

Seedling growth and leaf photosynthesis of *Acer grandidentatum* (Bigtooth maple, Sapindaceae) from isolated central Texas populations

Terri L. Nelson Dickinson

Department of Biology, University of Texas at San Antonio, One UTSA Circle,
San Antonio, TX 78249, USA terri.nelson.dickinson@gmail.com

and

O. W. Van Auken

Department of Biology, University of Texas at San Antonio, One UTSA Circle,
San Antonio, TX 78249, USA oscar.vanauken@utsa.edu

ABSTRACT

Two experiments were completed to address issues concerning apparent recruitment failure of native relict populations of *Acer grandidentatum* Nutt. (Bigtooth maple) found in the Edwards Plateau Region of Central Texas. In the first experiment seedlings were grown in pots at 20, 40, 60 and 100% (open or full sun, $1615 \pm 8 \mu\text{mol}/\text{m}^2/\text{s}$). In the second experiment leaf photosynthetic rates of seedlings growing in sun or shade below a canopy were examined. Growth of seedlings was greatest at 40% of the maximum light treatment or at a light level of $705 \pm 22 \mu\text{mol}/\text{m}^2/\text{s}$. Mortality was zero in the 40% light treatment and 100% at the highest light level tested. Light response curves were generated using photosynthetic rates of five leaves of separate juvenile maples growing in full sun or understory canopy shade. Rates were measured in the field at light levels from 0-2000 $\mu\text{mol}/\text{m}^2/\text{s}$. From these measurements a number of photosynthetic parameters were calculated and compared. No significant differences were seen between the curves for sun and shade leaves of *A. grandidentatum*. The only significantly different photosynthetic parameter measured was the maximum photosynthetic rate (A_{max}). The A_{max} was low at $3.89 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ for shade leaves and $5.23 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ for sun leaves. The light saturation point, the light compensation point and other calculated factors were low as well, but not significantly different. *Acer grandidentatum* is a shade tolerant species with a low photosynthetic rate which seems to be part of the reason it can persist in isolated Central Texas canyon woodland populations. Published on-line www.phytologia.org *Phytologia* 99(1): 11-21 (Jan 19, 2017). ISSN 030319430.

KEY WORDS: light levels, CO₂ uptake, gas exchange rates, shade plants

It has been challenging to understand factors controlling growth and recruitment of woody species in woodland and forest communities, although many research papers have dealt with the topic (Baker et al. 2005). This is true for native relict populations of *Acer grandidentatum* Nutt. and other woody species that are present in the Edwards Plateau Physiographic Region of Central Texas (Van Auken 1988; Russell and Fowler 2004; Nelson Dickerson and Van Auken 2016). *Acer grandidentatum* is a small, deciduous, hardwood tree commonly known as bigtooth maple, but it has many other common names such as canyon maple, western sugar maple and others (Correll and Johnston 1970; Tollefson 2006). There has been some debate over the systematics of *A. grandidentatum*, but most current papers refer to it simply as *A. grandidentatum*, which is the convention that we will follow (Cronquist et al. 1997; Stevens 2001; Atha et al. 2011). The 129 *Acer* species have been traditionally grouped into the family Aceraceae, but more recently they have been considered as members of the subfamily Hippocastanoideae within the family Sapindaceae (Buerki et al. 2009; Watson and Dallwitz 2011).

Anecdotal reports suggest a decline of recruitment of juvenile *A. grandidentatum* in central Texas (Riskind 1979; McCorkle 2007; Adams 2010; BCNPSOT 2010; Heidemann 2011). These

same reports suggest the decline in recruitment is caused by browsing by large herbivores specifically by *Odocoileus virginianus* (white-tailed deer). A recent study confirmed that *A. grandidentatum* seedlings protected from large herbivores had a greater rate of survival than unprotected seedlings (Nelson Dickinson and Van Auken 2016). With leaf removal, a reduction in plant net photosynthesis occurs. This leaf loss compromises the ability of the plant to replace lost biomass (Ellsworth et al. 1994), which is most readily shown in juveniles. A plant's photosynthetic parameters affect its inherent growth rate and thus its biomass (Jones and McLeod 1989). Thus, understanding a plant's photosynthetic characteristics can help explain how an individual plant is able to compensate for episodes of herbivory and how it adapts to an environment that's been altered by herbivory (Crowley 1997). Nevertheless, until now, there have been no studies that we could find concerning photosynthetic rates of *A. grandidentatum*.

PURPOSES

The purposes of the present study were to determine the light requirements of juvenile *A. grandidentatum* plants and to compare differences in gas exchange rates at various light levels for leaves of sun and canopy shade *A. grandidentatum* plants.

METHODS

STUDY AREAS-There were two study areas. The plant growth experiment was carried out on a non-shaded roof patio of the science building of the University of Texas San Antonio (98°34'26"W and 29°37'19"N). The gas exchange measurements were made at Lost Maples State Natural Area, in Bandera and Real counties about 114 mi west of San Antonio, Texas (29°49'11"N and 99°34'59"W).

SEEDLING GROWTH-On March 29, 2010, a total of twenty first-year seedlings were obtained from a commercial source (Janzow, Boerne, TX), transplanted and randomly placed into one of four light treatments (five plants/treatment). Plants were randomly placed (one each) into 15.0 cm diameter x 14.5 cm tall pots lined with 3.79 L Ziploc® plastic bags containing 1350 g of soil. Additional nutrients were added as 5.5 g Osmocote per pot (14/14/14 NPK equivalent to 436 kg/ha nitrogen, 436 kg/ha phosphorous, and 436 kg/ha potassium). Plants were watered with deionized water as needed, usually 150 mL every day (Janzow 2007). They were placed on a non-shaded roof-top patio on UTSA's Science building within each of the light treatments.

Plants' sunlight exposure was limited using shade boxes measuring 0.5 m wide, 0.5 m long, and 1.0 m high. They were constructed with 1.3 cm diameter PVC pipe covered with zero to three layers of commercial black polyethylene shade cloth on five sides secured with plastic zip ties (Rainbow Gardens and Lowe's Home Improvement Stores, San Antonio, TX) to adjust light levels in each treatment.

Light levels were measured in each plant location, in each shade box on a clear day in May and October 2010 within ± 30 minutes of solar noon using a Li-COR® LI-188 integrating quantum sensor (Li-COR, Inc. Lincoln, NE). Each shade box contained five *A. grandidentatum* seedlings (one/pot). Light levels were 100 % or maximum ($1615 \pm 8 \mu\text{mol}/\text{m}^2/\text{s}$, no shade cloth), 60 % ($977 \pm 42 \mu\text{mol}/\text{m}^2/\text{s}$), 40 % ($705 \pm 22 \mu\text{mol}/\text{m}^2/\text{s}$), and 20 % ($281 \pm 1 \mu\text{mol}/\text{m}^2/\text{s}$). Boxes were affixed to railings with zip ties and weighted with sand bags to prevent movement. Pots were covered with clear plastic during rainy weather to prevent flooding, nutrient and soil loss.

Survival, aboveground, belowground and total dry mass were determined and recorded. Other plant responses were measured but not reported here (Nelson Dickinson 2011). Plants were harvested on October 14, 2010, dried to a constant mass at 80°C, and weighed. Data were tested for normality using the Shapiro-Wilks test and for homogeneity of variance using Bartlett's test (Sall et al. 2005). If probability

values fell below 0.05 on either test, data were transformed and retested. Aboveground dry mass, belowground dry mass, and total dry mass were log transformed, and then analyzed using a one-way ANOVA followed by Tukey-Kramer HSD. ANOM for proportions was used with a probability level of 0.05 to determine if there were differences in mortality across treatments (McKinley and Van Auken 2005).

GAS EXCHANGE MEASUREMENTS-Ten *Acer grandidentatum* saplings were randomly selected in and adjacent to a deer enclosure at Lost Maples State Natural Area, in Sabinal Canyon, Texas. One fully expanded, complete leaf was selected on each plant; five leaves from the shaded canopy understory plants and five from the open no canopy, full sun plants. The Li-Cor 6400 portable photosynthetic meter was used to measure gas exchange as a function of light level, or photosynthetically active radiation (PAR), for each leaf. Measurements were made with plants fully leafed out in May 2011, within \pm three hours of solar noon using a gas flow rate of 400 $\mu\text{mol/s}$ and a CO_2 concentration of 390 $\mu\text{mol/mol}$ at PARs of 2000, 1600, 1200, 1000, 800, 600, 400, 200, 100, 50, 25, 10, 5, and 0 $\mu\text{mol/m}^2/\text{s}$. Each leaf used covered the entire chamber.

Two light response curves were generated, one for sun leaves and one for shade leaves. Photosynthetic rates along each curve were tested for normality using the Shapiro-Wilks test and for homogeneity of variance using Bartlett's test (Sall et al. 2005). A repeated measures ANOVA was completed to determine if there were significant differences between the two leaf types. A one-way ANOVA with Tukey's HSD was used to determine differences in photosynthetic rates at different light levels. For the sun and shade treatments, the maximum rate of photosynthesis (A_{max}) was determined, along with transpiration and conductance at the A_{max} . The initial slope of the curve, or quantum yield efficiency, was also measured. The PAR value at which this line reached A_{max} was the light saturation point (L_{sp}). Other factors measured were the dark respiration (R_d), the curve's y-intercept and the light compensation point (L_{cp}), the line's x-intercept. These values were also tested for normality using the Shapiro-Wilks test and for homogeneity of variance using Bartlett's test, then compared using a one-way ANOVA (Sall et al. 2005).

RESULTS

SEEDLING GROWTH-Total dry mass was significantly different across the four light treatments (One-way ANOVA; $F = 4.6639$, $P = 0.0159$) (Figure 1). The mean total dry mass in the 100 % sunlight treatment was 0.52 ± 0.11 g/plant. This was significantly different from the 40 % treatment, but was not significantly different from 20 % or 60 % treatments ($P = 0.01290$, 0.8802, 0.5003 respectively) (Tukey- Kramer HSD). The mean total dry mass in the 40 % sunlight treatment was greatest at 1.40 ± 0.67 g/plant. This was significantly different from the 100 % treatment ($P = 0.0129$), marginally different from the 20 % treatment ($P = 0.0555$), but not significantly different from the 60 % treatment ($P = 0.1335$).

Aboveground dry mass was significantly different across the four treatment levels (one-way ANOVA, $P = 0.0156$), but only slightly different and only significantly different between the 20 and 100 % treatments (Figure 1). Belowground dry mass was significantly different across all four light treatment levels (one-way ANOVA, $P = 0.0492$), but we could not determine where the differences were with the Tukey-Kramer HSD (multiple range test; Figure 1), thus the letters in the figure are all the same across all light levels.

Mortality was complete in the full sunlight treatment (100 %), while at the 40 % light level, there was zero mortality (Figure 2). Both of these values were significantly different from the mean at the 0.05 level (ANOM for Proportions; $\text{LDL} = 0$, $\text{UDL} = 0.868$). Twenty percent mortality occurred in the 60 %

light level and 40 % mortality in the 20 % light level, neither of which were statistically significant (ANOM for Proportions; LDL = 0, UDL = 0.868).

GAS EXCHANGE RATES-Photosynthetic light response curves for full sun and shade leaves of *A. grandidentatum* were not significantly different from each other (repeated measures ANOVA, $P = 0.0709$, Figure 3A and B). Mean photosynthetic rate for shade leaves of *A. grandidentatum* was $2.27 \pm 0.23 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, which was not significantly different from the mean photosynthetic rate for sun leaves that was $2.94 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ (one-way ANOVA, $P = 0.0709$).

Mean maximum photosynthetic rate (A_{max}) for shade leaves of *A. grandidentatum* was $3.89 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ at a PAR of $880 \mu\text{mol}/\text{m}^2/\text{s}$, while the A_{max} for sun leaves of was $5.23 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ at a PAR at of $1200 \mu\text{mol}/\text{m}^2/\text{s}$ (Table 1). A_{max} values were significantly different from each other (one-way ANOVA, $P = 0.0296$), while the PARs at the A_{max} values were not significantly different between treatments (one-way ANOVA, $P = 0.2861$).

The quantum yield efficiency or initial slope (ϕ or IS) for shade leaves ($0.030 \pm 0.010 \mu\text{mol CO}_2/(\mu\text{mol quanta})$) was not significantly different from that of sun leaves ($0.032 \pm 0.010 \mu\text{mol CO}_2/(\mu\text{mol quanta})$) (one-way ANOVA, $P = 0.0677$, Table 1). The light compensation point (L_{cp}), the light saturation point (L_{sp}) and dark respiration (R_d) for shade leaves were not significantly different from the sun leaves (one-way ANOVA, $P = 0.1431$, 0.2618 and 0.0758 respectively, Table 1).

There were no overall significant differences in mean transpiration rate between sun and shade leaves (repeated-measures ANOVA; $P = 0.2274$) (Table 1). However, the transpiration rate for sun leaves increased from $0.34 \pm 0.12 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ at the lowest light level to $1.47 \pm 0.12 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ at the highest light level tested with a few significant differences. Usually significant differences were between the lowest light level and the highest (one-way ANOVA; $P < 0.0001$; Tukey - Kramer HSD; $P < 0.05$) (data not shown). The mean transpiration rate for shade leaves increased from $0.36 \pm 0.08 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ to $1.04 \pm 0.08 \text{ mmol H}_2\text{O}/\text{m}^2/\text{s}$ with a similar trend in significant differences (one-way ANOVA; $P < 0.0001$; Tukey - Kramer HSD; $P < 0.05$) (data not shown).

There were no overall significant differences in mean stomatal conductance between sun and shade leaves (repeated-measures ANOVA; $P = 0.9305$) (Table 1). However, the conductance for sun leaves increased from $0.01 \pm 0.01 \text{ mol H}_2\text{O}/\text{m}^2/\text{s}$ to $0.05 \pm 0.01 \text{ mol H}_2\text{O}/\text{m}^2/\text{s}$ with few significant differences. Usually significant differences were between the lowest light level and the highest (one-way ANOVA; $P < 0.0001$; Tukey - Kramer HSD; $P < 0.05$) (data not shown). The conductance for shade leaves increased from $0.02 \pm 0.05 \text{ mol H}_2\text{O}/\text{m}^2/\text{s}$ to $0.04 \pm 0.05 \text{ mol H}_2\text{O}/\text{m}^2/\text{s}$ with few significant differences and trends similar to transpiration (one-way ANOVA; $P < 0.0001$; Tukey - Kramer HSD; $P < 0.01$) (data not shown).

DISCUSSION

Acer grandidentatum seedlings grew best in the 40 % light treatment, which was $705 \pm 22 \mu\text{mol}/\text{m}^2/\text{s}$, and most closely matches the light levels found below an *A. grandidentatum* canopy at Lost Maples State Natural Area. This was where there were higher numbers of *A. grandidentatum* saplings and mature trees and suggests better seedling survival (Nelson Dickerson and Van Auken 2016). All of the plants survived in the 40 % light treatment, whereas none of the *A. grandidentatum* seedlings in the highest light exposure survived, supporting the hypothesis that this species is a shade and not a sun species. Light levels far above a plant's light saturation point that do not cause an increase in

photosynthesis, may cause damage to leaf tissues and the photosynthetic apparatus or increase water loss to the point of wilting and possibly mortality (Crawley 1997).

Table 1. Mean \pm one standard error for the maximum net photosynthetic rates (A_{max}), light level (PAR) at the A_{max} light saturation (L_{sat}), light compensation points (L_{cp}), dark respiration rates (R_d), initial slope or quantum yield efficiency (IS), mean stomatal conductance (g_s) and mean transpiration rate (E) of *A. grandidentatum* leaves found in full sun and shade. Stars indicate a significant difference between values for the two treatments (one-way ANOVA; $P < 0.05$).

Parameter	Shade leaves	Sun leaves
A_{max} ($\mu\text{mol CO}_2/\text{m/s}$)	3.89 \pm 0.36*	5.23 \pm 0.36*
PAR at A_{max} ($\mu\text{mol/m/s}$)	880 \pm 198	1200 \pm 198
Mean photosynthetic rate	2.27 \pm 0.23	2.94 \pm 0.23
L_{sat} ($\mu\text{mol/m/s}$)	139.11 \pm 18.48	170.67 \pm 18.48
L_{cp} ($\mu\text{mol/m/s}$)	9.74 \pm 2.22	14.83 \pm 2.22
R_d ($\mu\text{mol CO}_2/\text{m}^2\text{s}$)	0.32 \pm 0.05	0.47 \pm 0.05
IS ($\mu\text{mol CO}_2/(\mu\text{mol quanta})$)	0.032 \pm 0.010	0.030 \pm 0.010
g_s ($\text{mol H}_2\text{O/m/s}$)	0.04 \pm 0.01	0.04 \pm 0.01
E ($\text{mmol H}_2\text{O/m/s}$)	0.83 \pm 0.08	0.99 \pm 0.12

When plants are grown with insufficient light, they may have decreased leaf area, basal diameter and dry mass (Jones and McLeod 1989), but may increase their shoot height or decrease their leaf to shoot ratios (Holt 1995). *Acer grandidentatum* seedlings in the present study that received 20 % of ambient sunlight had high mortality and low growth (Figure 2). Similar deep shading of *A. saccharum* and *Aesculus glabra* seedlings in early spring led to 80 % mortality after three years, compared to 27 % mortality in control plants (Augsburger 2008). Though *A. grandidentatum* seems to be best characterized as a shade plant, it still requires approximate 40 % sunlight to compensate for its respiration to allow growth and survival. The majority of growth for all experimental seedlings in the current study occurred in spring, during the first half of the experiment (not presented). Growth for all plants slowed through the intense heat and light of summer, and most mortality was observed late in the experiment (Nelson Dickerson 2011).

The current results differ somewhat from similar studies done on the closely related *A. saccharum*. First-year *A. saccharum* seedlings grown at 13, 25, 45 and 100 % sunlight for one year increased their number of leaves and dry mass as light level increased, with maximum values found at 100 % sunlight (Logan and Krotkov 1968). The study was conducted in Ontario, Canada, and does not disclose the actual light levels used in the experiment. It is quite possible that the amount of sunlight received by these plants was lower than the 100 % suggested. In addition, ambient temperature was significantly different than used in the current experiment due to the higher latitude and shorter day length or possibly other factors that were not the same as in the present study. However, *A. saccharum* is considered to be a shade plant (Logan and Krotkov 1968; Ellsworth et al. 1994; Kwit et al. 2010).

Gas exchange rates of members of the genus *Acer* indicates the genus includes both shade tolerant and shade intolerant species (Morrison and Mauck 2007; Verdu and Climent 2007). While no information on the photosynthetic parameters of *A. grandidentatum* have been identified in the literature, it is assumed to be at least moderately shade tolerant because of its distribution in protected canyon bottoms and as an understory late succession species (Correll and Johnston 1970; Bazzaz and Carlson 1982; Nelson Dickerson and Van Auken 2016). The slow growth of *A. grandidentatum* also suggests shade tolerance, as photosynthetic parameters are closely tied to relative growth rates (Coley et al. 1985; Poorter 1990; Tollefson 2006; Van Auken et al. 2016).

Acer grandidentatum maximum photosynthetic rates of $3.89 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ for shade leaves and $5.23 \pm 0.36 \mu\text{mol CO}_2/\text{m}^2/\text{s}$ reported for sun leaves in the present study are consistent with classification of as a shade plant. *Acer grandidentatum* sun plants found at higher elevations, higher rainfall and lower temperatures appear to have higher A_{max} values in full sun (Van Auken and Bush, in preparation, unpublished), but plants in shade had similar low A_{max} values. Succession in many cases is driven by temporal differences in resource availability and particularly by changes in available nutrients, especially nitrogen, and light levels (Tilman 1985; Van Auken and Bush 2013).

Early succession sites usually have high light levels and low soil nitrogen. Usually early successional species are shade intolerant and late successional species are shade tolerant (Boardman 1977; Tilman 1985; Mooney and Ehleringer 1997; Valladares and Niinemets 2008; Van Auken and Bush 2013). As successional time passes and communities mature, increased canopy shading decreases available light at the soil surface and shade tolerant and higher soil nitrogen requiring plants become more common (Tilman 1985; Bush and Van Auken 1986; Van Auken and Bush 2013). Early successional species exhibit higher rates of photosynthesis, transpiration, and conductance than late successional species, while late successional or climax community species are more likely to be shade tolerant and reach their light saturation points at much lower light levels (Horn 1974; Furuya and Van Auken 2009, 2010; Wayne and Van Auken 2009; Van Auken and Bush 2011). Early succession sites also have greater variability in abiotic conditions, such as swinging between environmental extremes, so early successional plants frequently have greater plasticity in their adaptive responses than late successional species (Horn 1974; Bazzaz and Carlson 1982; Holt 1995; Hull 2002; Van Auken and Bush 2011).

Bazzaz and Carlson (1982) measured photosynthetic rates of full sun and shade leaves of fourteen species. They found that the difference between initial slope, light compensation point, and dark respiration for full sun and shade leaves was much greater for herbaceous early succession species than for late succession hardwood species. The values they reported for late successional hardwoods are similar to the values obtained for *A. grandidentatum* in the present study (Table 1). The present study found no significant differences between most variables for sun and shade leaves, consistent with observations that *A. grandidentatum* is a late succession species (Bazzaz and Carlson 1982; Hull 2002).

Light response curves for *A. saccharum* seedlings in clearings had A_{max} values of $3.32 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, while understory individuals had A_{max} values of $1.81 \mu\text{mol CO}_2/\text{m}^2/\text{s}$, the only factors that were significantly different between locations (Ellsworth and Reich 1992). We found similar values for *A. grandidentatum* in the present study. These two species may be able to increase their photosynthetic rate to take advantage of sunflecks, short term increases in light availability, but limited data is available. *Acer grandidentatum* seems to exhibit lower plasticity in photosynthetic rate than other woody species, which may affect its growth as well as its ability to become a dominant member of the canopy (Hull 2002). Photosynthetic response curves below a forest canopy measured at four different times in a single growing season found that most light response parameters decreased during the growing season and affirmed that *A. saccharum* is shade tolerant, and seedlings must survive most of their first year in a densely shaded forest canopy (Kwit et al. 2010).

Measured transpiration rates (E) and stomatal conductance (g_s) rates for *A. grandidentatum* were low compared to values for shade intolerant species (Boardman 1977; Bsoul et al. 2007). These rates indicated the stomates were open and CO_2 uptake was probably normal. Rates are consistent with values for shade tolerant species but not shade intolerant species (Horn 1974; Boardman 1977; Bazzaz and Carlson 1982; Tilman 1985; Holt 1995; Mooney and Ehleringer 1997; Valladares and Niinemets 2008; Hull 2002; Van Auken and Bush 2013).

Photosynthetic rates of *A. grandidentatum* were lower at high light levels than those of most other dominant plant species in the community at Lost Maples State Natural Area, but not at low light sub-canopy conditions (Furuya 2007; Grunstra 2011; Grunstra and Van Auken 2015). Differing light requirements have been shown to affect succession and plant community composition (Bush and Van Auken 1986; Wayne and Van Auken 2009; Van Auken and Bush 2011). Plants with low photosynthetic rates may experience difficulty growing below the canopy and then through the canopy without a disturbance to canopy plants. When this lowered potential is combined with browsing pressure, the effect can become even stronger (Van Auken and Bush 2009). Community composition in Sabinal Canyon in Lost Maples State Natural Area and other central Texas communities are likely affected by complex interaction of inherent photosynthetic capacities and abiotic requirements of the species present. This would include preferential feeding of large herbivores, and the effect of that herbivory on the biotic and abiotic conditions present in the environment. There are a number of species found in these central Texas communities that can grow at high light levels, but most cannot grow in deep shade below a closed canopy (Furuya 2007; Grunstra 2011; Grunstra and Van Auken 2015).

THE FUTURE

Populations of *A. grandidentatum* in central Texas are relatively rare and are really outlier populations. Management of these populations in the past has mostly been hap-hazard at best and dependent on the whims of owners of properties where they have been found. Understanding that they are understory/sub-canopy species or shade species was unknown until the present study. Sensitivity to native and domestic herbivores has been suspected for many years but not demonstrated until very recently. What will happen to these populations in the future? This is uncertain and difficult to predict. If their reproductive cycle is continually disrupted, they will become extinct in central Texas. If herbivory by native and domestic species is not reduced the same thing will happen. What is the timeline of the potential extinction of these isolated native populations? This is uncertain at this time. It is hard to say because apparently individuals can live for hundreds of years and the death rate of adults is unknown and the rate of recruitment of juveniles into these populations is not known either.

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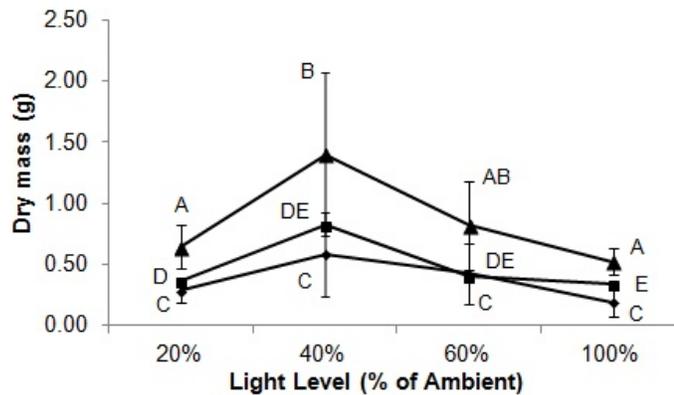


Figure 1. Mean aboveground (■), belowground (◆), and total dry (▲) mass of *Acer grandidentatum* at varying light levels as a percentage of ambient sunlight. Bars indicate \pm one standard deviation of the mean. Different letters on the same line indicate significant differences for that factor (one-way ANOVA; $P < 0.05$, Tukey - Kramer HSD; $P < 0.05$).

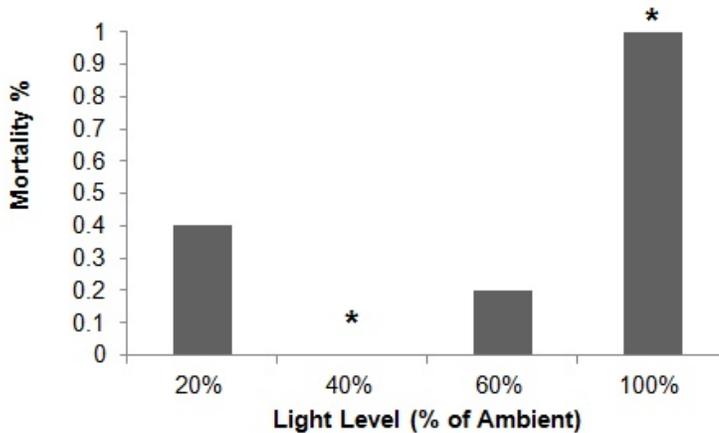


Figure 2. Relative mortality (1=100%) of *Acer grandidentatum* seedlings grown at varying light levels is presented as a percentage of ambient sunlight. The * indicates values which were significantly different from the mean (ANOM for Proportions, $\alpha = 0.05$, LDL [lower detection limit] = 0, UDL [upper detection limit] = 0.868). There were no mortalities in the 40% light treatment.

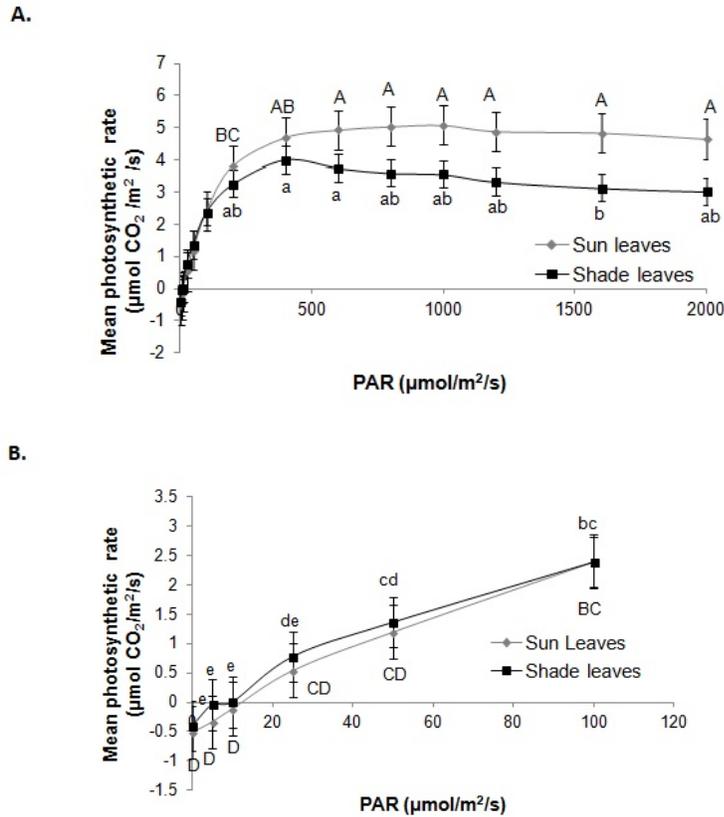


Figure 3. **A.** Mean photosynthetic rate of full sun and shaded leaves of *A. grandidentatum* as a function of light level (PAR). **B.** The lower portion of graph A between 0 and 100 PAR. Uppercase letters represent values for sun leaves, while lowercase letters represent values for shaded leaves. Different upper or lowercase letters indicate significant differences within the curve (one-way ANOVA; $P < 0.0001$; Tukey-Kramer HSD; $P < 0.05$). Error bars represent \pm one standard error.