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The Effects of Fire and Deer Herbivory on Oak Regeneration in an Eastern Deciduous Forest

Julie La Spina
Union College - Schenectady, NY

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By
Julie La Spina

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ABSTRACT

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In the past, oak was one of the most dominant species groups in the deciduous forests of the northeastern United States. More recently, a variety of factors, including interspecific competition, fire suppression and deer herbivory, have led to the decline of oaks. We studied how oaks regenerate and grow following a major disturbance, and how their growth interacts with deer herbivory. We measured the growth of seedlings of three tree species following the 1,200 hectare Overlook Fire that occurred in Minnewaska State Park, NY in April 2008. At each of three sites, we measured the growth of twenty *Quercus prinus*, *Quercus rubra*, and *Sassafras albidum* seedlings. Half of the individuals of each species were caged to prevent deer herbivory. The height of the seedlings and any evidence of herbivory were recorded in July, August, and September 2008. Several transects in each of the sites were used to determine species composition and relative abundance. The relative growth of *Q. prinus* varied by site – growth was highest where light levels were greatest ($p < 0.01$). This suggests that the *Q. prinus* grew better where fire-caused damage to the canopy was greatest. There was no significant difference in the relative growth of caged versus uncaged seedlings ($p > 0.05$). Overall, the abundance of *S. albidum* seedlings – frequently an early successional specialist – was greater than the abundance of either *Quercus* species. These results suggest that the severity of the damage to the canopy may influence the regeneration of oaks and that deer herbivory does not have a significant impact on their growth.

Introduction

Forest succession plays an important role in the species composition of a habitat and the ecological interactions within an ecosystem (Connell and Slayter 1977; Horn 1974). The gradual shift in community composition over time from one community to another is commonly seen after disturbances that can be natural (i.e. wildfires, floods, volcanoes) or anthropogenic (i.e. clearcutting, prescribed fires). While major disturbances may strip the land of nearly all of its vegetation, more minor disturbances may only partially clear the land of its plant life. In either case, the first species to recolonize an area are often extremely important to later successional species and community structure (Del Moral and Wood 1992; Olff et al., 1993; Reich et al., 1990). These early colonizers modify the environment so that it may become more or less suitable for other successional species (Connell and Slatyer 1977). Therefore, many times this post-disturbance community is different from the pre-disturbance community and a noticeable change can be seen in species composition. While certain species may prosper in the new environment, others may not be able to reestablish at all.

One example of shifting community composition as succession proceeds is oak (*Quercus*) communities in the eastern deciduous forest (Abrams, 1992; Iverson et al., 2008). In the past, oak was one of the most dominant species groups in the deciduous forests of the Northeastern United States. More recently a variety of factors, such as climate change, logging, animal grazing, insect defoliation, and disease, have contributed to a decline in the abundance of oaks (Abrams, 1992). In addition, closed-canopy conditions have caused shade-intolerant oak seedlings to perform poorly and be out competed by shade-tolerant species (Nowacki et al., 2008). When light is a limiting factor, oaks tend to be successionally replaced by other species such as sugar maple, red maple, and black cherry (Abrams, 1992). Today, oak species are increasingly restricted to certain conditions. Therefore, areas where oaks are found in abundance, such as the Shawangunk Ridge in New York State, are considered unique.

Fire suppression has contributed to the inability of oaks to regenerate. Such land-use changes as road construction, the development of towns, overgrazing, the conversion of forests and prairies to croplands, and safety issues have led to a decline in fire frequency in northeastern North America since European settlement (Nowacki and Abrams 2008; Abrams, 1992). This reduction in fire frequency may contribute to undesirable conditions for oak regeneration in several ways. First, a decline in disturbances prevents an open canopy which seems to be essential for the growth of shade-intolerant oaks. Second, without fires, the successional process cannot be reset. If early colonizers do not provide good conditions for the growth of oak species, it seems unlikely that the oaks will be able to establish themselves at a later point in time due to overwhelming interspecific competition. Fire suppression may prevent the process of succession and consequently, the successful growth of oaks.

In addition to fire suppression, deer herbivory has greatly affected oak regeneration and growth. Over the past decades, white-tailed deer (*Odocoileus virginianus*) populations have increased drastically throughout their range, including the Northeast (Garrott et al. 2003). These high deer densities have been found to impact species diversity and tree regeneration by reducing the growth and survival of seedlings that are consumed (Tilghman 1989). Rooney et al. (2003) reported that red oak (*Quercus rubra*) seedling densities declined sharply as browsing pressure from deer increased.

Similarly, Rossell et al. (2007) found that browsing had a negative effect on oak species richness. Together, these studies indicate that deer herbivory is another factor contributing to the decline of oaks.

In this study, we tested the aforementioned effects of white-tailed deer and fire suppression on an oak community in southern New York. We looked at how the regeneration, growth, and survival of chestnut oak (*Quercus prinus*), red oak (*Quercus rubra*), and sassafras (*Sassafras albidum*) seedlings were affected by deer herbivory following a major forest fire in April 2008. We compared the growth of seedlings that had been caged to exclude deer herbivory to the growth of seedlings that were not caged and open to herbivory. We also observed how seedlings regenerated after a disturbance by looking at species composition in burned areas. The specific questions we addressed are: (1) Which species were most successful in recolonizing the burned areas? (2) Does deer herbivory reduce seedling growth (in particular, the growth of oaks)? (3) Is there an interaction between species and deer herbivory?

Methods

Study Area

We established our experimental plots at Minnewaska State Park Preserve in Ulster County, New York, about 90 miles north of New York City. The 20,000-acre park is located on the Shawangunk Mountain ridge and is comprised of a dense hardwood forest. Although Minnewaska has experienced forest fires in the past, the Overlook Fire was the largest fire in nearly 60 years (Buckley 2008), burning approximately 3,000 acres over a span of four days (April 17, 2008 to April 20, 2008). This enormous fire, which is unusual in recent history in the Northeast, was believed to be fueled by winds and dry, thick underbrush composed of mountain laurel (*Kalmia latifolia*), huckleberry (*Vaccinium*), and pitch pine (*Pinus rigida*) litter.

The mean annual temperature for Minnewaska State Park during the year of our study (2008) was 50.0° F. This was 1.7° F above the 113-year average for the area. During the summer months, when a majority of our research was completed, the mean temperature was 69.4° F. The annual precipitation level (60.12 inches) was well above the normal (47.85 inches). In the 113 years of record, 2008 was the ninth wettest year for the area. The length of the growing season was 188 days, beginning April 15 and lasting until October 18. During the growing season, 27.99 inches of rain fell, close to the historical average of 29.35 inches.

Experimental Design

In July 2008, 20 chestnut oak, red oak, and sassafras seedlings were identified at three different sites within Minnewaska State Park Preserve (one near Awosting Parking Lot and two near Jenny Lane trail). At the Awosting site, few chestnut oak seedlings were found both in the understory and the canopy, so only red oak and sassafras seedlings were sampled. Half of the individuals of each species were caged. These cages, constructed of hardware cloth (1 cm^2 gauge) and poultry wire, were used to help prevent herbivory by deer and other large browsers (Hulme, 1994). They likely also reduced herbivory by small mammals, but not by insects. In total, 160 seedlings were flagged – 80 of them were caged while the other 80 were uncaged.

The initial height and evidence of herbivory for each seedling was recorded in July, August, and September 2008. The number of species was recorded in each site to determine their relative abundances. This was carried out by setting up three 20 meter transects in each site and counting the number of seedlings within 1 meter of the transect. Light intensity that each seedling received was collected in July using a LiCor LI-189 photometer. Twelve soil samples (four from each site) were sent to the Cornell Nutrient Analysis Laboratory to determine their soil moisture and nutrient contents. We left the seedlings caged through the winter and following growing season so as to assess seedling growth and survival one year following the fire.

Statistical analyses

The mean relative growth of chestnut oak, red oak, and sassafras amongst the three study areas were compared using ANOVA. The model used included species, site, caged/uncaged, and the interaction between site and species as independent variables. The interaction between site and caged/uncaged was also included in the model. Species composition at each site was analyzed using ANOVA in which the dependent variable was the average number of seedlings. Differences in light levels in each of the sites were tested using an ANOVA as well. Where ANOVA indicated a significant main effect of species or site, we performed an LSD analysis in order to test for differences between treatments.

Results

Soil Composition and Light Levels

Soil composition did vary between the three study sites. Although the only significant difference between the soils was found in phosphorus levels ($p < 0.05$; Table 1), this difference means that the soils did vary. Soil at Jenny Lane B had more than three times the amount of phosphorus as the soil at Awosting. In addition, a trend in the data suggests that Jenny Lane B had significantly more phosphorus in its soils than Jenny Lane A ($p = 0.06$). Another key finding was that available nitrate was very low at all sites.

In addition to variations in soil composition between the sites, there were also differences in light levels. At Jenny Lane B, light levels were significantly higher than at Awosting and Jenny Lane A ($p < 0.01$; Figure 1). However, light levels did not significantly differ between Jenny Lane A and Awosting ($p > 0.05$).

Species Composition and Relative Abundance

Huckleberry and mountain laurel made up approximately 75% of the vegetation in each of the three sites. However, aside from these two species, the relative abundance of sassafras was the greatest in two of the three study sites. In both Awosting and Jenny Lane A, sassafras seedlings were much more abundant than chestnut oak and red oak (Figure 2). However, in Jenny Lane B, the average number of seedlings of each of the three species was similar – although chestnut oaks were the most abundant, the number of sassafras and red oak seedlings were close in number to the chestnut oaks.

Seedling Growth

Seedling growth varied by site as well as by species (Table 2). Sassafras grew more than chestnut oak and red oak in all three study sites (Figure 3). The relative growth of red oak ranged from -11% to 92% while the relative growth of chestnut oak ranged from -13% to 63%. On average, red oak grew 26% at Awosting, 9% at Jenny Lane A, and 13% at Jenny Lane B. The mean relative growth of chestnut oak was 8% at Jenny

Lane A and 29% at Jenny Lane B. There was an interaction between site and species – chestnut oaks were present at Jenny Lane B, but not at Awosting. In addition, chestnut oak seedlings at Jenny Lane B grew almost as well as sassafras seedlings.

Caged vs. Uncaged

There was no significant difference in relative growth between species that were caged and those that were uncaged (Figure 4). The mean relative growth of caged seedlings was only 0.1% more than uncaged seedlings. Furthermore, there was no interaction between species and deer herbivory ($p > 0.05$).

Discussion

Seedling Regeneration

Sassafras was the most abundant species in two of the three study sites and had a much higher relative growth than chestnut oak and red oak in all three sites. Even though sassafras was most successful at recolonizing the area after the fire, the regeneration of chestnut oaks and red oaks was evident at the three sites, but in much smaller numbers. The oaks that were able to reestablish grew considerably between our initial measurements in July and our final measurements in September (Figure 3). Therefore, once oaks seedlings were established, they were successful as well.

Even though sassafras was successful as an early colonizer, species composition and relative abundance will likely continue to change over the years. Peterson and Pickett (1995) detailed the patterns and mechanisms of regeneration in an old-growth beech-hemlock forest following a tornado. In the six seasons following the tornado, *Betula alleghaniensis* and *Tsuga canadensis* established at high densities, but both declined significantly over the next five years. In addition, shade-intolerant and intermediate species did well initially, but declined in abundance thereafter. This study indicates that species composition continually changes over time following a disturbance. If a similar pattern holds in the Minnewaska community, sassafras could eventually be replaced by later successional species causing a shift in understory species composition as well as species in the forest canopy.

Chestnut oak, which is of special interest to ecologists at Minnewaska State Park, was particularly successful at Jenny Lane B. Variations in light levels between the three sites seem to be the main factor contributing to these differences in chestnut oak abundance and growth. Light levels were significantly higher at Jenny Lane B than at Awosting and Jenny Lane A, perhaps due to a more severe burn at Jenny Lane B. Since chestnut oaks are a shade-intolerant species, the open canopy at Jenny Lane B provided more suitable conditions for oak growth. Another factor that may have contributed to the success of chestnut oak at this specific site was the significantly higher phosphorus levels at Jenny Lane B than at Awosting and Jenny Lane A. Although the exact soil mechanisms are unknown the soil at Jenny Lane B may have been more favorable for chestnut oak growth than soil at Awosting and Jenny Lane A.

The paucity of oak regeneration at Minnewaska State Park is comparable to the lack of oak regeneration and growth in several other forests in the Eastern United States. Arthur et al. (1998) observed a decline in oak regeneration in the Southern Appalachian forests of Kentucky, which is believed to be largely in response to fire suppression in this region. Other studies have noted a compositional shift from fire-dependent xerophytic species, such as oak, pine, and chestnut, to fire-sensitive species such as maple, cherry, and hemlock (Nowacki and Abrams 2008; Abrams 1992). In these studies, fire suppression seemed to be the limiting factor in oak growth as well.

Effects of Deer Herbivory

Deer herbivory had no effect on seedling growth following the fire at Minnewaska – seedlings that were caged to prevent herbivory did not grow significantly more than seedlings that were uncaged. These results were unexpected considering the large deer population in New York State and the several studies that have shown that deer have a negative impact on oak regeneration (Tilghman 1989; Rooney and Waller 2003; Rossell et al. 2007). One possibility is that deer may have avoided these burned areas due to the initial lack of vegetation following the fire. This would allow oak species to reestablish the area and grow with minimal browsing by deer. It is also possible that deer consumed other abundant species such as herbs (Rooney and Waller 2003). Since the study was conducted over the summer, deer may have had a greater selection of vegetation and were not limited to oaks. Further study would be necessary to determine whether seasonal changes impact oak consumption as well as whether deer avoid the burned sites.

Implications for management of oak forests

Although oaks in our study seemed to regenerate no better or worse than oaks in similar studies due to widespread fire suppression, the reduced impact of deer herbivory on oaks at Minnewaska State Park may contribute to the minor success of the oak community in this area. Numerous studies have shown that high deer densities negatively impact species diversity and tree regeneration by reducing the growth and survival of seedlings that are consumed (Tilghman 1989; Rooney and Waller 2003). More specifically, Rossell et al. (2007) observed that deer browsing negatively affected oak species richness. Even though our study found that deer had no impact on oak regeneration, which would eliminate the negative consequences of herbivory on oak growth at Minnewaska, further study would be necessary to determine to what degree deer affected oaks during the winter when vegetation is limited.

Due to the importance of fire in oak-forest ecosystems, several studies have examined the use of controlled burns to reduce interspecific competition and promote the regeneration of oaks. Arthur et al. (1998) studied the impact of two single fires and a repeated fire on herb, shrub, and tree strata on an oak-pine ridgetop in eastern Kentucky. Although chestnut oak was found in fairly high densities in the understory of the single-burn plot, the highest density of chestnut oak was found in the understory of the twice-burned site. Chestnut oak also had the highest cover in the twice-burned plot. The results of this study suggest that prescribed fire may encourage chestnut oak regeneration and that repeated prescribed burns may positively affect the species' ability to regenerate while limiting the growth of non-oak species. Although further study would be necessary to determine the effectiveness of twice-burned sites, our results suggest that single fires may have a positive impact on oak regeneration and growth.

The severity of damage to the canopy by the Overlook Fire may influence the regeneration of oaks. Areas that were burned more severely had higher light levels which seemed to help shade-intolerant oaks grow. If this is the case, parks such as Minnewaska may want to consider high-intensity prescribed burns that mimic the severity of a natural fire. These high-intensity controlled burns would open up the canopy much more than the current prescribed burns at Minnewaska and would assist in oak species regeneration.

Deer herbivory may also have an effect on oak communities. Although deer did not have a significant impact on oak regeneration and growth in the present study, they may negatively affect oaks in other regions. In these areas, parks may want to regulate the deer population by allowing deer to be hunted. If implemented correctly, these management proposals may have profound impacts on the oak community and lead to their growth and success in the future.

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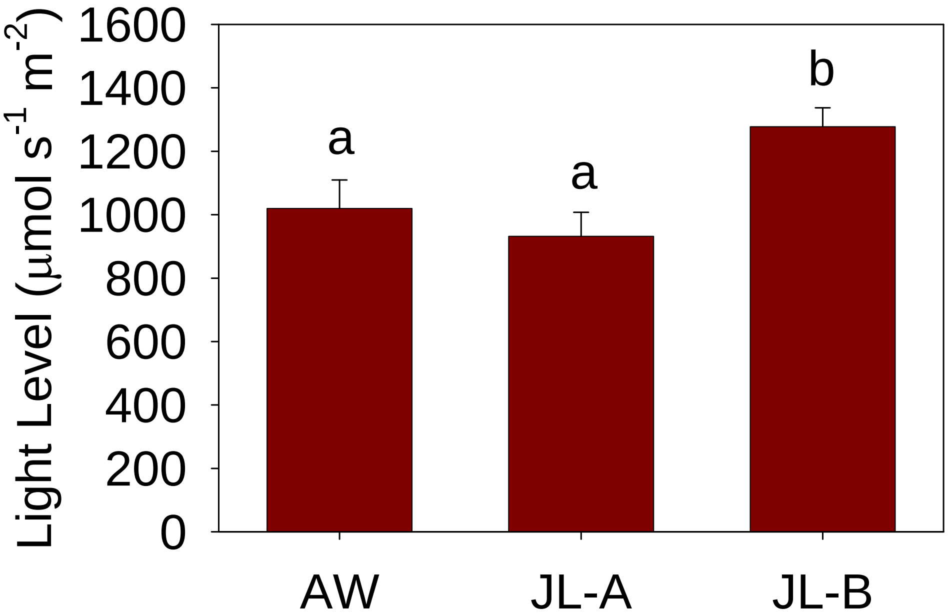

Figure 1. Average light levels at each site. Different letters indicate significant differences in light levels. AW = Awosting, JL-A = Jenny Lane A, JL-B = Jenny Lane B.

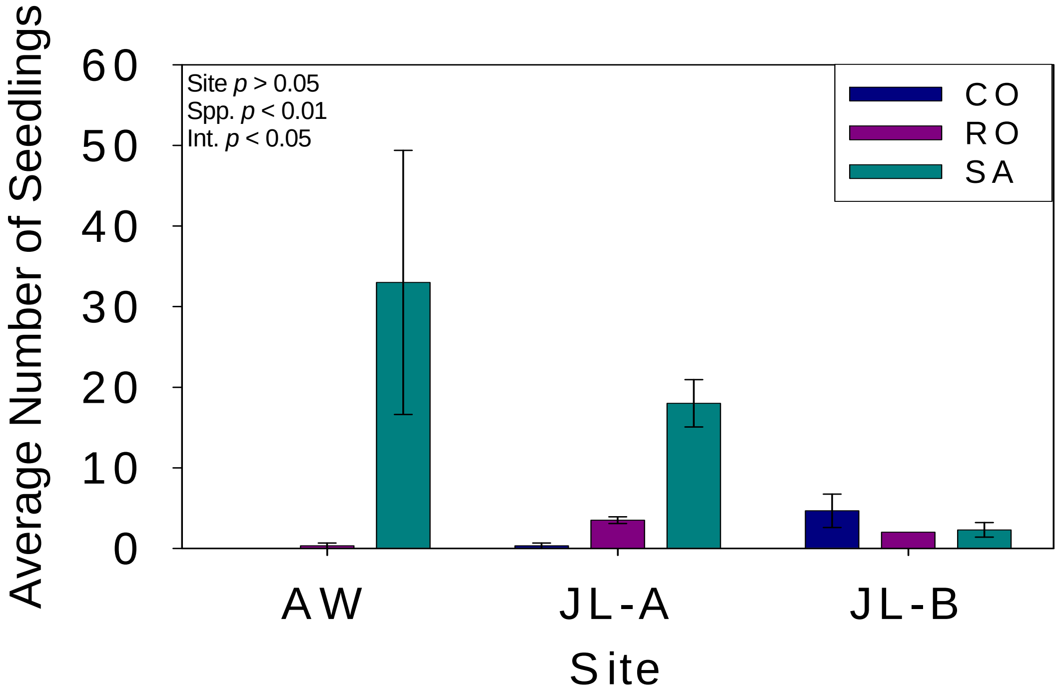

Figure 2. Species composition at each site. Significant differences between species and site are indicated by *P* values based on ANOVA tests. CO = chestnut oak, RO = red oak, SA = sassafras.

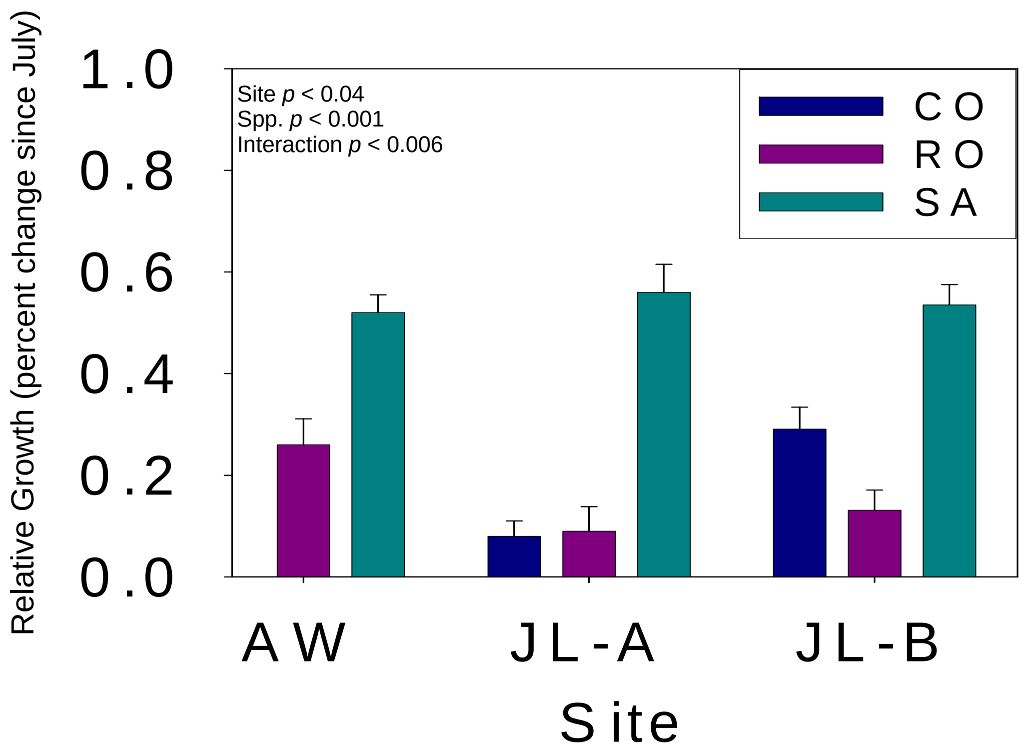

Figure 3. Mean relative growth of chestnut oak, red oak, and sassafras at each site. Significant differences between species and site are indicated by *P* values based on ANOVA tests. CO = chestnut oak, RO = red oak, SA = sassafras.

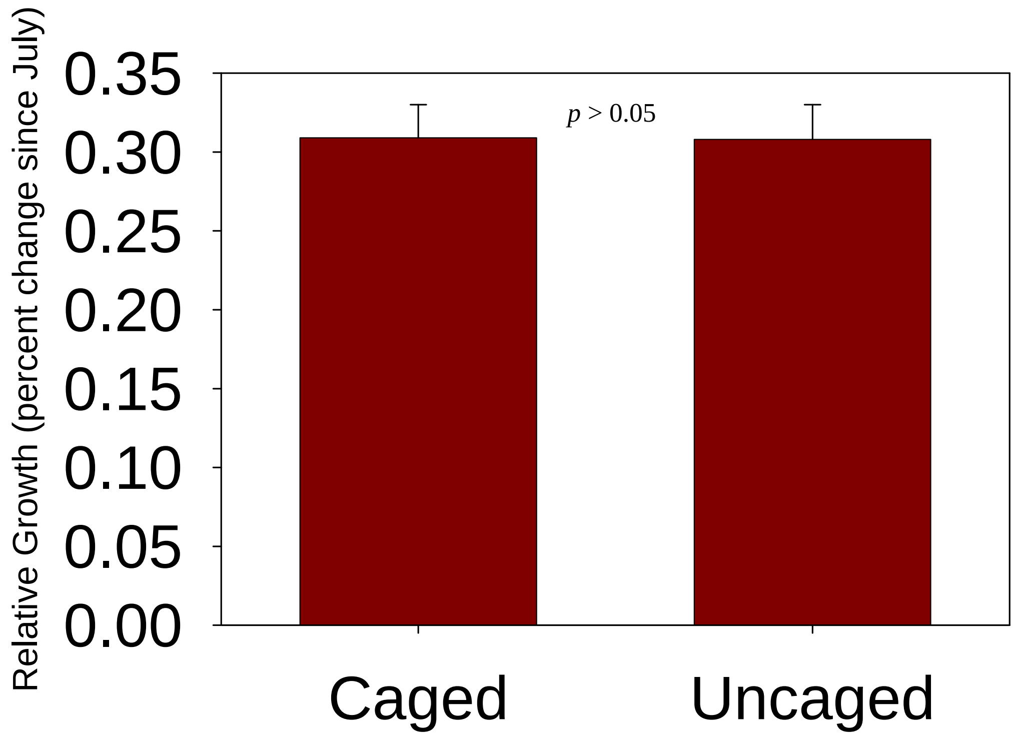

Figure 4. Mean relative growth of caged and uncaged seedlings. ANOVA indicated that there was no significant difference between caged and uncaged seedlings.

Table 1. General Study Site Characteristics (averages for each site are presented).

	Awosting	Jenny Lane A	Jenny Lane B
Organic Matter	4.850 %	6.250 %	6.875 %
Phosphorus	2.810 kg/ha	4.210 kg/ha	8.710 kg/ha
Calcium	61.800 kg/ha	140.450 kg/ha	103.930 kg/ha
pH	4.0	3.9	4.2
Moisture Content	1.078 %	0.925 %	1.510 %
Potassium	109.550 kg/ha	115.170 kg/ha	130.620 kg/ha
Magnesium	28.090 kg/ha	39.330 kg/ha	39.330 kg/ha
Iron	106.460 kg/ha	265.450 kg/ha	420.220 kg/ha
Aluminum	617.700 kg/ha	667.980 kg/ha	1327.530 kg/ha
Manganese	5.340 kg/ha	38.480 kg/ha	52.250 kg/ha
Zinc	23.370 kg/ha	6.830 kg/ha	8.120 kg/ha
Available Nitrate	0.000 kg/ha	0.000 kg/ha	0.000 kg/ha
Light Levels	1019.77	931.96	1277.79

Table 2. ANOVA of experimental treatments on relative growth.

Source	Type III Sum of Squares	df	Mean Square	F	Sig.
Corrected Model	5.798(a)	15	.387	10.559	.000
Intercept	13.856	1	13.856	378.453	.000
Site	**.250**	**2**	**.125**	**3.416**	**.036**
Species	**4.490**	**2**	**2.245**	**61.327**	**.000**
CagedUncaged	.005	1	.005	.149	.700
Site * Species	**.470**	**3**	**.157**	**4.277**	**.006**
Site * CagedUncaged	.009	2	.005	.125	.883
Species * CagedUncaged	.095	2	.048	1.298	.276
Site * Species * CagedUncaged	.050	3	.017	.456	.714
Error	5.126	140	.037		
Total	25.139	156			
Corrected Total	10.924	155			

a R Squared = .531 (Adjusted R Squared = .481)

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