Shrub Biomass Production Following Simulated Herbivory: A Test of the Compensatory Growth Hypothesis

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Abstract: The objective of this experiment was to test the hypotheses that 1) simulated herbivory stimulates increased biomass production in spiny hackberry (*Celtis pallida*), but decreases biomass production in blackbrush acacia (*Acacia rigidula*) compared to unbrowsed plants and 2) thorn density and length increase in blackbrush acacia to a greater extent than in spiny hackberry in response to tissue removal. Blackbrush acacia shrubs defoliated repeatedly at the 75 percent level produced about 66 percent more biomass than control shrubs, while shrubs receiving 100 percent repeat defoliation treatments produced double the biomass as control shrubs ($p < 0.05$), suggesting overcompensation. Spiny hackberry repeat defoliated shrub biomass production was double control shrub production at 25 percent treatment levels and 81 percent higher in repeat defoliated shrubs at 50 percent defoliation levels relative to control shrubs ($p < 0.05$). Biomass production during the third and fourth defoliation events was 90 percent lower than ($p < 0.05$) biomass removed in the initial defoliation. New twig and thorn production occurred only in 2003, but only in blackbrush acacia. These results suggest that spiny hackberry, a highly palatable shrub, is negatively impacted at high defoliation intensity, while the less palatable shrub, blackbrush acacia, responds to intense defoliation with increased biomass production.

Introduction

Compensation, over-compensation, and under-compensation were the three original plant responses to biomass removal by herbivores (McNaughton 1983). Production of mechanical and chemical defenses has been characterized as an induced response to biomass loss (Rhoner and Ward 1997). Increased thorn length and density may retard browsing (Cooper and Owen-Smith 1986). Our goal is to determine plant response to various levels of simulated herbivory in two important south Texas shrubs.

Spiny hackberry (*Celtis pallida*) and blackbrush acacia (*Acacia rigidula*) are important browse species for wildlife in southern Texas (Graham 1982, Varner and Blankenship 1987). Many wildlife species utilize spiny hackberry and blackbrush acacia during dry periods when other available forage has been exhausted (Varner and Blankenship 1987).

Spiny hackberry has spines, but no chemical defensive mechanisms against herbivory have been documented and the shrub appears to respond to removal of tissue with compensatory growth (Asah and others 1987, Schindler 2000). After top growth removal, new spiny hackberry shoots and tissue are often higher in nutritive value than previous tissues (Asah and others 1987, Schindler and others 2004). Blackbrush acacia is more heavily defended with thorns and chemical compounds (Clement and others 1998, Schindler and others 2003). Previous studies have suggested that thorn length and density increase on thorn scrub vegetation following mechanical brush clearing (Schindler and others 2004). It is therefore important to understand how these two important browse plants respond to biomass removal by herbivores.

We hypothesize that 1) simulated herbivory stimulates increased biomass production in spiny hackberry but decreases biomass production in blackbrush acacia compared to unbrowsed plants and 2) thorn density and length increase in blackbrush acacia to a greater extent than in spiny hackberry in response to tissue removal.

Materials and Methods

Study Site

Research was conducted on the Jack R. and Loris J. Welhausen Experimental Station in Webb County, about 56 km northeast of Laredo, Texas (27°40’57N, 98°56’51W), at an elevation of about 137 m. The surface layer soil at the site is a sandy clay loam with 0 to 3 percent slopes, with a caliche layer underlying the soil at depths of 1 to 5 m (Soil Conservation Service 1985). Precipitation, as recorded in Laredo (1947-2003), averages about 50 cm a year but varied during the 2 years of this study (fig. 1) and deviated from long term averages (National Climate Data Center 2004, Asheville, NC). Maximum temperatures above 35°C occur from June to August and the lowest temperatures, around 8°C, usually occur December to January (National Climate Data Center). Vegetation at the study site is a mixed shrub community with little grass cover (Varner and Blankenship 1987). Cattle and wildlife both are present on the ranch under a continuous grazing system. However, little use was observed by cattle or wildlife of the selected study site area. The area has been mechanically cleared of brush in the past, but sufficient time

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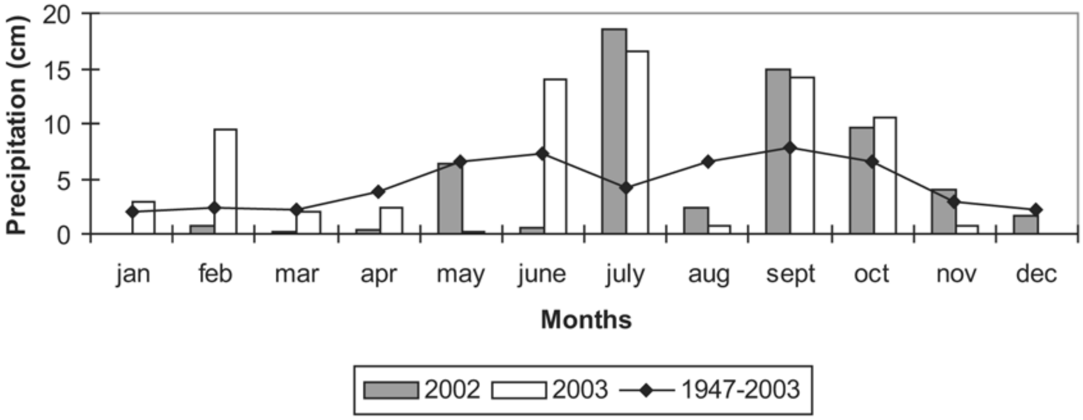

Figure 1. Precipitation by month as recorded in Laredo (1947-2003) and the Welhausen Research Station (2002, 2003), Webb County, TX.

has elapsed for vegetation to recover and form a mature shrub community. A representative area was selected in May 2002 and an exclosure about 60 x 80 m surrounded by a 1.2 m tall welded wire fence was established to prevent wildlife and livestock browsing on shrubs. Chicken wire with a 2.5 cm diameter mesh was used along the bottom 0.6 m of the fence to retard small mammals. A CM20 Campbell Scientific Weather Station located on the Welhausen Research Station < ½ km from the study site provided local hourly and daily weather conditions (Campbell Scientific Inc., Logan, UT).

Methods

A randomized, complete-block design was used in this experiment. Five blocks per species were used, with each treatment randomly assigned to a selected shrub in the block (n = 5). Twenty-five plants of each species, blackbrush acacia and spiny hackberry, were randomly selected in May 2002 from plants within the exclosure. Plants had a similar number of basal stems and were 1.5 to 2 m tall, which is considered the upper limit white-tailed deer (*Odocoileus virginianus*) browse. Plants of each species were randomly chosen and were assigned to one of five defoliation treatments on a randomly selected stem: 0 percent, 25 percent, 50 percent, 75 percent, and 100 percent. The 0 percent defoliation was the control group and was defoliated at the end of the experiment in October. For the 2003 field season, additional controls were added for harvest at the second and third defoliations to add a finer degree of resolution for temporal variations that might influence biomass production, such as tropical storms or insect defoliation. Shrubs were initially defoliated in late June and repeat removal of regrowth biomass was conducted at 6 week intervals until late October, resulting in one initial and three repeat defoliation periods for each year. Leaf tissue and new twig material was removed by hand, placed on dry ice, weighed, freeze dried for 48 hours, and then reweighed. Thorn length and density was measured on new season twig growth at the initial defoliation and then only on regrowth twig biomass at each repeat defoliation period. Leaf and twig biomass production, thorn length, and thorn density were analyzed separately by species using ANOVA and Proc Mixed commands in SAS version 8 (SAS Institute 1999). Independent variables consisted of defoliation intensity, clipping treatment (control or treated), and defoliation event. Dependent variables were biomass production, thorn length, and thorn density.

Results

Blackbrush acacia

There were no significant ($p > 0.05$) differences between years for blackbrush acacia biomass production. Total biomass production by repeat defoliated blackbrush acacia shrubs subjected to 25 percent and 50 percent defoliation did not differ ($p > 0.06$) from control shrubs (fig. 2). Blackbrush acacia shrubs subjected to 75 percent and 100 percent tissue removal produced more ($p < 0.01$) biomass, double the control production for 100 percent removal, than associated

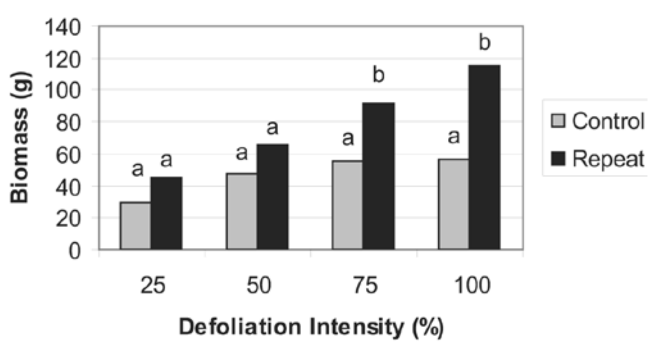

Figure 2. Mean of total blackbrush acacia biomass summed across defoliation events for each treatment, no difference between 2002 and 2003. Control plants were harvested only at end of growing season in October; repeat is sum of all biomass removed. Means within a defoliation intensity with a different letter are different (p < 0.05) at that defoliation level. Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

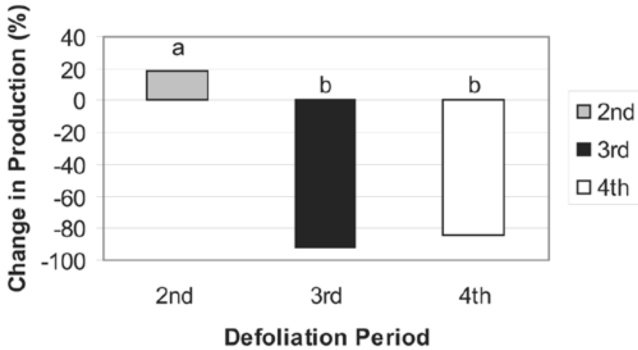

Figure 3. Change (percent) of blackbrush acacia biomass production as a percent of the original biomass removed. Years and treatment are not different. Means across defoliation periods with a different letter are different (p < 0.05). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

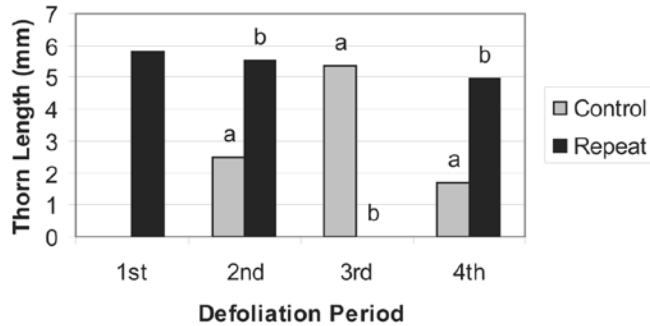

Figure 4. 2003 Blackbrush acacia thorn length. No thorn production in 2002. No repeat thorn production at 3rd defoliation period. Means within a defoliation period with a different letter are different (p < 0.02). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

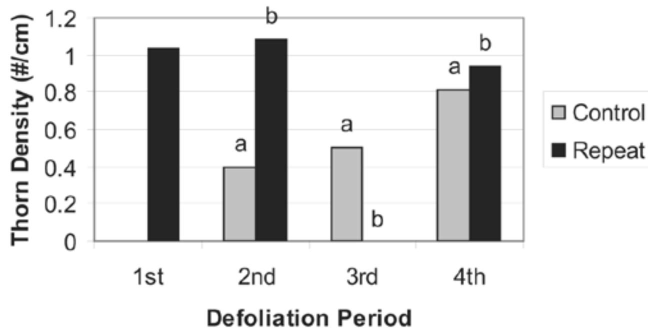

Figure 5. 2003 Blackbrush acacia thorn density (number of thorns per cm). No repeat thorn production at 3rd defoliation period. Means within a defoliation period with a different letter are different (p < 0.02). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

non-defoliated control shrubs. We reject our hypothesis that simulated herbivory decreases biomass production in blackbrush acacia because shrubs defoliated at 25 percent and 50 percent produced biomass amounts similar to control shrubs and shrubs defoliated at 75 percent and 100 percent levels overcompensated or produced more biomass than control shrubs.

The change (percent) in blackbrush acacia regrowth biomass compared to initial biomass removed demonstrated overcompensation during the second defoliation period, but a decrease or under-compensation during the third and fourth defoliation events (fig. 3). There was no difference ($p > 0.05$) in defoliation intensity (percent removed) or year for each of the three repeat defoliation periods. Biomass removed at the second defoliation was about 20 percent more than was originally removed. Biomass production 12 and 18 weeks post defoliation demonstrated an 80 percent reduction in biomass production compared to initial biomass amounts removed.

Blackbrush acacia did not produce new twig growth after defoliation events in 2002. We hypothesize the drought of 2001, coupled with low rainfall in early 2002, was partially responsible for this. In 2003, twig and thorn production occurred in treated and control blackbrush acacia shrubs, except during the third defoliation period when treated plants did not produce any twigs or thorns (figs. 4 and 5). Thorns on repeat defoliated plants were twice as long as thorns on control shrubs at the second defoliation event and were three times longer on treated plants at the final defoliation event than control shrubs ($p < 0.02$, fig. 4). Thorn density in treated plants was greater (0.76 thorns/cm) than control plants (0.57 thorns/cm) ($p < 0.02$). This appears to support our hypothesis that defoliation increased thorn density and length in treated shrubs.

Spiny Hackberry

There was no significant difference ($p > 0.05$) between years for spiny hackberry biomass production. Spiny hackberry shrubs exhibited the opposite compensation pattern than blackbrush acacia. Spiny hackberry shrubs repeatedly defoliated at 25 percent produced almost double ($p <0 .01$) the amount of biomass as control shrubs (fig. 6). Biomass production in shrubs subjected to repeat defoliation at 50 percent produced approximately 81 percent more ($p < 0.01$) biomass production than associated controls (fig. 6). However, there was no difference ($p > 0.09$) in biomass production in repeatedly defoliated and control shrubs defoliated at 75 percent and 100 percent levels (fig. 6). This suggests that spiny hackberry shrubs compensated for tissue removal at higher defoliation intensities and over-compensated for biomass loss at lower defoliation intensities, a partial validation of our hypothesis that simulated herbivory stimulates increased biomass production in spiny hackberry compared to non-defoliated controls.

The change (percent) of spiny hackberry regrowth biomass compared to biomass removed in the initial defoliation was higher in 2002 compared to 2003 (fig. 7). In 2002, repeatedly defoliated shrubs produced more biomass at the second defoliation than was originally removed, but less biomass was produced relative to the original biomass following the second and third defoliation events. In 2003, biomass production following defoliation never exceeded the biomass that was originally removed, resulting in under-compensation by the plant.

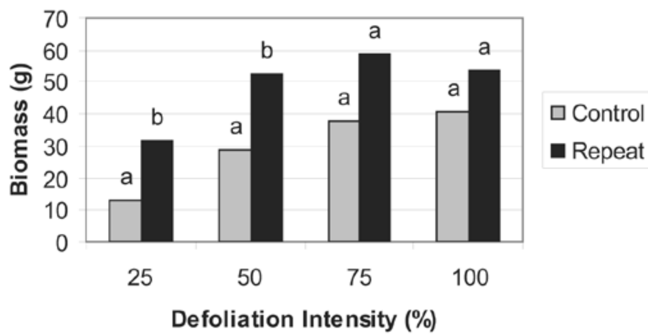

Figure 6. Mean of total spiny hackberry biomass production summed across defoliation events for each treatment, no difference between 2002 and 2003. Control plants were harvested only at end of growing season in October; repeat is sum of all biomass removed. Means within a defoliation intensity with a different letter are different ($p < 0.05$) at that defoliation level. Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

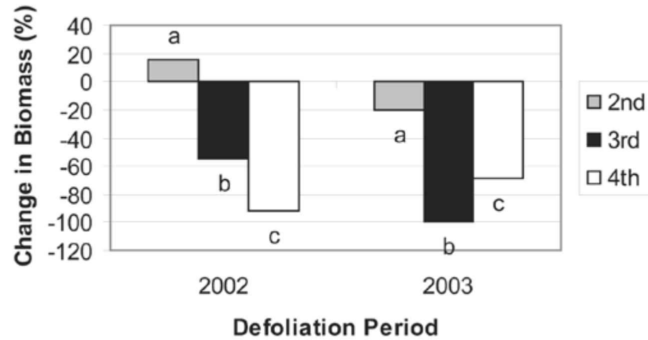

Figure 7. Change (percent) of spiny hackberry biomass production as a percent of the original biomass removed. Treatments not different; means across defoliation periods with a different letter are different ($p < 0.05$). Research conducted in 2002 and 2003 at Welhausen Research Station, Webb County, Texas.

Repeatedly defoliated spiny hackberry shrubs did not produce new twig browse or thorns following defoliation in 2002. In 2003, spiny hackberry produced new twigs, but no thorn production occurred in repeatedly defoliated shrubs. Many possible reasons exist for the lack of twig browse production in spiny hackberry. During summer 2001, leaf drop was observed in spiny hackberry. In 2002, spiny hackberry had delayed leaf bud until late May, almost 2 months past normal leaf bud as reported by Everitt and Drawe (1993). We hypothesize the drought of 2001 coupled with low early rainfall in 2002, was partially responsible for the lack of twig and thorn production.

Conclusions

The shrubs in this experiment demonstrated compensatory and over-compensatory biomass growth at different intensities of defoliation. In contrast to our original hypothesis, blackbrush acacia responded with overcompensation at high levels of tissue defoliation and compensation at lower levels. Spiny hackberry demonstrated over-compensation at low defoliation levels but not at high defoliation levels where compensation occurred. Repeat defoliation resulted in under-compensation in biomass production. This suggests that if defoliation occurs frequently, these shrub species may continue to under-compensate, possibly resulting in shrub death (Forbes and others 1995). Lack of precipitation appears to intensify the influence of tissue removal.

Implications

The summer months in southern Texas, May to August, are characterized by high temperatures and low rainfall. Late summer, the third and fourth defoliation periods, are normally the driest in southern Texas. The low biomass production during this study may reflect the combined influence of increased number of defoliations (frequency) and drought. The third defoliation of spiny hackberry in 2003 had a 99 percent reduction in biomass production (fig. 7) and during the 6 weeks before the third defoliation in <6 mm of precipitation was received. Forbes and others (1995) reported similar results concerning lack of biomass production and stem death following repeat defoliations of guajillo (*Acacia berlandieri*), another common south Texas shrub, during a period of low precipitation. Our results indicate that biomass removal and shrub response may be dependent upon the species of shrub, the intensity of biomass removal, the frequency of removal, and the amount of precipitation received.

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