Defoliation and woody plant (*Prosopis glandulosa*) seedling regeneration: potential vs realized herbivory tolerance

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Abstract

Herbivory by rodents, lagomorphs and insects may locally constrain woody plant seedling establishment and stand development. Recruitment may therefore depend either upon plant tolerance of herbivory, or low herbivore abundance, during seedling establishment. We tested potential herbivory tolerance by quantifying growth, biomass allocation, and survival of defoliated *Prosopis glandulosa* seedlings under optimal abiotic conditions in the absence of competition. Realized tolerance was assessed by clipping seedlings of known age grown in the field with and without herbaceous competition.

At 18-d (= 'young') or 33-d (= 'old') of age, seedlings in the growth chamber were clipped just above the first (cotyledonary) node, above the fourth node, or were retained as non-clipped controls. Potential tolerance to defoliation was high and neither cohort showed evidence of meristematic limitations to regeneration. Clipping markedly reduced biomass production relative to controls, especially belowground, but survival of seedlings defoliated 5 times was still ≥75%. Contrary to expectations, survival of seedlings defoliated above the cotyledonary node 10 times was greater ($P < 0.10$) for 'young' (75%) than 'old' (38%) seedlings. Under field conditions, survival of defoliated 11-month-old *P. glandulosa* seedlings was ≤59% after one defoliation and only ≤13% after six defoliations.

Results indicate *P. glandulosa* is potentially tolerant of repeated shoot removal early in its life cycle. Seedling tolerance to defoliation under field conditions therefore appears dependent upon abiotic stresses or resource limitations rather than a lack of intrinsic adaptations for shoot replacement or a depletion of the seedlings' bud bank. Curtailment of root growth, a consequence of top removal observed in the growth chamber experiment, may reduce the capacity of *P. glandulosa* seedlings to acquire soil resources needed for meristem activation and shoot growth under field conditions. The importance of resource availability to post-defoliation regeneration was implicated in the field experiment, where survival, shoot elongation, and aboveground productivity of clipped seedlings was greatest in plots without herbaceous interference.

In light of the marked increases in *P. glandulosa* abundance in grasslands in recent history, our results suggest that (1) utilization of *Prosopis* seedlings by herbivores may be infrequent or sporadic, (2) periodic episodes of seed production and germination may satiate herbivore populations, and/or (3) *Prosopis* seedling establishment occurs during periods of low herbivore density.

Introduction

The arborescent legume, honey mesquite [*Prosopis glandulosa* (Torr.) var. *glandulosa*] is a widespread and important component of many arid and semi-arid landscapes in southwestern North America (Simpson 1977, McKell 1989). Its abundance has increased markedly since the 1800s, apparently reflecting interactive changes in atmospheric CO_2 concentration, livestock grazing, and fire and climatic

regimes (Archer 1994; Archer et al. 1995). Germination and establishment of *Prosopis* can occur across a broad array of light, temperature, and moisture regimes (Scifres & Brock 1969, 1971) and soil types (Ueckert et al. 1979). Reductions in competition with grasses, as might occur from livestock grazing, increase its growth rate (Polley et al. 1994, Bush & Van Auken 1995), but seedling survival can be high in both lightly- and heavily-grazed grasslands which differ markedly in their herbaceous species composition and biomass (Archer 1996). Adult *Prosopis* plants are tolerant of disturbance and regenerate rapidly from lignotubers following chemical, mechanical or fire-induced aboveground mortality (Wright & Stinson 1970; Scifres and Hahn 1971). As a result, *Prosopis glandulosa* has been an aggressive invader of grasslands and savannas, and is highly persistent once established.

Research on the critical seedling establishment phase of the *P. glandulosa* life cycle has focused primarily on abiotic factors and herbaceous interference. However, field observations suggest defoliation by rodents, lagomorphs and insects may also be a significant source of mortality among *Prosopis* seedlings (Glendening & Paulsen 1955; Simpson 1977; Nilsen et al. 1987; Weltzin et al. 1997). The importance of herbivore-induced seedling mortality, known to be a determinant of adult plant distribution in other systems (McAuliffe 1986; Cooke 1987; Borchert et al. 1989; Myster & McCarthy 1989; Huntly 1991; Terborgh & Wright 1994) may depend on the extent to which *Prosopis* seedlings possess adaptations that confer defoliation tolerance. If young seedlings are highly susceptible to defoliation because of meristem, energy, or nutrient limitations, their recruitment would be confined to times or places where rodent, lagomorph or insect herbivore activity are low. Alternatively, seedlings may be well-adapted to regenerate following top removal, but abiotic stresses or competition from associated plants may limit their recovery under field conditions. To assess these possibilities, we quantified biomass allocation, growth, and survival of *Prosopis* seedlings subjected to repeated top removal in complementary controlled environment and field experiments. Our goal was to assess potential tolerance of seedling cohorts to repeated defoliation in a competition-free, controlled environment optimal for plant growth. Realized tolerance was assessed by clipping seedlings of known age under field conditions with and without herbaceous competition.

Materials and methods

Growth chamber experiment

On 17 February 1989, we planted five scarified *P. glandulosa* seeds (0.5 cm deep) into each of 129 (10 cm × 10 cm × 35 cm) plastic pots filled with commercial potting soil. This process was repeated on 4 March 1989 to produce a second cohort of *Prosopis* seedlings. Seedlings were thinned to two per pot 12 days after planting each cohort.

Mercury and sodium bulbs provided an average photosynthetically active photon flux density (PPFD, 400–700 nm) of 500 μmol m^{-2} s^{-1} over a 13 hour photoperiod. Air temperature was maintained at 21/15 °C (day/night). Soil water content was maintained near field capacity with distilled, deionized water. Water soluble fertilizer (2 g l^{-1} of 20–10–20 N, P, K [Peters Professional]) was applied biweekly.

Potential tolerance to defoliation was assessed on these seedlings grown at near-optimal conditions. Seedlings were first clipped on 22 March 1989, when the two cohorts were 18- (hereafter 'young') and 33- (hereafter 'old') days old. Seedlings received one of three treatments: no clipping (= control), partial clipping (PC), or complete clipping (CC). Seedlings in the CC treatment were clipped just above the cotyledonary node (cotyledons left intact), because prior work (Scifres & Hahn 1971) indicated that seedlings would not regenerate if clipped below the cotyledonary node. Seedlings in the PC treatment were clipped between the 4th and 5th node (ca. 4–6 cm above the cotyledonary node). Seedlings were subsequently clipped at 14-day intervals (i.e., on 5 April, 19 April, 4 May, and 19 May 1989). Clipped leaves and shoots were dried at 105 °C and weighed.

Prior to each clipping event, we counted the total number of leaves, and the number of long and short shoot buds initiated. Long shoot buds produced shoots with distinct nodes and elongated internodes. Short shoots did not elongate internodes, and lacked visible lateral buds (Dahl 1995).

Seedling above- and belowground biomass was determined on each clipping date by destructively harvesting a subset of seedlings. At treatment initiation (22 March 1989), we destructively harvested nine seedling pairs from each cohort. On subsequent clipping dates, we destructively harvested eight seedling pairs from each of the six treatment combinations. Leaves and stems were separated, dried at 105 °C and weighed. Biomass of individual leaves (mg leaf^{-1})

was determined for clipped seedlings at each harvest date, and for control seedlings at experiment termination. Roots were extracted from soil by hand washing and ash-free biomass determined.

Seedling survival was assessed 14 days after each clipping event; seedlings were considered dead if they had brittle stems and brown cambium. All biomass values are based on live seedlings.

To assess the impact of additional defoliations on seedling growth and survival, we retained seedlings in the CC treatments ($n = 8$), and continued clipping them at ca. 18-d intervals (11 clippings total) until 20 September 1989, whereupon they were harvested to determine belowground biomass.

Field experiment

Realized tolerance of *P. glandulosa* seedlings was assessed in a field experiment conducted in Wilbarger County in north-central Texas. The climate of the region is characterized by hot summers and mild winters. Average annual precipitation (682 mm) is distributed bimodally, with peaks in May (96 mm) and September (118 mm). The field site (33°48′ N, 99°29′ W) was characterized by well-drained clay loam soils dominated by the grasses *Stipa leucotricha* and *Buchlöe dactyloides* (see Weltzin et al. 1997 for further details on climate, vegetation and soils). Precipitation for the period encompassing the field experiment was well below-normal (1988 = 326 mm; 1989 = 564 mm).

In June 1988, we planted 20 scarified *P. glandulosa* seeds 0.5 cm deep within each of 60 1 m² randomly located plots assigned at random to one of two vegetation interference treatments: no interference (NI) or full interference (FI). The NI treatment was designed to minimize herbaceous interference (e.g., shading, competition for water or nutrients) with *Prosopis* growth. This was achieved through application of a non-specific contact herbicide (Roundup) and subsequent hand-weeding. The FI treatment was considered an indigenous control with full herbaceous interference. Exclosures constructed of 1-cm mesh hardware cloth protected seedlings from potential vertebrate herbivory.

On 18 May 1989, one-half of the surviving *Prosopis* seedlings (now 11 months old) in the NI ($N = 68$) and FI ($N = 78$) treatments were clipped just above the cotyledonary node; the other half were retained as unclipped controls. Seedlings in the defoliation treatment were subsequently clipped at 14-day intervals after determination of the number and length of newly-emerged shoots. Clipped leaves and shoots were dried at 105 °C, and weighed.

Clipping treatments were continued and seedlings monitored for survival through 8 August 1989. The experiment was terminated on 9 October 1989, 61 days after the last clipping event, when seedling survival was determined for the last time. Plants were considered dead when their stems were brittle and their cambium was brown.

Statistical analysis

For the growth chamber experiment, we used fixed-effects, repeated measures analyses of variance (ANOVA; Zar 1996) to evaluate the effects of initial age, clipping treatment, and clipping date on *Prosopis* shoot growth rate, belowground biomass accumulation, stem elongation and leaf number, and meristem activation. Means were computed using surviving plants only. We used Fisher's exact text (Fisher 1958) to evaluate differences in seedling survival at each clipping date for each initial age-clipping treatment combination ($\alpha = 0.10$ because of low seedling numbers).

Prosopis biomass accumulation and shoot elongation in the field were dependent on pretreatment stem length, so data were normalized by subtracting the mean pretreatment stem length. Normalized data were analyzed in a fixed-effects, repeated measures ANOVA model to evaluate effects of clipping and herbaceous interference on rates of stem elongation and production. Fisher's exact test (Fisher 1958) was used to evaluate effects of herbaceous interference on clipped seedling survival at each clipping date.

Arcsine transformations (Steel & Torrie 1980) were performed on proportional data and square-root transformations on all other data except seedling survival. Applicable first- and second-order interactions were included in all ANOVA models. To facilitate interpretation of results, significant interactions that contributed $<2\%$ to the model sum of squares were combined with the error term and the model reanalyzed. Tukey's HSD multiple means comparison test was used to compare levels within factors for significant ($P < 0.05$) main effects and first-order interactions. Non-transformed least-squares means are presented in all tables and figures.

Table 1. Survival (%) of *Prosopis* seedling cohorts (18- and 33-d old) clipped at two-week intervals in 1989 at two intensities (NC = non-clipped control, PC = partially clipped, and CC = completely clipped). We continued the CC treatment beyond 19 May and found that survival of CC seedlings defoliated a total of 10 times was greater ($P < 0.10$) for 'young' (75%) than 'old' (38%) seedlings (data not shown).

Initial age	Treatment	Date				
		22 Mar.	5 Apr.	19 Apr.	4 May	19 May
18-d	NC	100[1]	100	100	100	100
	PC	100	100	100	100	100
	CC	100	100	100	100	100
33-d	NC	100	100	100	100	100
	PC	100	100	100	100	100
	CC	100	100	100	88	75

[1] Within date and treatment, survival did not differ ($P > 0.10$.)

Results

Growth chamber experiment

Each seedling had a single stem on the initial clipping date (22 March 1989). Mean (± 1 SE) shoot length of 'young' and 'old' seedlings was 5.1 ± 0.3 and 11.9 ± 0.4 cm, respectively. 'Young' seedlings had initiated leaves at 3–5 nodes along the main axis, whereas 'old' seedlings had leaves at 8–11 nodes. Root biomass was 0.04 ± 0.02 g and 0.06 ± 0.01 g for 'young' and 'old' seedlings, respectively.

All seedlings in all age/treatment combinations survived at least three clipping events (Table 1). Intensity of defoliation (PC vs CC) and seedling age at initial defoliation ('young' vs 'old') did not affect seedling survival after five clipping events ($P > 0.10$).

Shoot growth rate was affected by an interaction between defoliation and time ($P < 0.05$). The growth rate of shoots of control seedlings was high and increased during the experiment, while CC and PC seedling shoot growth rates were low and constant (Figure 1).

Root biomass accumulation was affected by a three way interaction between defoliation treatment, seedling age, and time ($P < 0.05$). Root biomass of control seedlings increased throughout the experiment, whereas accumulation of root biomass in defoliated seedlings was virtually nil (Figure 2). Complete defoliation suppressed root biomass accumulation to a greater extent than partial defoliation, but by 19 May differences among 'old' seedlings were not significant ($P > 0.05$).
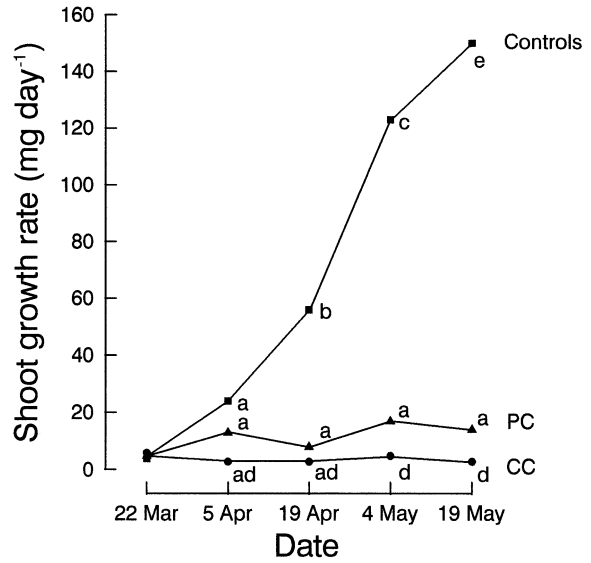

Figure 1. Mean shoot growth rate (mg d^{-1}) of *Prosopis* seedlings that were not clipped (control, squares), partially clipped (PC, triangles) or completely clipped (CC, circles) at biweekly intervals in a growth chamber in 1989. Within clipping treatment and within date, means with the same letter did not differ ($P > 0.05$).
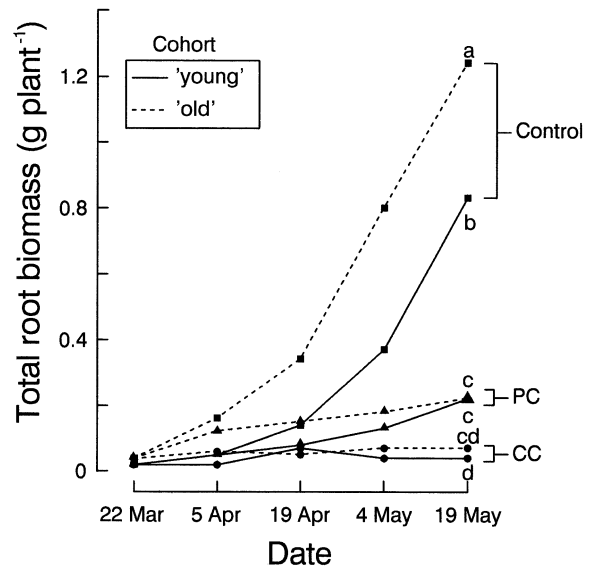

Figure 2. Mean ash-free root biomass (g plant^{-1}) of *Prosopis* seedlings that were not clipped (squares), partially clipped (PC, triangles) or completely clipped (CC, circles) at biweekly intervals in a growth chamber in 1989. Seedlings were initially clipped at 18 days (= 'young') and 33 days (= 'old') of age. Means on 19 May with the same letter did not differ ($P > 0.05$).

Table 2. Mean number of leaves and stem length (cm) increment generated for *Prosopis* seedlings clipped at two-week intervals in 1989 at three intensities (NC = non-clipped controls, PC = partially clipped, and CC = completely clipped) in a growth chamber. Mean number of leaves and stem length were used to calculate leaf number per unit stem length. For leaf number and stem length, means within treatment and within date with the same letter did not differ ($P > 0.05$). See text for seedling size at treatment initiation (22 March 1989).

Parameter	Treatment	Date			
		5 Apr.	19 Apr.	4 May	19 May
Number of	NC	8.9a	9.0a	8.9a	7.5a
leaves	PC	12.8b	17.5c	24.4d	17.6c
	CC	6.2a	9.0a	12.7b	7.6a
Stem length	NC	9.1a	14.9b	18.2c	17.5c
(cm)	PC	9.7ad	8.9ad	11.9a	8.0d
	CC	4.7e	4.5e	6.8e	4.3e
Number of	NC	1.0	0.6	0.5	0.4
leaves cm^{-1}	PC	1.3	2.0	2.1	2.2
of stem	CC	1.3	2.0	1.9	1.8

The incremental number of leaves produced and length (cm) of shoot generated was also affected by an interaction between defoliation and time ($P < 0.05$). Among clipped seedlings, the number of leaves produced per plant was comparable to or greater than controls (Table 2). Stems of clipped seedlings were substantially shorter than controls on most dates. As a result, the number of leaves produced per unit of stem length was greater in clipped than control plants.

Non-clipped seedlings typically were single-stemmed. At the termination of the experiment, the number of lateral stems per control plant averaged 0.2 and 0.4 among 'young' and 'old' cohorts, respectively. In contrast, the number of first-order long shoots (i.e., an elongated stem with at least one leaf) produced on clipped plants ranged from 1.8 to 2.7 over the five clipping dates and was comparable among cohorts ($P > 0.05$). After five clippings, CC seedlings had produced an average of 9.3 first-order long shoots per plant from the cotyledonary node (including the original stem). The number of short shoots (i.e., a single leaf emerging at a node) produced from the cotyledonary node of CC seedlings averaged 1.1 plant^{-1} and did not differ with seedling age or date ($P > 0.05$). PC seedlings produced between 0 and 1.8 long shoots node^{-1} at each date. At the 4th node, 4X as many long shoot meristems were activated than at the cotyledonary node, regardless of seedling age at initial

clipping. Similar to CC seedlings, PC seedlings produced fewer short than long shoots overall, and seldom activated short shoots from the cotyledonary node.

By 19 May, individual leaf biomass generated by 'old' control plants averaged 64 mg leaf^{-1} while 'young' control plants averaged 76 mg leaf^{-1}. In contrast, leaf biomass of clipped seedlings, which were pooled across age cohorts and clipping treatments because they did not differ ($P > 0.05$), was 2.4 mg leaf^{-1}. Individual leaf biomass of clipped seedlings was greatest (6.2 mg leaf^{-1}) on 5 April, and generally decreased with increasing numbers of clipping events.

The cotyledons of clipped seedlings generally persisted longer than those of non-clipped seedlings. By 19 May (ca. 3 months after seedling emergence), all cotyledons had abscised from both cohorts of control seedlings. In contrast, 50% and 63% had abscised from 'young' and 'old' PC seedlings, respectively, and 0% and 25% had abscised from 'young' and 'old' CC seedlings, respectively.

Seedlings in the extended portion of the CC treatment (i.e., that were clipped a total of 11 times) were relatively tolerant of multiple defoliation, depending on seedling age at initial defoliation and the number of clipping events. Contrary to expectations, survival of 'young' seedlings (75%) exceeded survival of 'old' seedlings (38%) after 10 clipping events ($P < 0.10$; data not shown). However, at experiment termination (i.e., after 11 clipping events), survival of 'young' (63%) and 'old' (38%) seedlings did not differ ($P > 0.10$). Shoot growth rate and root biomass of these seedlings were comparable to seedlings clipped 5 times (data not shown).

Field experiment

Survival of non-clipped (control) seedlings was 100% in plots with no herbaceous interference (NI) and in plots with full herbaceous interference (FI). Defoliation of seedlings significantly reduced their survival (Table 3). After the first and second clipping events, the number of 11-month-old *Prosopis* seedlings that initiated new shoots was statistically comparable on plots with and without herbaceous interference ($P > 0.10$). After the third and subsequent clipping events, more seedlings regenerated in NI plots than FI plots.

Prosopis shoot elongation was affected by clipping date and the interaction between clipping treatment and herbaceous interference ($P < 0.05$). Shoot elongation of clipped seedlings was greater ($P < 0.05$) in NI plots (0.054 cm day^{-1}) than in FI plots (0.033 cm

Table 3. Survival (%) of *Prosopis* seedlings clipped at two-week intervals in 1989 in field plots with no herbaceous interference (NI) or full herbaceous interference (FI). Survival of non-clipped control plants was 100% for both levels of herbaceous interference.

Treatment	Date					
	18 May	7 June	21 June	5 July	22 July	8 Aug.
FI	53[1]	35	32*	3**	3*	0*
NI	59	56	56	26	18	13

[1] Within date, * $P < 0.10$, ** $P < 0.01$.

day^{-1}). In contrast, stem elongation of non-clipped seedlings was statistically comparable ($P > 0.05$) on NI (0.088 cm day^{-1}) and FI (0.072 cm day^{-1}) plots. Productivity of clipped seedlings was greater ($P < 0.05$) on NI (8.2 mg day^{-1}) than FI (6.8 mg day^{-1}) plots.

Discussion

Mature woody plants are often highly tolerant to defoliation or top removal, the response varying with lifeform, growthform, season, frequency and extent of defoliation, and environmental conditions prior to and following herbivory (e.g., Garrison 1953; Merz & Boyce 1956; Wright & Stinson 1970; Haas et al. 1973; Archer & Tieszen 1980; Bergstrom & Dannell 1987; Du Toit et al. 1990; Bilbrough & Richards 1993; Ernest 1994). By comparison, little is known of the defoliation impacts at the seedling stage of the woody plant life cycle. Survival of *P. glandulosa* seedlings in the growth chamber was high ($\geq 75\%$) after 5 consecutive clipping events (Table 1), and exceeded 38% after as many as 11 clipping events. These results indicate *P. glandulosa* is potentially tolerant of repeated shoot removal early in its life cycle. Seedling tolerance to defoliation under field conditions therefore appears dependent upon abiotic stresses or resource limitations rather than a lack of intrinsic adaptations for shoot replacement. The importance of resource availability to post-defoliation regeneration was implicated in the field experiment, where survival, shoot elongation, and aboveground productivity of clipped seedlings was greatest in plots without herbaceous interference.

We expected the detrimental effects of herbivory to be most pronounced on younger, smaller plants whose bud bank and energy/nutrient stores would be less well-developed. However, survival of 'young'

seedlings exceeded that of 'old' seedlings after as many as 10 clipping events. This counter-intuitive outcome has also been observed with *Acacia senegal* seedlings (Seif el Din & Obeid 1971) and may reflect the decline in physiological performance associated with the advanced senescence observed on cotyledons of the older seedling cohorts relative to younger seedling cohorts (cf., Ampofo et al. 1976).

Cotyledons (Seif el Din & Obeid 1971; Ampofo et al. 1976; Andersson & Frost 1996) and leaves (cf., McNaughton 1979, Nowak & Caldwell 1984; Belsky 1986) retained after defoliation play a key role in bud activation, shoot growth, and the maintenance of root biomass and activity. Delayed senescence and stimulated photosynthesis of leaves remaining on partially defoliated plants has been reported for various plant growth forms (Briske & Richards 1995). The leaf area retained by PC seedlings presumably enabled plants in this treatment to maintain higher rates of shoot and root growth than CC plants. Cotyledons may have similarly contributed to unexpectedly high rates of seedling survival, especially for the 'young' CC cohort. This interpretation is supported by observations of cotyledon life-span, which increased with increasing intensity of defoliation (control < PC < CC), and decreased relative to age at initial defoliation ('old' < 'young'). In other experiments, *P. glandulosa* cotyledon abscission has been observed 15–20 days after seedling emergence; however, when shoots were removed cotyledons remained functional until new shoots emerged ca. 2 weeks later (Scifres & Hahn 1971). Further, when cotyledons were removed with shoots, seedlings did not regenerate.

Clipped seedlings produced mostly long shoots throughout the growth chamber experiment. Initiation of long shoots after defoliation has been widely reported for woody species (Scifres & Hahn 1971; Willard & McKell 1978; Archer & Tieszen 1980; Du-Toit et al. 1990; Bilbrough & Richards 1993) and the ability of shrubs to initiate long shoot growth is an important component of browsing tolerance (Wandera et al. 1992). Although long shoots constitute a potentially greater energetic investment than short shoots, such tissue would enable damaged *Prosopis* seedlings to gain vertical stature more rapidly after defoliation. Even so, clipped seedlings had shorter internodes and more leaves per unit shoot length than control seedlings (Table 2). This suggests that seedlings responded to clipping by preferentially allocating resources to photosynthetic tissue over structural tissue.

Meristematic limitations may affect the capacity of some grasses (Richards & Caldwell 1985) and shrubs (Hobbs & Mooney 1985) to respond to top removal. One would expect this constraint to be especially acute in seedlings. This does not appear to be the case for *Prosopis*. The 18-day-old seedlings in the most severe clipping regime (CC) initiated >10 shoots plant^{-1} over the 6-month period, all from buds activated at the cotyledonary node. No shoots originated from the cambium of the hypocotyl or from the cortical collar at the root/shoot interface, which is reported to be the primary mode of regeneration in juvenile and adult *Prosopis* plants (Haas et al. 1973). The high mortality of *Prosopis* seedlings observed under field conditions after four clippings (Table 3) thus appears to reflect environmental limitations on shoot development rather than a depletion of the bud bank.

Competition between grasses and *Prosopis* seedlings is primarily below ground (Van Auken & Bush 1997). However, one-year-old *Prosopis* seedlings can access soil moisture at depths not effectively exploited by grasses (Brown & Archer 1990), thus facilitating their co-existence and minimizing competition (Brown & Archer 1989; Bush & Van Auken 1991). In our field study, survival and growth of non-clipped seedlings were comparable on plots with extant and reduced herbaceous interference, suggesting that *Prosopis* and herbaceous plants may have been partitioning soil resources. However, root initiation, elongation, and survival are dependent upon the supply of photosynthate (Coyne et al. 1995) and each of these parameters is typically affected adversely by shoot removal (Briske & Richards 1995). Under field conditions, where water and nutrients are scarce and patchy, curtailment of root biomass production and elongation associated with top removal would reduce the capacity of *P. glandulosa* seedlings to acquire soil resources needed for meristem activation and shoot growth. Thus, clipping-induced reductions in root biomass (Figure 2) were likely responsible for the high rates of mortality observed among seedlings defoliated in the field (Table 3).

Although our growth chamber experiment indicated that *P. glandulosa* is well-adapted to cope with defoliation early in its life cycle, the realization of its potential tolerance to shoot removal under field conditions was relatively low. A variety of small mammals (e.g., *Lepus* spp., *Perognathus* spp., *Dipodomys* spp., *Cynomys* spp.; Vorhies & Taylor 1933, 1940; Arnold 1942; Glendening & Paulsen 1955; Simpson 1977; Nilson et al. 1987; Weltzin et al. 1997) and insects

(e.g., Geometridae, Psychidae, Noctuidae as reviewed in Simpson 1977) are known to feed on *Prosopis* stem and leaf tissue. Activities of these organisms could therefore impose a significant constraint to *P. glandulosa* seedling establishment. The fact that *P. glandulosa* abundance has increased markedly over the past century therefore suggests that (1) utilization of *Prosopis* seedlings by herbivores is rare, infrequent, or sporadic, (2) periodic mast production of seed and episodes of widespread dispersal and germination (as by livestock [Brown and Archer 1989]) produces more seedlings than herbivores can consume (i.e., predator satiation), and/or (3) *Prosopis* seedlings establish during periods of low herbivore density and grow to sufficient size to 'escape' or better tolerate defoliation before herbivore densities increase. Additional experiments are needed to test these hypotheses.

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