Mortality and growth of C*haptalia texana* (silver-puff) in full sun and canopy shade

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ABSTRACT

We completed a transplant experiment with *Chaptalia texana* Greene (silver-puff, Asteraceae) to determine its habitat preference. Sixty days after seedling emergence in a greenhouse, plants were transplanted into the field at Hardberger City Park in San Antonio, Texas. One half of the 40 plants were planted below a *Juniperus/Quercus* woodland canopy and half into an adjacent open grassland. Total mortality was 70% with 12 plants that survived 192 days to the end of the experiment. Nine plants below the canopy and three in the open grassland survived. Growth increased rapidly during the first 60-90 days of the experiment (spring). Full sun (open or grassland) plants were smaller than those below the canopy. Plant response variables decreased during the latter part of the experiment (summer and early fall). Survival and growth variables for canopy plants were greater than for open plants. We believe *C. texana* is found mostly below woodland canopies, but time to demonstrate this seemed to exceed one growing season. The amount and timing of rainfall and the presence of neighbors are also important. Published on-line www.phytologia.org *Phytologia 98(3): 156-163 (July 6, 2016).* ISSN 030319430.

KEY WORDS: canopy, open, sun species, shade species, sunflower, *Juniperus/Quercus* woodland, grassland, neighbors

Chaptalia texana Greene (silver-puff) is a member of the sunflower family (Asteraceae). The genus includes about 56 species, with two found in the southern United States, and the remainder in Mexico, Central America and much of South America (Correll and Johnston 1979; Enquist 1987; USDA 2009). In southwestern North America, *Chaptalia texana* occurs in parts of central and western Texas, southern New Mexico, northern, central and southern Mexico. In central Texas, it is reported in savanna communities, usually below the canopy of *Juniperus/Quercus* (juniper/oak) mottes or woodlands (Van Auken and Bush 2015). It is an herbaceous perennial and grows as a rosette in the woodland phase of some of these central Texas savanna communities, flowering and producing numerous seeds that will germinate within 16 days (Van Auken 2013).

Chaptalia texana seems to be a shade adapted species that can carry out photosynthesis below a woodland canopy (Van Auken and Bush 2015). Differences in photosynthetic rates of plants growing in full sun habitats compared to those found in shady habitats are fairly well known (Hull 2002; Begon et al. 2006; Valladares and Niinemets 2008). Gas exchange rates for shade leaves of *C. texana* placed in full sun were as high as full sun leaves of some sun species (Van Auken and Bush 2015). Thus, its maximum carbon uptake rate is higher than typical understory plants at high light levels (Hull 2002). Carbon uptake rates suggest that this species should occur in grasslands or open areas, but it was not found there.

Few ecological studies have been located that consider the habitat preference of various species of *Chaptalia* or why they seem to be found below canopies rather than grassland environments. The successional status, disturbance requirements, densities and resource requirements of the various species of *Chaptalia* are unclear. One study of coastal plain longleaf and slash pine forests found *C. tomentosa* after winter fires with 50% cover reduction eight years later with grass regrowth (Lemon 1949). Reports of *Chaptalia* species in South American grasslands showed that frequent disturbances including fire, clipping or herbivory of adjacent species promoted *Chaptalia* density (Fidelis et al. 2010; Joiner et al. 2011). Accordingly, it seems to require disturbances but its ecological niche and factors affecting its distribution are not well understood (Begon et al. 2006). *Chaptalia texana* is mostly found below canopies suggesting that light level is the obvious but not necessarily the only factor controlling its habitat.

THEORY: Our theory is that *Chaptalia texana* is a canopy understory or shade species and will not grow in high light open grassland habitats.

METHODS

This project was completed in "Phil Hardberger Park" in San Antonio, Texas, USA (N-29°33'41.3", W-98°31'11.8"). Subsurface of the study area is Cretaceous limestone, and soils are usually shallow, rocky or gravelly, dark colored, calcareous with neutral or slightly basic pH. They are clayey-skeletal, smectitic, thermic, lithic, calciutolls usually Austin silty clays, Whitewright-Austin complex, or Eckrant cobbly clay (Taylor et al. 1962; NRCS 2006). The Park is approximately 20 km south of the Edwards Plateau region of central Texas just south of the Balcones Escarpment in north central Bexar County (Correll and Johnston 1979; Van Auken et al. 1981; Van Auken and McKinley 2008). Elevation is approximately 350 m above mean sea level (AMSL) (Taylor et al. 1962; NRCS 2006). January mean temperature is approximately 9.6°C and July mean is 29.4°C (NOAA 2004). Precipitation is bimodal totaling 78.7 cm/yr with peaks in May and September (10.7 cm and 8.7 cm), highly variable, with little summer rainfall and high evaporation (Thornthwaite 1931; NOAA 2004).

Chaptalia texana is a native, herbaceous, perennial that grows as a rosette of basal leaves with scapose, monocephalous stems (single flowering head or inflorescence) (Nesom 1995). It is similar to other species of *Chaptalia*. The flowering scapes can be 13-34 cm tall at flowering (anthesis) and become taller in fruit. Leaves are obovate to ovate or elliptical and relatively thick with dense, gray-white pubescence below and dark green and glabrescent above (Enquist 1987; Nesom 1995). This species is reported from thin, rocky, limestone soils and mostly from oak, pine-oak and juniper-oak woodlands (Enquist 1987; Nesom 1995; Harms 2011). It theoretically flowers year round, but mainly when temperatures and rainfall are moderate. Achenes (one seeded fruits) start to germinate soon after maturation with 100% germination at 25ºC in low light 16 days after the start of incubation, with slight or no innate seed dormancy (Van Auken 2013).

Area vegetation of the study site was savanna or woodland with *Juniperus*/*Quercus* (juniper and oak) being dominant throughout this region (Van Auken et al. 1981; Van Auken and McKinley 2008). High density woody species were *Juniperus ashei* (Ashe juniper) and *Quercus virginiana* (=*Q. fusiformis*, Live oak) followed by *Diospyros texana* (Texas persimmon) and *Sophora secundiflora* (Texas mountain laurel). *Ulmus crassifolia* (cedar elm) is sometimes found in these communities at lower density and on the deeper soils (Gagliardi and Van Auken 2010). There were also former grasslands of various sizes that are woodlands today with *Prosopis glandulosa* (mesquite), *Aloysia gratissima* (whitebrush) and *Diospyros texana* as major woody species (Van Auken and Leonard 2016). These areas seem to be on deeper soils and were not used in the current study. Within the *Juniperus*/*Quercus* woodlands there are sparsely vegetated intercanopy patches or gaps on shallow soil (openings in the woodlands) (Van Auken 2000). This is where the high light or open treatments were placed.

The highest density herbaceous species below the canopy were *Carex planostachys* (Cedar sedge) (Wayne and Van Auken 2008), *Verbesina virginica* (Gagliardi and Van Auken 2010) and occasionally *Chaptalia texana*. In the gaps, *Aristida longiseta* (Red three-awn), *Bouteloua curtipendula* (Side-oats grama), *Bothriochloa* (=*Andropogon*) *laguroides* (Silver bluestem), *Bothriochloa ischaemum* (KR bluestem), various other C_4 grasses, and a variety of herbaceous annuals are common (Van Auken 2000).

Experimentally, there were two treatments, canopy or no canopy (+ or - canopy). The experiment included 20 replications for each treatment for a total of 40 pots or plants. Plants were started from seed and grown for 60 days in 10.1 x 10.1 cm peat pots (in a greenhouse) in native area soil from the study site (dried, sifted Whitewright-Austin complex) with 100 ml of a complete nutrient solution added initially (Van Auken, et al. 2005). Plants were randomized and planted in the field February 26, 2013. All plants were watered initially and then every other day with 500 ml of tap water for two weeks. After that, plants were given 500 ml tap water once/week to maintain the soil at or near field capacity. Rosette diameter, number of leaves, as well as the size of the largest leaf were measured monthly. Largest leaf and plant area were calculated. Live and dead plants were counted monthly. Upon harvesting, when growth had stopped (day 192), plants were clipped at the soil surface just below the rosette and dried at 75°C to a constant level and then dry mass was determined. Roots were not collected. Mid-day light levels on a clear spring day were measured at each plant position using a LI-COR® LI-190 SA integrating quantum sensor. Soil depth was determined using a piece of re-bar pounded into the ground, removed and measured (Wayne and Van Auken 2008). The study site was re-visited 56 d after the end of the experiment to look for missing plants.

Analysis of variance and *Student's t-test* was used for parametric results and X^2 tests were used for non-parametric results (Sall et al. 2001). This was used to test the effect of canopy position on response variables. Least square regressions were completed to examine how response variables changed in time. Data were compared to various functions and significance level for all tests was 0.05.

RESULTS

The experiment was planted on February 26, 2013 and harvested 192 days later on September 6, 2013. At the end of the experiment, overall mortality was 70% or 28/40 dead and survival was 30% with 12/40 total plants surviving. Mortality of *Chaptalia texana* increased through the experiment (Figure 1) and appeared to be greatest on day 192 with a total of 70% dead. Below the canopy in shade, mortality was 10/20 or 50% mortality. Total plant mortality was a significant linear function (R^2=0.80 and P<0.05), but the R^2 and P value were improved using a 2nd or 3rd order polynomial function (Figure 1). Time (days) explained 95% of the variation of mortality of *C. texana* using a 2nd or 3rd order polynomial function. On day 192, there was a significant difference between percent survival in the open versus canopy plants (X^2, P < 0.05). At this time, total survival was 30% and survival in the open was 15% while below the canopy it was 45%.

Several plant growth factors were measured during the experiment including number of leaves, length and width of the largest leaf, and length and width of the largest plant. Leaf area and plant area were calculated. These factors were regressed on time in days that they were measured or counted. Linear as well as logarithmic and polynomial (2nd, 3rd and 4th order) regressions were examined. None of the linear and logarithmic regressions were significant (P>0.05 in all cases).

The mean number of leaves for all living plants in time was a highly significant third order polynomial. The R^2 for all plants was 0.91. For plants grown in the open (no canopy) the R^2 was 0.94 and for plants growing below the canopy it was 0.88. Thus, the R^2 for the polynomial functions explained 88-94% of the variation in number of leaves of *C. texana* over the time in days of the experiment (Figure 2). Mean number of leaves on canopy plants was greatest on day 52 with 7.4 leaves per plant compared to 3.6 leaves per plant in the no canopy treatment (Figure 2). Mean number of leaves on open grown plants declined to approximately 0.1 leaf/per plant by day 192, because of leaf and plant mortalities. Mean number of leaves on the plants below the canopy decreased to about 1.5 leaves/plant.

The largest leaf area and mean plant area were significantly related to time and were 3rd or 4th order polynomial functions (Figure 3 shows plant area, leaf area followed the same trend but is not presented). These polynomial regressions explained 73-95% of the variation of that factor in time. Mean number of leaves, leaf area and plant area increased from the start of the experiment in March of 2013 through the early spring months (day 52-73) and then declined through late summer and early fall.

Considering final plant dry mass, canopy plants were larger (0.406 g/plant) than plants in the open (0.155 g/plant) (*Student's t-test* with P values < 0.05). There was more dry mass produced by the plants below the canopy, 7.71 g total dry mass compared to 2.48 g total in the open or 3.1 times more produced below the canopy. Cause of the difference was more plants surviving and growing below the canopy. Light level in the open areas was 1985±242 µmoles/m^2/s compared to canopy at 130±64 µmoles/m^2/s and significantly different (*Student's t-test*, P values < 0.05). Soil depth was the same below the canopy (19.4±4.5 cm) as it was in the open (20.0±6.1 cm) (*Student's t-test*, P > 0.05).

DISCUSSION

Chaptalia texana has been found below the canopy of *Juniperus ashei/Quercus virginiana* woodlands, but not in associated grasslands (Van Auken and Bush 2015). When *C. texana* was planted, in the open (no canopy) mortality was higher than for canopy plants (Figure 1). No *C. texana* plants were noted in any grassland during the current experiment or in a prior study (Van Auken and Bush 2015). Literature reports are ambiguous concerning its habitat (Enquist 1987; USDA 2009; Harms 2011). The importance of light level was noted, with no *C. texana* plants found in the high light open grassland habitat and fewer survived when they were planted in the grassland compared to plants planted below the canopy. Soil depth did not seem to be a factor, as open or grassland soil was as deep as soil below the canopy (20.0±6.1 cm versus 19.4 ± 4.5 cm), but light levels were significantly higher in the open grassland.

Neighbors, especially the common C_4 warm season grasses, appeared to be essential in preventing the establishment, growth and presence of *C. texana*, in C_4 grasslands but was not examined in the current experiment. Earlier work suggested the various species of *Chaptalia* are found below *Quercus* or *Pinus-Quercus* woodlands or savannas (Nesom 1984; 1995; Flora of North America 2003) and *Juniperus-Quercus* woodlands and savannas (Harms 2011; Van Auken and Bush 2015). In parts of the range of the genus *Chaptalia*, some species or individuals of all species of *Chaptalia* may establish and grow in low density grasslands outside of the woodland canopy. However, all of the *C. texana* plants that we found were below the *Juniperus-Quercus* woodland canopy (current study and Van Auken and Bush 2015). Thus, the presence of neighbors seems to be a more subtle but not a less important factor in influencing or determining the density and the distribution of *C. texana* in these communities. Neighbor effects seemed to be combined with one or more other factors, which were not readily apparent in the current or previous study. The various C_4 grasses in the open and the C_3 sedge, *Carex planostachys*, below the canopy may be more efficient in taking up water and possibly nutrients and thus reduce the possibility of *C. texana* easily establishing and persisting in habitats where these species are found (Wayne and Van Auken 2009). The inhibiting effects of the C_4 grasses seems to be paramount, but may be transitory and neighbor effects were not determined in the current research.

Growth of *C. texana* plants early in the current experiment (first five months) was greater for plants below the canopy, while plants in the open did not change very much compared to their initial size (Figures 3). However, by the end of the experiment plants in both treatments decreased in size. Plants below the canopy grew to be about seven times larger than at the start by two months into the experiment (Figure 3), but then decreased in size toward the end of the growing season. Open plants grew less in the first three months, then lost leaves and area until they had an average of < 1 leaf plant. After the experiment was terminated and after fall rains we revisited the study site and found some *C. texana* plants. This was a surprise, because we did not expect to find any *C. texana* plants. Apparently some *C. texana* plants lose all of their leaves during drought and survive until rainfall reappeared. However, we could not relate these plants to our dead or lost study plants. Loss of leaves is known to happen for a number of herbaceous plants like the rain lilies (*Cooperia*), wild onions (*Allium*), the sego lily (*Calochortus*) and the C_4 grasses (Enquist 1987; Epple and Epple 1995). However, as far as we know, it has never been reported for *C. texana* or any other species of *Chaptalia*. Survival of *C. texana* in the rhizome stage was not expected.

A canopy habitat preference was demonstrated for *C. texana*. However, to determine neighbor effects will take more experimental time, a larger number of replications and probably a canopy that allows additional light to reach the understory species. Canopy light level in the current study was 130±64 µmoles/m^2/s which was < 10% of light levels found below a canopy where nearby populations of *C. texana* were previously noted and < 50% of measured light saturation for shade leaves of *C. texana* (Van Auken and Bush 2015).

Sorting out the causes that determine why a species is present in a given habitat is challenging (Begon et al. 2006; Smith and Smith 2012). While *C. texana* is usually found growing in shade, light levels and gas exchange characteristics are not the only factors controlling its habitat preference (Van Auken and Bush 2015). Further appraisal of the drought tolerance of *C. texana* is necessary to determine if they are restricted to the canopy because they cannot compete with associated species especially in the open or is it other factors. Other environmental conditions may limit *C. texana* to shaded understory habitats but they are not known at this time. A factor that may partially control the distribution of *C. texana* is covering or being buried by leaf litter. Covering *C. texana* by the leaves of various oaks especially *Quercus virginiana* seemed to occur but was not measured. Similar sun or shade distribution patterns have been reported for other species, but boundaries were caused by differential herbivory (Louda and Rodman 1996; Maron and Crone 2006; Leonard and Van Auken 2013).

Chaptalia texana growth may be limited by water availability or water use by more drought tolerant C_4 grasses that keep *C. texana* restricted to canopy habitats where these grasses cannot grow because of low light (Wayne and Van Auken 2009). Possibly higher soil water levels found below the canopy, which would be available to *C. texana*, are important. These conditions are dynamic and individuals respond to them all of the time, which makes it difficult to know which one or ones are controlling the species' responses and thus community composition. Because a species is present in a community today does not mean it was there yesterday or will be there tomorrow and determining the controlling factor or factors is difficult.

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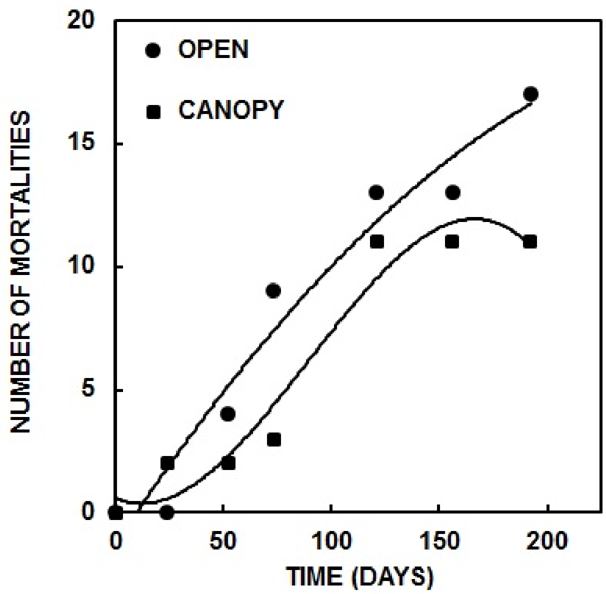

Figure 1. Mortality of Chaptalia texana plants at Hardberger City Park in San Antonio, Texas, USA is presented. Mortality of 40 plants (20 plants below a canopy and 20 plants in the open) was followed for 192 days in 2013. Total mortality at experiment end was 70% (12/40). Mortality in the open at the end of the experiment was 85% (17/20) and it was 55% (11/20) for plants below the canopy. Plotted lines are polynomial functions (no canopy or open, $y=-0.0002x^2 +0.1345x-1.2786$, $R^2=0.95$, $P<0.001$; canopy, $y=-6E-06x^3+0.0017x^2-0.0379+0.5909$, $R^2= 0.95$, $P<0.0001$).

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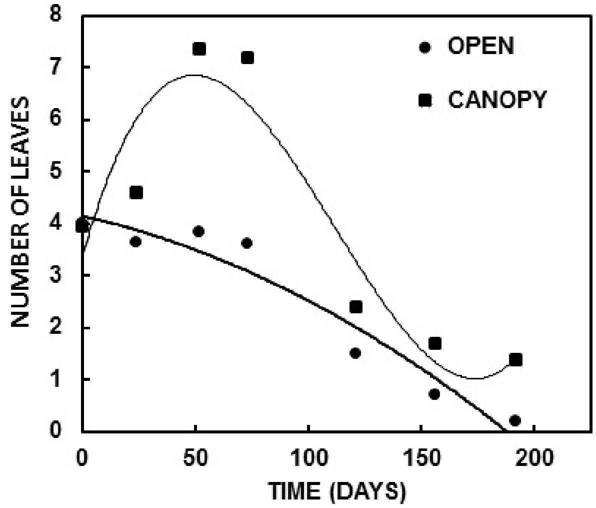

Figure 2. Presented is the mean number of leaves present on Chaptalia texana plants at Hardberger City Park in San Antonio, Texas, USA is. All leaves greater than 0.5 cm were counted approximately once per month over the course of the experiment. Plotted lines are polynomial functions (no canopy or open, y=-7E-05x^2-0.0097x+4.1457, R^2=0.94, P<0.0001; canopy y=6E-06x^3-0.002x^2+0.156x+3.362, R^2=0.88, P<0.001).

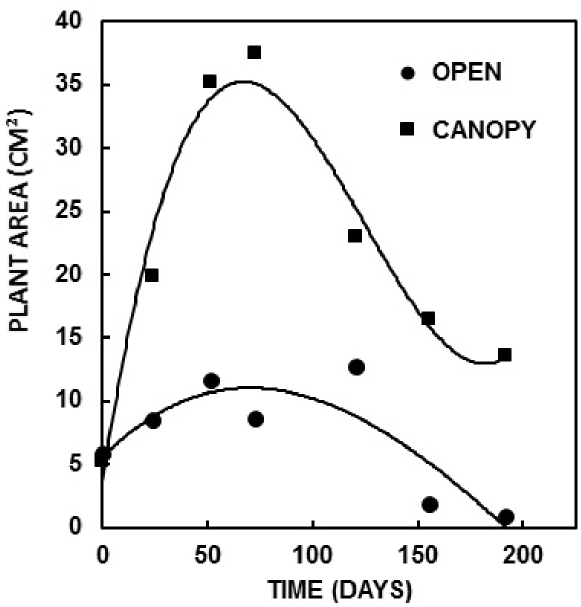

Figure 3. Presented is the mean area (cm2) of Chaptalia texana plants at Hardberger City Park in San Antonio, Texas, USA. Length of the two largest plant dimensions were measured and area was calculated. Plants were measured approximately once per month over the course of the experiment. Plotted lines are polynomial functions (no canopy or open, y=2E-06x^3-0.0014x^2+0.1651x+5.5883, R^2=0.73, P<001; canopy, y= 3E-05x^3-0.011x^2+1.0756+3.6675, R^2=0.95, P<0.0001).