlling the replacement of *Q. gambelii* trees in *Q. gambelii* woodland communities. We report surface light levels below the canopy of *Q. gambelii* communities and in associated open meadows in the Lincoln National Forest, New Mexico, USA.
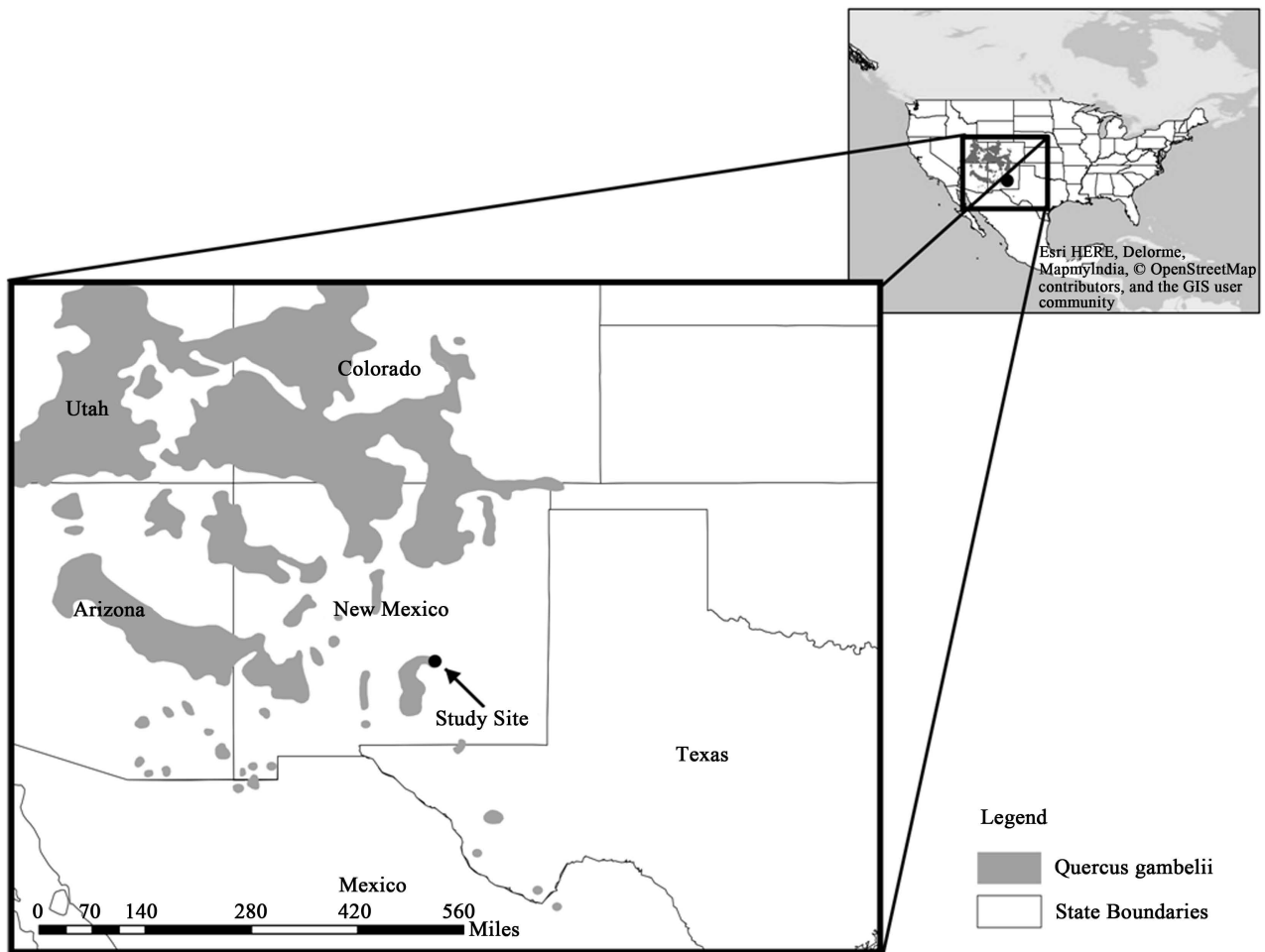
Figure 1. Map of distribution of *Quercus gambelii* in the United States and the location of the study site.

We measured light response curves and gas exchange rates of potential replacement species below the *Q. gambelii* canopy and compared them to rates for *Q. gambelii*. In addition, we measured and compared growth in height and wood specific gravity of *A. concolor* and *Q. gambelii*.

2. Methods

We completed this study near the White Mountain Wilderness Area in the Sacramento Mountains in the northern portion of the Lincoln National Forest (105°50'W and 33°28'N, **Figure 1**). Mountain ranges in this area are biogeographical islands or mountain islands [31] [32]. They are isolated, forested, and heavily faulted. Elevation of the study site is approximately 2700 m. Average annual precipitation is 60 cm, with approximately 60% as rain in July and August and 100 cm of snowfall in winter. Usually there are 100 frost-free days per year, but killing frosts have been documented in every month except July. Mean maximum temperature is 26°C in July and the mean minimum temperature is −5°C in January [33] [34]. The mean midday (solar noon) photosynthetic flux density (PFD) below the *Q. gambelii* canopy and the daily average was calculated as was the mean midday PFD in the adjacent open meadow [20].

It is likely that the study area was a meadow or grassland 150 years ago. Heavy grazing by domestic animals occurred in the study areas followed by encroachment of *Q. gambelii* and other species [31]. No evidence of past clear-cutting was observed. Seventeen fires between 0.1 and 3.0 ha were reported within 10 km of the study area in the last 35 years, but none from the specific study site [35].

We selected one mature *Q. gambelii* community and associated meadow or grassland with scattered *Q. gambelii* plants (see [5]). The communities were 2 - 3 ha in total area and showed signs of browsing but no other signs of recent disturbances. The *Q. gambelii* community was approximately 137 years old (based on tree ring analysis) and the mean height of the canopy trees was 10.75 m [5]. Density of *Q. gambelii* trees (greater than 3 cm in circumference at 150 cm in height) was 3740 plants/ha and juvenile density was 4767 plants/ha. Basal area was 40.5 m^2/ha which was 96.7% of the total [5]. We also found *Abies concolor*, *Acer glabrum* (Rocky Mountain maple), *Fraxinus velutina* (velvet ash), *Pinus edulis* (pinyon pine), and *Pseudotsuga menziesii* (Douglas fir) (Table 1). We used Correll and Johnston [36] and USDA [37] to identify plants. There were 233 *Abies concolor* juvenile/ha below the *Q. gambelii* canopy. *Pinus ponderosa* was found in the adjacent grassland.

The majority of juvenile plants were *Q. gambelii*, and most appeared to be root sprouts. Although we did not find *P. ponderosa* in this specific community, we did find it in the adjacent meadow and other nearby communities (density of 30 plants/ha, mean basal area of 3.6 m^2/ha, and mean juvenile density of 17 plants/ha) [5]. *Pinus ponderosa* trees were large and were present before the encroachment of *Q. gambelii*. The open community was a high elevation meadow or grassland adjacent to the *Q. gambelii* community with few scattered woody plants. The woody plant density was low at approximately 40 plants/ha consisting of *Q. gambelii* (20 plants/ha), *P. ponderosa* (10 plants/ha) and *P. edulis* (10 plants/ha).

Table 1. Composition of a 137-year-old *Quercus gambellii* community in the Lincoln National Forest, New Mexico, USA. Data from Ryniker [5]. No *Pinus ponderosa* were found in this community, but an adjacent grassland had 30 trees/ha and 17 juveniles/ha.

Tree Species	Tree Density (plants/ha)	Tree Basal Area (m^2/ha)	Juvenile Density (plants/ha)
Quercus gambelii	3740	40.5	4767
Abies concolor	73	1.0	233
Acer glabrum	60	0.4	480
Fraxinus velutina	53	0.1	113
Pinus edulis	-[a]	-	40
Psuedotsuga menziesii	-	-	20
Total	**3926**	**42.0**	**5653**

a. Indicates no trees of that species were found.

We measured photosynthetic flux densities (PFD's) in the field in both communities with Spectrum® quantum sensors (Item # 36681, Plainfield, IL). We place three light sensors in each community at ground level connected to a Spectrum® Watch Dog® Data Logger (Model 450). We measured PFD's for two days, averaged the values, and presented by community type. We used a *Student's* t-*test* to determine if the mean PFD was significantly different between the two communities.

We constructed light response curves using shade leaves of *P. ponderosa, F. velutina, A. glabrum,* and *A. concolor*. We had three replications (individuals) for each species except *F. velutina*, which had five replications. Overall the variation in CO_2 uptake was low and doubling the sample size would have little effect of the variation [38]. We used one terminal leaf or leaflet per plant for the two deciduous species. Each leaf covered the entire chamber (2×3 cm). We used three adjacent leaves from each replicate plant of the two evergreen species for each light curve. We measured leaf area for the conifers with a Li-Cor® portable area meter (LI 3000A). We made measurements within ±2 hr of solar noon with a Li-Cor® infrared gas analyzer (LI-6400). We generated irradiances by the Li-Cor LED red-blue light source using the auto light curve program of the LI-COR with a flow rate of 400 μmol/s and CO_2 concentration of 400 μmol/mol. We used mature, undamaged, fully expanded leaves in the 2×3 cm chamber. We used ambient temperature (20˚C - 23˚C) and relative humidity (19% - 29%) and we calibrated daily. We recorded response data after two minutes until a stable total coefficient of variation was reached (1%). We started light response curves at a PFD of 2000 $\mu mol/m^2/sec^{-1}$ and decreased incrementally to 0 $\mu mol/m^2/sec$.

We measured net photosynthesis (A_{net}, μmol $CO_2/m^2/sec$), stomatal conductance (g_{leaf}, mol $H_2O/m^2/sec$), and transpiration (E_{leaf}, mmol $H_2O/m^2/sec$) over 14 light levels. We used a repeated measure ANOVA to determine significant differences in A_{net}, g_{leaf}, and E_{leaf} between species when measured over the PFD's tested, with PFD as the repeat variable [38]. We made photosynthetic measurements at the same time as ambient air temperature (T_{air}, ˚C) and incident photosynthetic flux density (PFD, $\mu mol/m^2/sec^1$).

We fitted replicated measurements to the model of Prioul and Chartier [39] using Photosyn Assistant a software package (Dundee Scientific, Dundee, Scotland). We calculated maximum photosynthesis (A_{max}), light saturating photosynthesis (L_{sat}), dark respiration (R_d), light compensation point (L_{cp}), the quantum yield efficiency (QE), g_{leaf} (stomatal conductance), E_{leaf} (transpiration)and WUE (water use efficiency) [20]. We calculated means from the replications. We determined the photosynthetic rate at 2000, 835, and 125 $\mu mol/m^2/sec$ (approximate maximum in the open, average in the open, and average below the canopy) for each replicate. We calculated water-use efficiency at 125 $\mu mol/m^2/sec$ for each replication.

Significant differences in photosynthetic rates (A_{max}, A_{835}, A_{125}, PFD at A_{max}, g_{leaf}, E_{leaf}, L_{cp}, R_d, QE and WUE) occurred between species, and we used analysis

of variance with species as the main effect [38]. We also included photosynthetic measurements for *Q. gambelii* made under similar conditions from a previous study in the analyses [20]. We used Tukey-Kramer HSD multiple comparison tests to determine differences between species. We determined homogeneity of variance using Bartlett's Test. We found significant differences in variances of g_{leaf} and E_{leaf}, however we used a log-transformation and variances were equal. Therefore, for these two parameters we performed analysis of variance and Tukey-Kramer HSD on transformed data. We used a significance levels of 0.05 for all tests. Using sequential methodology, only three replicates were needed because of the low variation except five *F. vetulina* plants were used.

We calculated and examined annual photosynthetic rates for all seasons and species [40]. We measured the height growth rates for *A. concolor* and compared them with height growth of *Q. gambelii*. We examined the time it would take for *A. concolor* to grow to and through the *Q. gambelii* canopy. Others have measured the wood specific gravity of these two species and we present that information as well [10] [41].

We determined diameter, height, and age for 28 *Q. gambelii* plants from communities in a previous study [5]. Diameter ranged from 1.6 to 16.6 cm (we measured and converted circumference to diameter). Height, measured with a marked extension pole, ranged from 1.70 to 10.75 m. We did not measure juveniles. We determined age by increment boring and then counting annual rings. Age ranged from 11 - 102 years [5]. We also measured diameter, height and age of 69 *A. concolor* juveniles and trees. Diameter ranged from 0.07 to 25.00 cm. For *A. concolor* plants < 10.0 cm in basal diameter, we measured with a Mitutoyo® digimatic caliper in two directions and averaged. For larger plants, we used a cloth metric tape to measure circumference and calculate diameter. We measured height to the nearest cm with a meter stick. Height ranged from 5 to 703 cm.

Abies concolor exhibits excurrent growth, and usually produces one major internode per year [42]. The beginning of each internode is easily recognized because of persistent terminal bud scale scars or the presence of a series of relatively thick, easily viewed lateral branches at each annual node. We measured the distance from the center of each annual internode to the center of the next higher one (in cm) then summed them to get total height and counted the number of years of growth [43] [44]. We plotted the height as a function of age followed by regression analyses to determine the type of curve, the r^2 and level of significance [38]. We also compared *A. concolor* growth for trees in productive sites (low density, [45]) and low production sites (high density, [45]).

3. Results

Meanphotosynthetic flux densities (PFDs) within the two communities were highly variable. The mean midday PFD level below the *Q. gambelii* canopy was 425 μmol/m²/sec and the daily average below the canopy was 125 μmol/m²/sec. The mean midday PFD level in the open meadow was 2100 μmol/m²/sec and the daily average in the open was 835 μmol/m²/sec.

There were significant differences in net photosynthesis between species when light response curves were examined (Table 2; repeated measures ANOVA; $F = 5.35$; $P = 0.0002$). Maximum photosynthetic rate (A_{max}) for leaves of *P. ponderosa* was highest at a mean PFD of 2000 µmol/m²/sec, which was significantly greater than the A_{max} for other species (Table 2). Mean A_{max} for leaves of *A. concolor* was lowest at a PFD of 900 µmol/m²/sec, which was 74% lower than the A_{max} of *P. ponderosa* and significantly different than the A_{max} of the other species (Table 2).

The photosynthetic rates for *P. ponderosa*, *F. velutina*, *Q. gambelii*, and *A. glabrum* at the daily mean PFD (835 µmol/m²/sec) in the open were not significantly difference from one another, but were significantly greater than *A. concolor*. Photosynthetic rate for *A. concolor* at the daily canopy mean PFD (125 µmol/m²/sec) was lowest of all species (Table 2).

Light saturation (L_{sat}) and light compensation points (L_{cp}) for *P. ponderosa* were significantly greater than for the other species, with *A. concolor* being lowest (Table 2). Dark respiration (R_d) of *P. ponderosa* and *A. concolor* were not significantly different and both were significantly greater than the other species (Table 2). *Pinus ponderosa* had the lowest quantum yield efficiency (*QE*). *Abies concolor* stomatal conductance (g_{leaf}) and transpiration (E_{leaf}) were lowest, with no differences among the other species (Table 2). Differences in water use efficiency were small with the sun species being equal and the shade species were all significantly higher.

Table 2. Maximum photosynthetic rates (A_{max}), photosynthetic flux densities (PFDs) at A_{max}, photosynthetic rate at mean canopy light levels, light saturation levels (L_{sat}), light compensation point (L_{cp}), dark respiration rate (R_d), quantum yield efficiency (*QE*), stomatal conductance (g_{leaf}), transpiration (E_{leaf}) and water use efficiency (WUE) for leaves of *Pinus ponderosa*, *Abies concolor*, *Acer glabrum*, *Fraxinus velutina* and *Quercus gambelii* plants in the Lincoln National Forest, New Mexico. Values are means ± standard deviations and means with the same letter within a row are not significantly different. The *Quercus* data was taken from [20].

Parameter	*Pinus*	*Abies*	*Acer*	*Fraxinus*	*Quercus*
A_{max} (µmol CO_2/m²/sec)	14.13 ± 0.02[a]	3.71 ± 0.79[c]	9.78 ± 1.64[b]	10.89 ± 2.35[b]	11.21 ± 1.68[ab]
PFD (µmol/m²/sec) at A_{max}	2000	900	900	1500	2000
A_{net} at PFD 125 (µmol/m²/sec)	4.20 ± 1.12[ab]	2.44 ± 0.56[b]	5.48 ± 0.42[a]	5.13 ± 0.27[a]	4.07 ± 0.65[ab]
A_{net} at PFD 835 (µmol/m²/sec)	10.72 ± 0.44[a]	4.02 ± 0.93[b]	9.77 ± 1.65[a]	10.20 ± 1.45[a]	10.69 ± 0.98[a]
L_{sat} (µmol/m²/sec)	513 ± 19[a]	165 ± 34[c]	247 ± 71[bc]	254 ± 27[b]	335 ± 6[b]
L_{cp} (µmol/m²/sec)	42 ± 6[a]	4 ± 2[c]	10 ± 1[b]	9 ± 3[b]	14 ± 6[b]
R_d (µmol CO_2/m²/sec)	1.79 ± 0.15[a]	1.39 ± 0.39[a]	0.77 ± 0.13[b]	0.62 ± 0.11[b]	0.69 ± 0.27[b]
QE (µmolCO_2/m²/sec)/ (µmol/m²/sec)	0.031 ± 0.007[b]	0.044 ± 0.008[a]	0.046 ± 0.006[a]	0.046 ± 0.006[a]	0.061 ± 0.003[a]
g_{leaf} (µmolH_2O/m²/sec)	0.21 ± 0.03[a]	0.03 ± 0.05[b]	0.08 ± 0.01[ab]	0.10 ± 0.07[a]	0.18 ± 0.05[a]
E_{leaf} (µmolH_2O/m²/sec)	4.10 ± 0.42[a]	1.09 ± 0.43[b]	2.31 ± 0.24[a]	2.21 ± 1.44[a]	3.63 ± 0.74[a]
WEU (Amax/E_{leaf})	1.02 ± 0.10[a]	2.24 ± 0.24[b]	2.37 ± 0.21[b]	2.32 ± 0.26[b]	1.12 ± 0.14[a]

Temperature data indicated that the evergreens could photosynthesize every day of the year while the deciduous plants could photosynthesize for 184 days [34]. The evergreens in this area could photosynthesize for almost twice as long as the deciduous plants from this study. Consequently, *P. ponderosa* annual photosynthetic rate would be ca. 130 mol $CO_2/m^2/yr$ (in high light) but low light would be 31% of that value (**Table 3**). The annual photosynthetic rate for *A. concolor* would be ca. 86 mol $CO_2/m^2/yr$ (in low light) and would be equivalent to the other two potential replacement species, *Acer* and *Fraxinus*. The annual photosynthetic rate for *A. concolor* would be ca. 1.39 times higher than the understory *Q. gambelii* plants, increasing the potential for *A. concolor* to grow to the canopy and overtop the *Q. gambelii* canopy trees.

We examined the growth rates of *Q. gambelii* and *A. concolor* (**Figure 2**). When height (y) in meters of *Q. gambelii* was plotted versus age (x) in years, the plot was found to be a significant 3rd order quadratic function with $R^2 = 0.87$ with a *P* value < 0.0001. Growth in height of *Q. gambelii* reached a plateau of
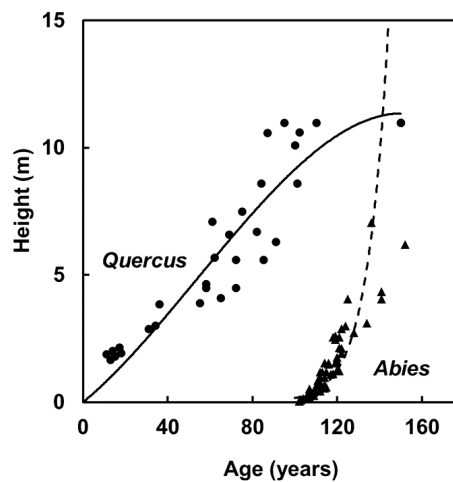
Figure 2. Plot of height of *Quercus gambelii* (●) and *Abies concolor* (▲) versus age in years from our study sites in New Mexico. For *Q. gambelii* growth in height is a 3rd order quadratic function (y = −5E−06x^3 + 0.0009x^2 + 0.0473x, $R^2 = 0.87$, *p* < 0.0001). For *A. concolor* growth in height is an exponential function (y = 6E−06e$^{0.1019x}$, $R^2 = 0.75$, *p* < 0.0001).

Table 3. Annual carbon uptake rates for the five study species, *Pinus ponderosa* (grown in the sun and shade), *Abies concolor, Acer glabrum, Fraxinus veluntina,* and *Quercus gambelii.*

Tree Species	% of Maximum	Annual CO_2 Uptake (mol $CO_2/m^2/yr$)	Habitat
Pinus ponderosa	100	130	Sun
Pinus ponderosa	31	40	Shade
Abies concolor	66	86	Shade
Acer glabrum	67	87	Shade
Fraxinus velutina	61	79	Shade
Quercus gambelii	48	62	Shade

about 11 m in 100 years. Growth in height of *A. concolor* below the canopy was exponential. Based on this population in New Mexico, these growth rates would allow *A. concolor* seedlings to reach the *Q. gambelii* canopy in approximately 35 years. Two groups of *A. concolor* from California (**Figure 3**) had exponential or 2nd order quadratic growth rates (higher in more productive sites, [45]). *Abies concolor* plants from California at the most productive sites could reach the *Q. gambelii* canopy in the same number of years. Comparisons of *Q. gambelii* growth factors with *A. concolor* are summarized in **Table 4**. *Abies concolor* A_{net} below the *Q. gambelii* canopy is 60% of the *Q. gambelii* rate; however, *Abies concolor* has leaves for 365 days of the year and fixes 1.39 times more carbon per year than *Q. gambelii*. Additionally, it has an exponential growth rate in height. *Abies concolor* wood specific gravity is 56% lower than *Q. gambelii* wood specific gravity (**Table 4**), which means ~44% more carbon is put into growth in height to reach the canopy at low light levels and low photosynthetic rates.
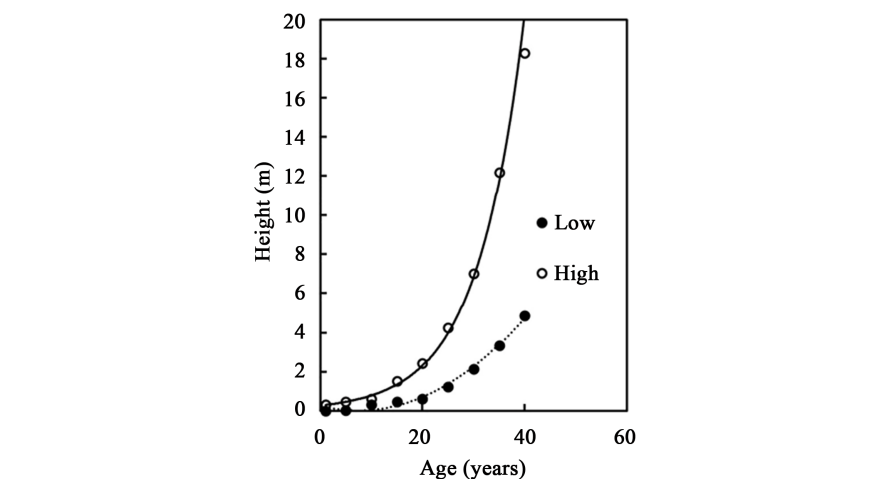
Figure 3. Plots of pooled height data in m of *Abies concolor* versus age of extrapolated data from high (O) and low (●) productivity growth plots [45]. High productivity growth is exponential (y = $0.26e^{0.11x}$, R^2 = 0.99, $p < 0.0001$), while low productivity growth is second order quadratic (y = $0.00x^2 − 0.7x + 0.25$, R^2 = 0.99, $p < 0.0001$).

Table 4. Comparison of growth parameters for *Quercus gambelii* and *Abies concolor*.

Parameter	Species	
	Quercus	*Abies*
A_{net} at PFD 125 (μmol/m²/sec)	4.07	2.44
% *Quercus* low light	-	60
Days with leaves	184	365
Annual net carbon uptake (mol CO_2/m²/y)	62	86
% of annual *Quercus* growth rate	-	139
Growth rate	2nd order quadratic	exponential
Height at 50 years (m)	~4.25	~7.50
Height at 140 years (m)	~10	~14
Wood specific gravity (g/cm³)	0.62 [10]	0.35 [41]
% of *Quercus* specific gravity	-	56

4. Discussion

There has been some debate regarding the successional status of *Quercus gambelii* (see [10] [11]). Major changes in the plant communities in the mountains of southwestern North America occurred more than 150 years ago [46] [47]. At that time, large herds of domestic livestock were introduced into the area with concomitant community changes. High levels of herbivory reduced the light fluffy fuel (grass dry-mass), reducing the fire frequency or increasing the fire return rate [19] [48]. About this time many *Q. gambelii* populations expanded, encroached or established in mountain grasslands or meadows (see [5]) and the canopies of some of these communities remain mono-specific today but there is a recruitment bottleneck for *Q. gambelii* [20]; that is, juvenile plants are not being recruited into the adult community.

Many studies demonstrated *Pinus* and *Quercus* establishment in grasslands with reduced fire frequency (see [12]). However, understanding the dynamics of tree replacement in woodland or forest communities throughout the world has been difficult in spite of numerous papers on the topic (see [25] [49] [50]). This includes existing *Q. gambelii* communities in mountainous western North American [9] [11]. The factors that control recruitment into mature populations have also been difficult to determine [51] [52].

Succession directed or controlled by the ratio of at least two limiting resources may be the best explanation for tree replacement [53] [54] [55] [56]. Surface light and soil nitrogen in woodland or forest succession change through time, with surface light levels decreasing and soil nitrogen levels increasing (see [22]). High light (shade intolerant) and low soil nitrogen requiring species dominate early in succession; while shade tolerant and high soil nitrogen requiring species dominate later in succession [22] [57]. In open forest canopies, disturbances allow the establishment of early successional species [49] [50] [58] [59]. These species would have high light requirements and possibly other requirements that occur in gaps, but not below a closed canopy [49].

On low-elevation xeric sites that occasionally burn, *Q. gambelii* may establish and become the dominant and remain the dominant species (see [10]). However at higher elevations which are wetter and cooler, more shade tolerant conferences probably replace *Q. gambelii* (see [11]). We showed previously that a bottleneck in recruitment of *Q. gambelii* occurs in these older communities [5]. In the current study, we wanted to show that photosynthetic rates would allow us to determine the replacement species in *Q. gambelii* communities. However, we found that *Q. gambelii,* like many other oaks and early successional species, is a sun plant ([20] [28] [60]-[66]). Based on the photosynthetic rate of *Q. gambelii* and demographic data [5], *Q. gambelii* will not be the dominant species in future communities. There are reports of seedlings of some *Quercus* species survival in low light environments [67] [68], but most members of the genus appear to be shade intolerant [20] [62] [69] [70] [71] [72] [73].

It has been suggested that both *Pseudotsuga menziesii* (Douglas-fir) and *Abies concolor* (or other species of fir) could replace the *Q. gambelii* populations or

communities, depending on the area rainfall, temperature, fire frequency, and herbivory (see [10] [11]). Based on community data from the current study area, potential replacement species include *Pinus ponderosa*, *Fraxinus velutina*, *Acer glabrum*, and *A. concolor* [5]. Most of these species establish best in partial shade and some of them under a closed canopy in dense shade [12] [50] [74] [75] [76] [77]. Most of these species are present in the understory of mature *Q. gambelii* communities (Table 1).

It is difficult to predict, which of the species tested would replace *Q. gambelii*, based on the photosynthetic rates (Table 2). At 125 μmolm²/sec the light level found beneath the canopy of *Q. gambelii*), four of the study species have similar photosynthetic rates. The rate for *A. concolor* at 125 μmol/m/sec is significantly lower than the other species suggesting it would not be present in older communities. However, closer examination of other photosynthetic parameters and growth rates from this study and work of others would alter this prediction. Gas exchange rates at high light levels (Table 2) suggest that *P. ponderosa* is an early successional species [78], and not a replacement species of *Q. gambelii*. Its annual photosynthetic rate at lower light levels is lower than all species examined (Table 2 and Table 3). Transpiration rates and water-use efficiency reported in this study, which are similar to those reported elsewhere [79], further support the fact that *P. ponderosa* would not replace *Q. gambelii*.

In addition, the photosynthetic abilities of *P. ponderosa* are more reduced at lower temperatures than *Abies grandis* and other fir species [80]. Therefore, even though both *P. ponderosa* and *A. concolor* can photosynthesize year round, *A. concolor* can fix carbon at higher rates than *P. ponderosa* during the coldest months and at low light (Table 3). We have not identified any studies of photosynthetic or respiratory rates of *A. concolor*. However, a number of United States Forest Service studies reported seedling establishment in the shade of several different canopy trees and growth rates in canopy shade [11]. Photosynthetic rates that we report here for *A. concolor* are similar to rates for other fir species [78] and similar to rates reported for shade species [81].

While we evaluated the changes in photosynthetic rates at various light levels, we did not evaluate these changes at various temperature, or other environmental conditions. By evaluating growth rates, a response variable that takes into account all of the conditions that a species is exposed to at a given site, we can better predict the replacement of one species by another in a successional sequence [57]. When growth rates are compared, *A. concolor* would be a better competitor than *Q. gambelii* in canopy shade (Table 4). Mature *Q. gambelii* communities are reported to be 100 to 150 years old [5] [10]. Various studies suggest that *Q. gambelii* trees start to die at about 100 years of age. This is probably density dependent self-thinning occurring as plant communities get older [54]. What we have shown is that *Q. gambelii* trees between 80 and 100 years old stop increasing in height (Figure 2). These trees grow to 9 - 12 m. Their growth is a second order quadratic function reaching a plateau at about 90 years and 10 - 11 m in height. They do not seem to replace themselves [5]. *Abies concolor*

appears to be a *Q. gambelii* replacement species based on its annual CO_2 uptake (Table 3 and Table 4). In addition, its growth rate in the communities we examined was exponential (Figure 2). Furthermore, *A. concolor* grown in plots with high productivity had exponential growth rates as well (Figure 3, [45]). We calculate that *A. concolor* would reach the *Q. gambelii* canopy in 35 years and continue to grow, overgrowing or overtopping the *Q. gambelii* canopy. At this time, *A. concolor* would start to shade the oaks further reducing their growth. It is not known how much time is required for *A. concolor* to overgrow the *Q. gambelii* community.

Physiological factors are probably one dimension of the replacement dynamics in these forests. Additionally, differential herbivory by large ungulates and fire susceptibility of the various species potentially influence replacement dynamics [20]. When the age of *Q. gambelii* and *A. concolor* are plotted together as in Figure 2, growth lines would cross at 140 years. This assumes that *Q. gambelii* trees grow to approximately 10 - 12 m tall. We did not find any *A. concolor* seedlings below the canopy of *Q. gambelii* until the communities were over 100 years of age based on tree ring analysis [5]. Communities that were 137 years old had an average of 73 adult *A. concolor* per hectare, and as many as 233 seedlings/ha. Thus, in Figure 2 we started the *A. concolor* growth curve at 100 years and after approximately 35 years of growth they would reach the *Q. gambelii* canopy. *Abies concolor* grown in productive sites in California (Figure 3, [45]) would reach the *Q. gambelii* canopy in 35 years. We assume these were even-aged plots with little or no shade and spacing to prevent competition.

The above does not seem consistent with other studies that suggest that species with low wood specific gravity and high growth rates would be poor competitors [25]. It seems that the low wood specific gravity would permit more carbon going to growth in height, allowing *A. concolor* to reach the canopy and to shade and probably outcompete *Q. gambelii*, and become the future community dominant. *Quercus gambelii* may suppress the early entry and growth of *A. concolor* for about 100 years; but once established, *A. concolor* growth becomes exponential and would reach the *Q. gambelii* canopy in 35 - 40 years.

Acknowledgements

References

[1] Lorimer, C.G. (1993) Causes of the Oak Regeneration Problem. In: Loftis, D.L. and McGee, C.E., Eds., *Oak Regeneration: Serious Problems, Practical Recommendations*, USDA Forest Service, Southeastern Forest Experiment Station, Knoxville, Tennessee, 14-39.

[2] Loftis, D.L. and McGee, C.E. (1993) Oak Regeneration: Serious Problems, Practical Recommendations. USDA Forest Service, Southeastern Forest Experiment Station, Knoxville, Tennessee.

[3] Cowell, C.M. and Hayes, J.J. (2007) Structure, History and Dynamics of a Mature Oak-Beech Forest in Western Indiana. *Journal of the Torrey Botanical Society*, **134**,

215-222. https://doi.org/10.3159/1095-5674(2007)134[215:SHADOA]2.0.CO;2

[4]   Shumway, D.L., Abrams, M.D. and Ruffner, C.M. (2001) A 400-year History of Fire and Oak Recruitment in an Old-Growth Oak Forest in Western Maryland, U.S.A. *Canadian Journal of Forest Research*, **31**, 1437-1443.
https://doi.org/10.1139/x01-079

[5]   Ryniker, K.A., Bush, J.K. and Van Auken, O.W. (2006) Structure of *Quercus gambelii* Communities in the Lincoln National Forest, New Mexico, USA. *Forest Ecology and Management*, **233**, 69-77. https://doi.org/10.1016/j.foreco.2006.06.008

[6]   DeVelice, R.L. and Ludwig, J.A. (1983) Forest Habitat Types South of the Mongollon Rim, Arizona and New Mexico. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

[7]   DeVelice, R.L., Ludwig, J.A., Moir, W.H. and Ronco, F.J. (1986) A Classification of Forest Habitat Types of Northern New Mexico and Southern Colorado. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado.

[8]   Dick-Peddie, W.A. (1993) New Mexico Vegetation: Past, Present and Future. University of New Mexico Press, Albuquerque, New Mexico.

[9]   Peet, R.K. (1988) Forests of the Rocky Mountains. In: Barbour, M.G. and Billings, W.D., Eds. *North American Terrestrial Vegetation*, Cambridge University Press, New York, 63-101.

[10] Simonin, K.A. (2000) *Quercus gambelii*.
https://www.fs.fed.us/database/feis/plants/tree/quegam/all.html

[11] Zouhar, K. (2001) Abies Concolor.
https://www.fs.fed.us/database/feis/plants/tree/abicon/all.html

[12] Abrams, M.D., Orwig, D.A. and Demeo, T.E. (1995) Dendroecological Analysis of Successional Dynamics for a Presettlement-Origin White-Pine-Mixed-Oak Forest in the Southern Appalachians, USA. *Journal of Ecology*, **83**, 133-143.
https://doi.org/10.2307/2261156

[13] Beschta, R. and Ripple, W. (2009) Large Predators and Trophic Cascades in Terrestrial Ecosystems of the Western United States. *Biological Conservation*, **142**, 2401-2414. https://doi.org/10.1016/j.biocon.2009.06.015

[14] Bowles, M.L., Jacobs, K.A. and Mengler, J.L. (2007) Long-Term Changes in an Oak Forest's Woody Understory and Herb Layer with Repeated Burning. *Journal of the Torrey Botanical Society*, **134**, 223-237.
https://doi.org/10.3159/1095-5674(2007)134[223:LCIAOF]2.0.CO;2

[15] Jenkins, L.H., Murray, B.D., Jenkins, M.A. and Webster, C.R. (2015) Woody Regeneration Response to Over a Decade of Deer Population Reductions in Indiana State Parks. *Journal of the Torrey Botanical Society*, **142**, 205-219.
https://doi.org/10.3159/TORREY-D-14-00047.1

[16] Long, Z.T., Pendergast, T.H. and Carson, W.P. (2007) The Impact of Deer on Relationships between Tree Growth and Mortality in an Old-Growth Beech-Maple Forest. *Forest Ecology and Management*, **252**, 230-238.
https://doi.org/10.1016/j.foreco.2007.06.034

[17] Royo, A.A., Stout, S.L., de Calesta, D.S. and Pierson, T.G. (2010) Restoring Forest Herb Communities through Landscape-Level Deer Herd Reductions: Is Recovery Limited by Legacy Effects? *Biological Conservation*, **143**, 2425-2434.
https://doi.org/10.1016/j.biocon.2010.05.020

[18] Schumacher, H.B. and Carson, W.P. (2013) Biotic Homogenization of the Sapling Layer in 19 Late-Successional and Old-Growth Forest Stands in Pennsylvania. *The*

Journal of the Torrey Botanical Society, **140**, 313-328.
https://doi.org/10.3159/TORREY-D-11-00002.1

[19] Van Auken, O.W. (2000) Shrub Invasions of Semiarid Grasslands. *Annual Review of Ecology and Systematics*, **31**, 197-216.
https://doi.org/10.1146/annurev.ecolsys.31.1.197

[20] Van Auken, O.W. and Bush, J.K. (2009) The Role of Photosynthesis in the Recruitment of Juvenile *Quercus gambelii* into Mature *Q. gambelii* Communities. *Journal of the Torrey Botanical Society*, **136**, 465-478. https://doi.org/10.3159/09-RA-035.1

[21] Ripple, W.J. and Beschta, R.L. (2012) Trophic Cascades in Yellowstone: The First 15 Years after Wolf Reintroduction. *Biological Conservation*, **145**, 205-213.
https://doi.org/10.1016/j.biocon.2011.11.005

[22] Bush, J.K., Richter, F.A. and Van Auken, O.W. (2006) Two Decades of Vegetation Change on Terraces of a South Texas River. *Journal of the Torrey Botanical Society*, **133**, 280-288. https://doi.org/10.3159/1095-5674(2006)133[280:TDOVCO]2.0.CO;2

[23] Davis, M.B. (1996) Extent and Location. In: Davis, M.B., Ed., *Eastern Old-Growth Forests: Prospects for Rediscovery and Recovery*, Island Press, Washington DC, 18-32.

[24] Horn, H.S. (1974) The Ecology of Secondary Succession. *Annual Review of Ecology and Systematics*, **5**, 25-37. https://doi.org/10.1146/annurev.es.05.110174.000325

[25] Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., *et al.* (2016) Plant Functional Traits Have Globally Consistent Effects on Competition. *Nature*, **529**, 204-207. https://doi.org/10.1038/nature16476

[26] Van Auken, O.W. and Bush, J.K. (1985) Secondary Succession on Terraces of the San Antonio River. *Bulletin of the Torrey Botanical Club*, **112**, 158-166.
https://doi.org/10.2307/2996412

[27] Tirmenstein, D.A. (1991) *Quercus alba*.
https://www.fs.fed.us/database/feis/plants/tree/quealb/all.html

[28] Abrams, M.D. (1990) Adaptations and Responses to Drought in *Quercus* Species of North America. *Tree Physiology*, **71**, 227-238.
https://doi.org/10.1093/treephys/7.1-2-3-4.227

[29] Neilson, R.P. and Wullstein, L.H. (1986) Microhabitat Affinities of Gamble Oak Seedlings. *Great Basin Naturalist*, **46**, 294-298.

[30] Christensen, E.M. (1958) Growth Rates and Vegetation Change in the Oak-Maple Brush in Lower Provo Canyon, Utah. *Proceedings of Utah Academy of Sciences, Arts, and Letters*, **35**, 167-168.

[31] Alexander, B.G., Ronco, F.J., Fitzhugh, E.L. and Ludwig, J.A. (1984) A Classification of Forest Habitat Types of the Lincoln National Forest, New Mexico. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colorado.

[32] Gehlbach, F.R. (1981) Mountain Islands and Desert Seas: a Natural History of the US-Mexico Borderlands. Texas A & M University Press, College Station.

[33] Hanks, J.P. and Dick-Peddie, W.A. (1974) Vegetation Patterns of the White Mountains, New Mexico. *Southwestern Naturalist*, **18**, 371-382.
https://doi.org/10.2307/3670295

[34] USDA (2005) Snotel Data Network. http://www.wcc.nrcs.usda.gov/snotel

[35] USDA (2005) Lincoln National Forest GIS Data.
http://www.fs.fed.us/r3/lincoln/contact/gis/index.htm

[36] Correll, D.S. and Johnston, M.C. (1979) Manual of the Vascular Plants of Texas.

Tex. Res. Found., Renner.

[37] USDA (2016) Plant Database. http://plants.usda.gov/java/

[38] Sall, J., Lehman, A. and Creighton, L. (2001) JMP Start Statistics: A Guide to Statistics and Data Analysis Using JMP and JMP IN Software. Duxbury Thomson Learning, Pacific Grove.

[39] Prioul, J.L. and Chartier, P. (1977) Partitioning of Transfer and Carboxylation Components of Intracellular Resistance to Photosynthetic CO_2 Fixation: A Critical Analysis of the Methods Used. *Annals of Botany*, **41**, 789-800.

[40] Givnish, T.J. (2002) Adaptive Significance of Evergreen vs. Deciduous Leaves: Solving the Triple Paradox. *Silva Fennica*, **36**, 703-743.

[41] Gerhards, C.C. (1964) Strength and Related Properties of White Fir. United States Department of Agriculture Forest Service Forest Products Laboratory, Madison.

[42] Wilson, C.L. and Loomis, W.E. (1952) Botany. Holt, Rinehart and Winston Inc., New York.

[43] Kozlowski, T.T. (1964) Shoot Growth in Woody Plants. *Botanical Review*, **30**, 335-392. https://doi.org/10.1007/BF02858538

[44] Wakeley, P.C. and Marrero, J. (1958) Five-Year Intercepts as Site Index in Southern Pine Plantation. *Journal of Forestry*, **56**, 332-336.

[45] Schumacher, F.X. (1926) Yield, Stand, and Volume Tables for White Fir in the California Pine Region. University of California, College of Agriculture Experimental Station, Berkeley.

[46] Savage, M. and Swetnam, T.W. (1990) Early 19th-Century Fire Decline Following Sheep Pasturing in a Navajo Ponderosa Pine Forest. *Ecology*, **71**, 2374-2378. https://doi.org/10.2307/1938649

[47] Swetnam, T.W., Allen, C.D. and Betancourt, J.L. (1999) Applied Historical Ecology: Using the Past to Manage for the Future. *Ecological Applications*, **9**, 1189-1206. https://doi.org/10.1890/1051-0761(1999)009[1189:AHEUTP]2.0.CO;2

[48] Scholes, R.J. and Archer, S.R. (1997) Tree-Grass Interactions in Savannahs. *Annual Review of Ecology and Systematics*, **28**, 517-544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

[49] Baker, P.J., Bunyavejchewin, S., Oliver, C.D. and Ashton, P.S. (2005) Disturbance History and Historical Stand Dynamics of a Seasonal Tropical Forest in Western Thailand. *Ecological Monographs*, **75**, 317-343. https://doi.org/10.1890/04-0488

[50] Foster, D.R., Orwig, D.A. and McLachlan, J.S. (1996) Ecological and Conservation Insights from Reconstructive Studies of Temperate Old-Growth Forests. *Tree*, **11**, 419-423. https://doi.org/10.1016/0169-5347(96)10047-1

[51] McKinley, D.C. and Van Auken, O.W. (2005) Influence of Interacting Factors on the Growth and Mortality of *Juniperus* Seedlings. *American Midland Naturalist*, **154**, 320-330. https://doi.org/10.1674/0003-0031(2005)154[0320:IOIFOT]2.0.CO;2

[52] Van Auken, O.W., Jackson, J.T. and Jurena, P.N. (2004) Survival and Growth of *Juniperus* Seedlings in *Juniperus* Woodlands. *Plant Ecology*, **175**, 245-257. https://doi.org/10.1007/s11258-005-0022-z

[53] Begon, M., Townsend, C.R. and Harper, J.L. (2006) Ecology: From Individuals to Ecosystems. Blackwell, Oxford.

[54] Grace, J.B. and Tilman, D. (1990) Perspectives on Plant Competition. Academic Press, New York.

[55] Smith, T.M. and Smith, R.L. (2012) Elements of Ecology. Pearson Benjamin Cummings, Boston.

[56] Tilman, D. (1988) Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton Press, Princeton.

[57] Van Auken, O.W. and Bush, J.K. (2013) Invasion of Woody Legumes. Springer, New York. https://doi.org/10.1007/978-1-4614-7199-8

[58] Abrams, M.D. and Orwig, D.A. (1996) A 300-Year History of Disturbance and Canopy Recruitment for Co-Occurring White Pine and Hemlock on the Allegheny Plateau, USA. *Journal of Ecology*, **84**, 353-363. https://doi.org/10.2307/2261198

[59] Lorimer, C.G. and Krug, A.G. (1983) Diameter Distributions in Even-Aged Stands of Shade-Tolerant and Midtolerant Tree Species. *American Midland Naturalist*, **109**, 331-345. https://doi.org/10.2307/2425414

[60] Bond, W.J. (2008) What Limits Trees in C_4 Grasslands and Savannas? *Annual Review of Ecology, Evolution, and Systematics*, **39**, 641-659. https://doi.org/10.1146/annurev.ecolsys.39.110707.173411

[61] Groom, Q.J., Baker, N.R. and Long, S.P. (1991) Photoinhibition of Holly (*Ilex aquifolium*) in the Field during the Winter. *Physiologia Plantarum*, **83**, 585-590. https://doi.org/10.1111/j.1399-3054.1991.tb02472.x

[62] Hamerlynk, E.P. and Knapp, A.K. (1994) Leaf-Level Responses to Light and Temperature in Two Co-Ocurring *Quercus* (Fagaceae) Species: Implications for Tree Distribution Patterns. *Forest Ecology and Management*, **68**, 149-159. https://doi.org/10.1016/0378-1127(94)90042-6

[63] Hollinger, D.Y. (1992) Leaf and Simulated Whole-Canopy Photosynthesis in Two Co-Occurring Tree Species. *Ecology*, **73**, 1-14. https://doi.org/10.2307/1938716

[64] Knapp, A.K. (1992) Leaf Gas Exchange in *Quercus macrocarpa* (Fagaceae): Rapid Stomatal Responses to Variability in Sunlight in a Tree Growth Form. *American Journal of Botany*, **79**, 599-604. https://doi.org/10.2307/2444875

[65] Kozlowski, T.T., Kramer, P.J. and Pallardy, S.G. (1991) The Physiological Ecology of Woody Plants. Academic Press, New York.

[66] Strickan, W. and Zhang, X. (1992) Seasonal Change in CO_2 and H_2O Gas Exchange of Young European Beech (*Fagus sylvatica* L.). *Tree*, **6**, 90-102.

[67] Callaway, R. (1992) Morphological and Physiological Responses of Three California Oak Species. *International Journal of Plant Sciences*, **153**, 434-441. https://doi.org/10.1086/297049

[68] Fuchs, M.A., Krannitz, P.G. and Harestad, A.S. (2000) Factors Affecting Emergence and First-Year Survival of Seedling of Garry Oaks (*Quercus garryana*) in British Columbia, Canada. *Forest Ecology and Management*, **137**, 209-219. https://doi.org/10.1016/S0378-1127(99)00329-1

[69] Gardiner, E.S. and Hodges, J.D. (1998) Growth and Biomass Distribution of Cherrybark Oak (*Quercus pagoda* Raf.) Seedlings as Influenced by Light Availability. *Forest Ecology and Management*, **108**, 127-134. https://doi.org/10.1016/S0378-1127(98)00220-5

[70] Kelly, D.L. (2002) The Regeneration of *Quercus petraea* (Sessile Oak) in Southwest Ireland: A 25-Year Experimental Study. *Forest Ecology and Management*, **166**, 207-226. https://doi.org/10.1016/S0378-1127(01)00670-3

[71] Quintana-Ascencio, P.F., Gonzalez-Espinosa, M. and Ramirez-Marcial, N. (1992) Acorn Removal, Seedling Survivorship, and Seedling Growth of *Quercus crispipilis* in Successional Forests of the Highlands of Chipas, Mexico. *Bulletin of the Torrey Botanical Club*, **119**, 6-18. https://doi.org/10.2307/2996914

[72] Riley, J.M.J. and Jones, R.H. (2003) Factors Limiting Regeneration of *Quercus alba* and *Cornus florida* in Formerly Cultivated Coastal Plain Sites, South Carolina. *For-*

est Ecology and Management, **177**, 571-586.
https://doi.org/10.1016/S0378-1127(02)00449-8

[73] Russell, F.L. and Fowler, N.L. (1999) Rarity of Oak Saplings in Savannahs and Woodlands of the Eastern Edwards Plateau, Texas. *Southwestern Naturalist*, **44**, 31-41.

[74] Abrams, M.D. (2003) Where Has All the White Oak Gone? *Bioscience*, **53**, 927-939. https://doi.org/10.1641/0006-3568(2003)053[0927:WHATWO]2.0.CO;2

[75] Hodges, J.D. and Scott, D.R. (1968) Photosynthesis in Seedlings of Six Conifer Species under Natural Environmental Conditions. *Ecology*, **49**, 973-980. https://doi.org/10.2307/1936548

[76] Jackson, L.W.R. (1967) Effect of Shade on Leaf Structure of Deciduous Tree Species. *Ecology*, **48**, 498-499. https://doi.org/10.2307/1932686

[77] Lorimer, C.G., Chapman, J.W. and Lambert, W.D. (1994) Tall Understory Vegetation as a Factor in the Poor Development of Oak Seedlings beneath Mature Stands. *Journal of Ecology*, **82**, 227-237. https://doi.org/10.2307/2261291

[78] Korol, R.L. (2001) Physiological Attributes of 11 Northwest Conifer Species. United States Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins.

[79] Monson, R.K. and Grant, M.C. (1989) Experimental Studies of Ponderosa Pine III. Differences in Photosynthesis, Stomatal Conductance, and Water-Use Efficiency between Two Genetic Lines. *American Journal of Botany*, **76**, 1041-1047. https://doi.org/10.2307/2444526

[80] Nippert, J.B., Duursma, R.A. and Marshall, J.D. (2004) Seasonal Variation in Photosynthetic Capacity of Montane Conifers. *Functional Ecology*, **18**, 876-886. https://doi.org/10.1111/j.0269-8463.2004.00909.x

[81] Hull, J.C. (2002) Photosynthetic Induction Dynamics to Sunflecks of Four Deciduous Forest Understory Herbs with Different Phenologies. *International Journal of Plant Sciences*, **163**, 913-924. https://doi.org/10.1086/342633