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Growth and Architecture of Small Honey Mesquites under Jackrabbit Browsing: Overcoming the Disadvantage of being Eaten

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Browsing is an important mortality factor in seedlings and small plants. However, the induced changes in the architecture of plant survivors may influence subsequent browsing, opening the possibility of compensating for the damage done. How jackrabbit (*Lepus californicus*) browsing affects the growth and architecture of small individuals of honey mesquite, *Prosopis glandulosa* var. *torreyana*, a tree/shrub that produces spines at every node, was explored. Naturally established mesquites of unknown age were selected in one site, and 2-year-old mesquites were transplanted in another site. In both cases, half of them were exposed to jackrabbits and the other half were excluded as controls. After 4 years, shoot production (height, length and number of derived shoots) and plant growth (height and cover) increased 1·4–2·5-fold in naturally established controls relative to exposed plants, depending on the measured variable. In the transplant experiment, the increases were 2·8–7·1-fold in controls relative to exposed plants 2 years after initiation of the experiment. The net loss of biomass in treatment *vs.* control plants in these experiments suggests a negative response to browsing which has been defined as under-compensation. Alternative architectures in honey mesquites were evident at the end of the exclusion experiments: controls had long branches and an extended crown cover, while exposed plants had short branches and a compact crown cover. Results indicated that mesquites were able to grow under browser pressure by packing many stems in a compact matrix armed with spines and producing one or more shoots tall and wide enough to escape from jackrabbits. © 2003 Annals of Botany Company

Key words: Exclusion treatments, honey mesquite, jackrabbit browsing, *Lepus californicus*, spines as mechanical defences, plant architecture and growth, *Prosopis glandulosa* var. *torreyana*, semi-arid communities, stem modular demography.

INTRODUCTION

Through their effect on reproduction, growth and dispersion, herbivores can change the structure of plant communities (McNaughton, 1984, 1988; Risenhoover and Maass, 1987; Dirzo and Miranda, 1991; Huntly, 1991). In arid environments, cattle have become one of the main regulators of the structure and function of grasslands and scrublands (Fisher, 1977; Scholes and Archer, 1997). However, in these and other ecosystems (Huntly and Inouye, 1988; Ostfeld and Canham, 1993), small mammals are typically the most pervasive herbivores. For example, herb and forb cover increased when rodents or lagomorphs were experimentally excluded in North and South American semi-arid zones (Brown and Heske, 1990; Gibbens *et al*., 1993; Gutiérrez *et al*., 1997).

The initial effect of herbivory is mostly demographic (through enhanced mortality), followed by structural impacts that increase as the surviving plant develops. Herbivores cause persistent damage to meristems, buds, leaves and/or stems. Damage to apical meristems or stem segments may also induce the production of new leaves and shoots (Seen and Haukioja, 1994), allowing plants to compensate for the damage done (Danell *et al*., 1985). In this paper the definitions of Belsky (1986) are adopted, where over-compensation, exact compensation or under-compensation are understood as differences in size gain and/or reproduction of browsed plants which are significantly greater, equal or lower, respectively, than unaffected control plants. Plant compensation depends on growth form (Archer and Tieszen, 1980), meristem availability (Richards and Caldwell, 1985) and timing of herbivory (Danell and Bergström, 2002), and may vary due to light availability, soil humidity and soil texture (Cox and McEvoy, 1983; van der Meijden *et al*., 1988; Maschinski and Whitham, 1989). By promoting the development of lateral meristems and branching, herbivory also has important consequences for plant architecture (Whitham and Mopper, 1985; Du Toit *et al*., 1990; Danell *et al*., 1994).

Browsing may cause profuse basal branching and maintain plants at an early stage of growth and development (Bryant *et al*., 1983; Archer, 1995). However, Paige and Whitham (1987) found that seedlings of the biennial herb *Ipomopsis aggregata* (Pursh) V. Grant. (Polemoniaceae) produced multiple stems after damage by herbivores instead of a single apical-dominant one. If each stem bears flowers, more seeds are produced and basal branching will thus have an adaptive value. Such consequences are difficult to follow

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in long-lived plants (Whitham *et al.*, 1991), and the study of compensation after browsing should then be methodologically divided into growth stages. In this respect, there seems to be a strong selection for chemical (Bryant, 1981; Chapin *et al.*, 1985) and physical (Cooper and Owen-Smith, 1986; White, 1988) defences in juveniles that may be relaxed in adults, especially if defences are metabolically costly (Strauss *et al.*, 2002). In adult plants, the production of longer spines as induced defences due to browsing have been demonstrated (Young, 1987; Gómez and Zamora, 2002), but their length may be again reduced if herbivores are excluded (Young and Okello, 1998). Spines and prickles physically deter the access to food by small mammals (Cooper and Ginnett, 1998) and increase the handling time of herbivores per unit of food ingested (Cooper and Owen-Smith, 1986). Finally, plants within a population may have different susceptibilities to herbivores and can become more (Ernest, 1994) or less (Du Toit *et al.*, 1990) resistant after damage, probably depending on the genetic basis of resistance and whether they produce chemical and/or physical defences (Karban and Baldwin, 1997).

The purpose of the study described here was to explore the effects of jackrabbits (*Lepus californicus* Gray) (Lagomorpha, Leporidae), an important primary consumer in arid and semi-arid zones of North America (Best, 1996), on the modular growth and architecture of small plants and saplings of the honey mesquite, *Prosopis glandulosa* var. *torreyana* (L. Benson) MC Johnston (Fabaceae), a spine-producing woody plant which is a conspicuous component in many semi-arid communities of the Chihuahuan and Sonoran deserts, where it may function as the nucleus of plant clustering (Archer *et al.*, 1988) and of 'islands of fertility' (De Soyza *et al.*, 1996). Species of *Prosopis* (*P. glandulosa* and *P. juliflora*) are preferentially chosen by jackrabbits in the few areas where their diets have been described (Hoagland, 1992; Daniel *et al.*, 1993). In the study site described here, jackrabbit browsing accounted for a 40 % mortality of honey mesquite shoots lower than 0·6 m (López-Portillo *et al.*, 1996). Lastly, the geographic distribution ranges of both browser and plant overlap quite well (Rzedowski, 1988; Best, 1996), suggesting a long relationship. Through a whole-plant and modular approach, the answers to the following questions were sought: How do small mesquites grow under constant browsing pressure? Are there inter-individual susceptibilities to jackrabbits? How does browsing modify mesquite architecture?

MATERIALS AND METHODS

Study site

The study site is within the Bolsón de Mapimí, a closed basin in the Chihuahuan Desert (103°44′W, 26°41′N, 1170 m altitude), at the junction of the states of Chihuahua, Durango, and Coahuila, Mexico. Average annual rainfall is 264 mm, 71 % occurring in summer (62 % at the end of this season) and 9 % in winter showers. Mean annual temperature is 20·8 °C with a seasonal variation of 16·2 °C, and a mean daily range of 20 °C (Cornet, 1988). Vegetation consists of xerophytic scrub (Rzedowski, 1978) or Chihuahuan Desert scrub (Brown, 1982). The study area was in scrubland dominated by *P. glandulosa* var. *torreyana*, *Larrea tridentata* (DC) Coville (Zygophyllaceae), *Opuntia rastrera* Weber and *O. leptocaulis* DC. (Cactaceae).

Plant species

The honey mesquite, *Prosopis glandulosa* var. *torreyana*, is a common and frequently dominant long-lived woody perennial that grows as a tree or shrub in the Chihuahuan desert. This and other species of *Prosopis* are considered as facultative phreatophytes, i.e. with roots that can take water from shallow and deep soil horizons (Ansley *et al.*, 1990). The buds from a mesquite shoot may produce leaves, spines (modified shoots; Mooney *et al.*, 1977) and inflorescences (if reproductive). Each new shoot consists of a series of nodes and internodes and each node may produce a leaf plus two or three apical meristems (Mooney *et al.*, 1977). In our study site, leaf, shoot and inflorescence production was simultaneous and occurred from March to May, although shoot growth can continue at a slower rate until September. The taller and reproductive mesquites loose their leaves completely in January (López-Portillo *et al.*, 1996), but small mesquites were observed to be capable of producing new shoots all year round. Shoots produced in a recent growing period are easily distinguishable from former shoots, since spines are flexible. Spine flexibility is lost within the first months after shoot expansion. In small (<0·60 m height) mesquites from the study site, median spine density in shoots was 1·1 spines cm^{-1} and spine length was 1·2 ± 0·03 cm (average ± s.e., n = 50 shoots from different trees; A. Martínez, unpubl. res.). However, several branches may overlap, increasing spine density per unit area.

Animal species

The black-tailed jackrabbit *Lepus californicus* is distributed along the highlands of Mexico, from north of Sonora and Baja California to Hidalgo and south of Querétaro, and is the most common jackrabbit species in western United States of America, from the Pacific coast to western Missouri and Arkansas, and from South Dakota southward to Texas (Best, 1996). The individuals are solitary and territorial, and display greater activity at early morning (Flux and Angermann, 1990). Their home range can vary from 16 to 20 ha and their population density from 0·2 to 2·5 individuals ha^{-1}, depending on season and quality of the environment (Dunn *et al.*, 1982; Daniel *et al.*, 1993). The estimated population density around our study site, obtained by night tallying during a 3-year study period (April 1996 to November 1999), was as low as 1·9 individuals ha^{-1} in March 1999 and as high as 3·9 in June 1997 (G. L. Portales, L. Hernández, F. Cervantes; Instituto de Ecología, AC and Instituto de Biología, UNAM, unpubl. res.).

When standing up, jackrabbits cannot reach higher than 0·7 m, so their effect is restricted to seedlings, relatively small plants and low branches of taller plants. They browse a wide range of perennial plants like *Prosopis glandulosa*,

FIG. 1. Naturally established small honey mesquites (*Prosopis glandulosa* var. *torreyana)* in a scrubland within the Northern Chihuahuan desert. A plant with two relatively tall stems surrounded by a dense mass of lower ones is shown at front left. The arrow at the upper right points to a plant excluded from jackrabbit (*Lepus californicus*) browsing; the arrow at the front points to a control plant, where tags can be distinguished. The footprint at the front is 30 cm long.

Larrea tridentata, *Opuntia rastrera* and *Machaerocereus gummosus* (Engelmann) Britton & Rose (Cactaceae) and may also feed on annual plants and forbs when available during the rainy season (Steinberger and Whitford, 1983; Ernest, 1994; Mandujano *et al*., 1998). *Prosopis* species such as *P. glandulosa* or *P. juliflora* account for 10–56 % of lagomorph diets (Vorhies and Taylor, 1933; Nilsen *et al*., 1987; Hoagland, 1992; Wansi *et al*., 1992). Jackrabbits may eat up to 390 g and produce an average of 545 faecal pellets per day (Best, 1996). They affect a larger proportion of plant tissue than they consume, since they cut down the shoots to minimize search time for leaves and buds and thus the risk of predation while feeding, leaving much of the bark and wood intact. It was noted also that some stems are cut down to open up space below the shrubs that can be used as refuges. Based on the measurements of 1050 shoots distributed among 60 trees, the average ± s.e. diameter of stems at the point of browsing was 3·5 ± 0·9 mm; the minimum and maximum diameters were 1·36 and 6·76 mm, respectively (A. J. Martínez, unpubl. res.). By comparison, the maximum diameter of stems browsed by moose feeding on *Betula pendula* and *B. pubescens* was less than 4 mm (Danell *et al*., 1985) and large browsers, such as giraffes and impalas, cut stems of *Combretum apiculatum* (Bergström *et al*., 2000) at diameters around 6 mm. The ability of jackrabbits to browse stems of equal or greater diameter than those consumed by much larger animals may be explained by the fact that large browsers eat mostly leaves and young shoots, while jackrabbits cut older stems to feed on young shoots, buds, leaves and bark.

Sampling method and exclusion treatments

A 100 × 100 m undisturbed plot with natural vegetation was subdivided into 10 × 10 m subplots to aid in the plant census. All mesquite plants were numbered regardless of their size and their location registered in a Cartesian coordinate system. The following were measured on every mesquite plant: individual height; the longest and shortest canopy diameters, which were used to estimate crown cover; and the diameter of the thickest basal branch. The 524 plants measured ranged in height from 0·04 to 3·3 m, from 0·2 to 18·5 cm in maximum stem basal stem diameter, and from 0·001 to 29 m^2 in crown cover. On the database, the mesquites were grouped by cover and height and a subgroup of plants that were 0·1–0·6 m tall and with 0·06–0·6 m^2 cover (277 mesquites), the sizes most susceptible to jackrabbit browsing, was separated. From that subgroup, 60 mesquites were randomly chosen for the experiment. Each selected plant was randomly assigned to a treatment with or without jackrabbit exclusion, 30 plants per treatment. The plant enclosures, 0·7 m high, square or circular in shape and closed at the top (Fig. 1) were constructed using a 0·025-m aperture metallic mesh.

Crown cover and height of the taller shoot of the selected plants were measured at yearly intervals from July 1996 to November 2000. Also in July 1996, the length and height of ten recent shoots, evenly distributed on each plant, were marked and measured. To represent the spring–summer and autumn–winter seasons, shoot length and height from base were measured, the number of secondary (current season) shoots, and the number of shoots bitten by browsers at 6-month intervals from December 1996 to July 1998, and later in July 1999 and November 2000 were counted. The total (cumulative) length of each tagged shoot was calculated as the sum of all shoots derived from it at every measurement occasion. Average plant height was considered as the mean height of the tagged shoots since these were evenly distributed within the individual.

Since the age of the naturally established plants could not be determined, a similar experiment was also conducted with 2-year-old plants that were grown from seeds from 20 mesquites in $9 \times 6 \times 12$ cm containers filled with clayey soil from our 1-ha study site. Sixty plants (hereafter referred to as transplanted mesquites) were randomly selected from a pool of 200 and in July 1996 were transplanted at random within a 25×25 m bare area about 1 km from the 1-ha site, excluding half of them from jackrabbits as previously described. This area lacked plant cover because it was part of an abandoned airstrip made within a scrubland similar to the 1-ha site. The same variables were measured as in the previous experiment and at the same time intervals, except that in this experiment all derived shoots were measured. Data corresponding to whole plants in naturally established and transplanted mesquites, when considering cover and maximum and average height, were used. However, the number of current and bitten shoots, and current and total (accumulated) shoot length were calculated on a stem basis in naturally established plants and on a whole plant basis in transplanted mesquites due to their much smaller size.

Data analyses

Repeated-measures ANOVAs (using module DGLM, Statistica for Windows, StatSoft 2000) was used, one for each of the response variables, to test the effect of exclusion through time. For every plant, the numbers of seasonally produced (current) shoots and of shoots bitten by browsers per (initial) shoot in naturally established plants per plant in transplanted mesquites were obtained, and log-transformed prior to analysis. Multiple comparisons (Scheffé tests; Zar, 1999) and 95 % confidence intervals were used to determine if there were significant differences between the experimental factors or their interactions.

Spearman-rank correlations between sampling dates were conducted to determine if shoot production was consistent through time in both excluded and non-excluded plants, generating a total of 15 possible correlations per treatment. The sequential Bonferroni technique was used to increase the power of detecting more than one false null hypothesis while making many simultaneous tests (Rice, 1989; Ernest, 1994). The same statistical methods were used to explore if browser damage in non-excluded plants was proportional to shoot production within and between sampling dates (36 correlations), since damage done by browsers in one time interval could affect future shoot production, and because greater shoot production may lure browsers towards certain plants. Finally, it was investigated whether there were different susceptibilities to browsing (i.e. were some plants consistently browsed in time while others were not?) during the six sampling dates comprising the study period (15 correlations).

RESULTS

Plant survival and inflorescence production

Three exposed naturally established plants and two plants inside enclosures died during the study period, a total of five plants out of the 60 (8·3 %) used in this experiment. Since the number of dead plants was similarly low between treatments, there was no evidence that browsers had a significant impact on the survival of these naturally established exposed mesquites. In contrast, there were significant differences between exclusion/non exclusion treatments in the survival functions of transplanted mesquites (Wilcoxon test, $\chi^2 = 18{\cdot}8$, 1 d.f., $P < 0{\cdot}0001$). Thirteen exposed mesquites compared with only five controls died by December 1996, 6 months after transplanting. Half of the exposed plants died by December 1997, whereas half the controls died by July 1998. Since the treatments were randomly assigned, it is inferred that greater mortality at these stages was due to browser exposure. This inference is supported by the field notes, which indicated that plants outside enclosures died after most basal meristems were removed by browsers. Although the exact causes of death of these plants were ignored, they were possibly unable to recover from browsing damage (i.e. resume growth) because they had few remaining meristems or no meristems at all. Differences in survival between treatment and control plants decreased through time, finally resulting in 80 % mortality of controls and 90 % in exposed plants 4 years after transplanting, probably due to water stress. In March 2001, almost 5 years after the exclusions were placed, five naturally established mesquites within enclosures produced a few inflorescences (two to five) while none of the exposed plants produced them. None of the surviving transplanted mesquites within enclosures produced inflorescences.

Data censoring

As a consequence of the high mortality in transplanted mesquites, it was not possible to analyse the whole data series due to missing data and it was decided to restrict it to the dates where there were at least seven surviving plants exposed to browsers and ten controls, eliminating the other plants from the database. Consequently, the reported results for the transplanted mesquite experiment encompass a 2-year period, from July 1996 to July 1998. To be consistent between experiments, the five trees that died in our naturally established site were also eliminated, giving a total of 27 plants exposed to browsers and 28 controls for our repeated-measures ANOVAs (in this case the analyses encompassed the complete 4-year period of the experiment).

Plant size

There were significant differences between control and exposed plants in crown cover, average plant height, and maximum stem height both in naturally established and transplanted mesquites ($P < 0{\cdot}001$). The interaction between sampling date and jackrabbit exclusion treatment was also significant in all cases ($P = 0{\cdot}003$), indicating that differences between treatments increased with time. In naturally established plants excluded from browsers, there were significant increases in crown cover and average and maximum height (Fig. 2A–C), while final values for these characteristics in exposed plants were similar to those at the

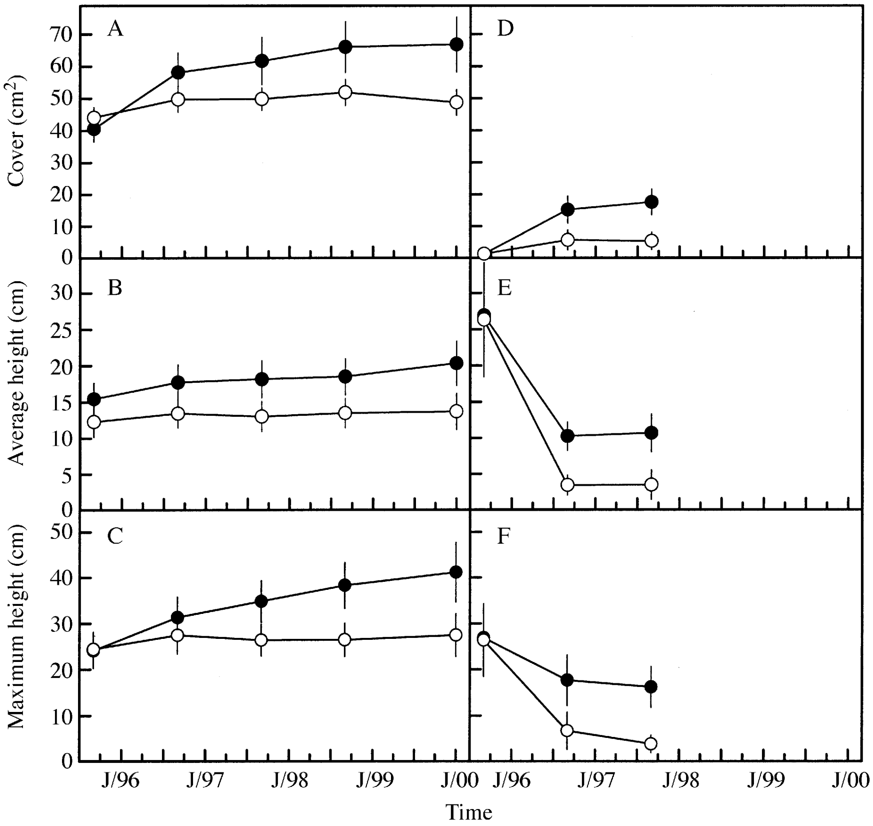

FIG. 2. Crown cover (A and C), and average (B and D) and maximum (E and F) shoot height over a 4-year period for naturally established (A–C) and 2-year period for transplanted (D–F) mesquites excluded from (filled circles) or exposed to (open circles) jackrabbits in the Northern Chihuahuan desert. Vertical lines indicate 95 % confidence intervals. Data in D–F were truncated due to plant mortality and the consequent loss of degrees of freedom. J, January followed by the year of measurement.

beginning of the experiment. As in the naturally established mesquites, there was a significant increase through time in the cover of transplanted mesquites within browser exclosures and none in exposed plants (Fig. 2D). Dieback after transplanting reduced average and maximum plant height, but such loss was greater in exposed plants than in controls, indicating that browsing added to dieback (Fig. 2E and F).

After 4 years, it was found that cover, average height, and maximum height were 37 % (66·7 *vs.* 48·7 cm^2), 48 % (20·3 *vs.* 13·7 cm) and 50 % (41·1 *vs.* 27·4 cm) greater, respectively, in naturally established controls *vs.* exposed plants. In the same order as these size variables, the differences between control and exposed plants after 2 years in transplanted mesquites were 411 % (32·2 *vs.* 6·3 cm^2), 175 % (17·3 *vs.* 6·3 cm) and 609 % (23·4 *vs.* 3·3 cm) greater when comparing control with exposed plants. Architectural differences between excluded and non-excluded mesquites were increasingly evident in time: exposed plants were more compact in form than excluded plants. Since the plants from both treatments produce a similar amount of shoots per unit time, and what varied was their individual length, shoots were intertwined in a smaller area in the exposed plants. As a consequence, spines were more concentrated on a unit volume basis, possibly restricting jackrabbit access to some parts of the plant.

Shoot size and browsing

There were no significant differences (P = 0·4) between treatments in the number of current shoots per stem in naturally established mesquites and per plant in transplanted mesquites, but there were significant differences (P = 0·007) between treatments in the number of bitten shoots, and in their current and total length. The treatment × sampling date interactions were significant in all cases (P = 0·02) except two (number of current and of bitten shoots, P = 0·3), for the transplanted mesquites. The current shoots per stem × sampling date interaction in naturally established mesquites was due to lower production in exposed plants in July 1999 (Fig. 3A). The number of current shoots per plant tended to decrease in exposed transplanted mesquites by the second year, but was always similar between treatments (Fig. 3B). The number of bitten shoots per plant was negligible within enclosures, but the average in the exposed plants tended to increase from 0·3 to 1·7 bitten shoots per stem in naturally established mesquites and varied somewhat (two or three bitten shoots per plant) in transplanted mesquites (Fig. 3C and D). Jackrabbit bites are characterized by a clean diagonal cut, while mule deers (*Odocoileus hemionus,* Cervidae) and cows leave fibres at the surface; no such cuts were recorded in exposed parts. From the initiation of the experiment, current (Fig. 3E and F) and total (Fig. 3G and H) shoot length tended to increase

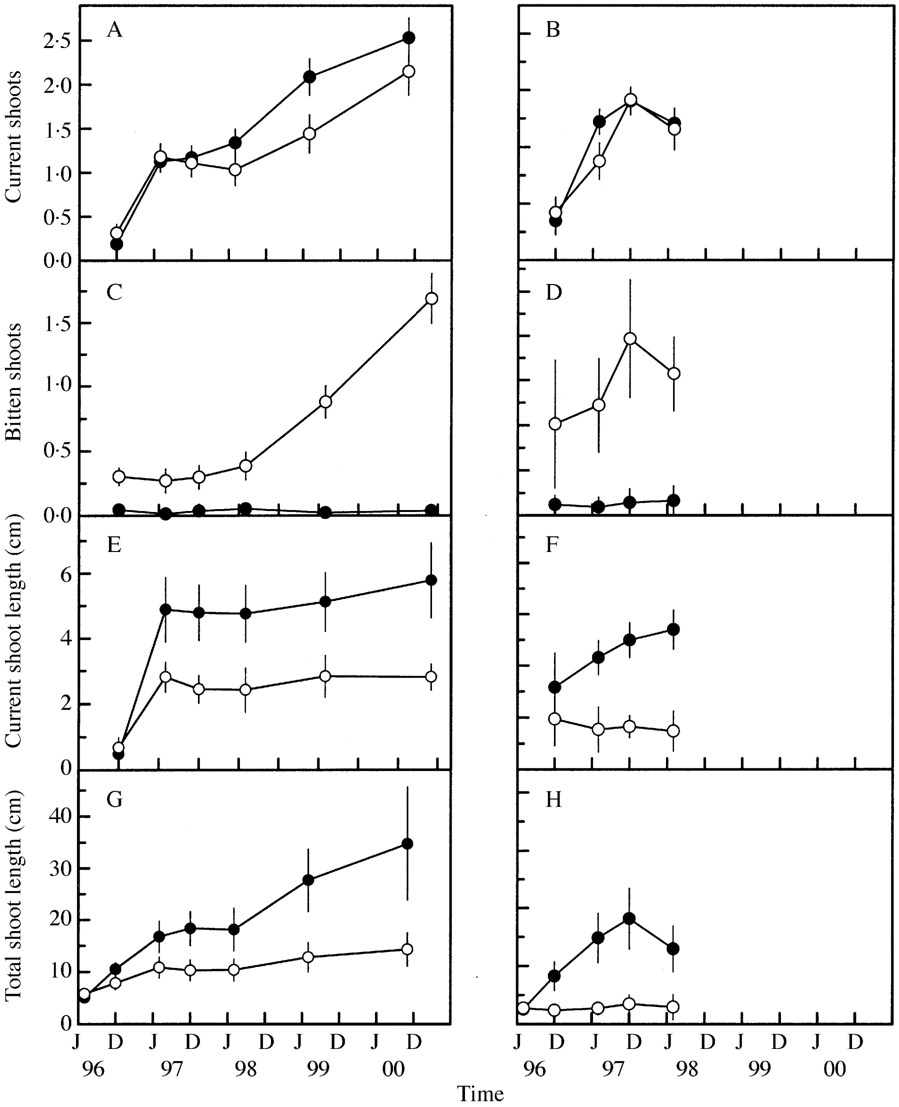

FIG. 3. Current shoots (A and B), bitten shoots (C and D), current shoot length (E and F) and total shoot length (G and H) per stem of naturally established mesquites (left), and per plant in transplanted mesquites (right) either excluded from (filled circles) or exposed to (open circles) jackrabbit browsing. Vertical lines indicate 95 % confidence intervals. Data in B, D, F and H were truncated due to plant mortality and the consequent loss of degrees of freedom. J and D in the abscissae correspond to January and December; numbers below indicate year of measurement.

within enclosures in both naturally established and transplanted mesquites. Both shoot lengths increased much less in naturally established exposed plants, and did not change in transplanted mesquites. In other words, plants exposed to jackrabbits had either little or no shoot growth.

At the end of the experiments, current shoot length of control *vs.* exposed plants was 100 % greater (2·8 cm *vs.* 5·8 cm) in naturally established mesquites and 290 % greater (1·4 cm *vs.* 5·4 cm) in transplanted mesquites. Total shoot length was 150 % greater (14 cm *vs.* 34·7 cm) in naturally established mesquites and 340 % greater (29·3 cm *vs.* 129 cm) in transplanted mesquites.

Stem height increase

When comparing maximum stem height in January 1996 with that of November 2000 (Fig. 4), we found that all naturally established controls gained height or at least did not loose it, as indicated by their values above and over the 1 : 1 slope line (Fig. 4, filled symbols). An interesting result is that after 4 years, 16 of the surviving 27 exposed plants did not loose height and that six of them increased their maximum height by at least 50 % of their initial value (Fig. 4, open symbols).

Correlations within and between dates in shoot production and browsing

Because patterns in plant and stem dimensions in naturally established and transplanted mesquites have similar trends, and due to high mortality and the consequent loss of degrees of freedom in transplanted mesquites, only patterns for naturally established plants were reported. In these, seasonal shoot production was correlated with

TABLE 1. *Spearman rank correlation coefficients for the number of shoots per stem at time* t vs. *the number of shoots per stem at time* t + i (i = *each of the sampling dates) in naturally established mesquites exposed (above diagonal) or excluded (below diagonal) from jackrabbit browsing*

	Dec. 1996	July 1997	Dec. 1997	July 1998	July 1999	Nov. 2000
Dec. 1996	–	**0·49**	**0·46**	0·40	0·19	0·02
July 1997	**0·50**	–	**0·90**	**0·79**	**0·63**	**0·52**
Dec. 1997	**0·71**	**0·74**	–	**0·83**	**0·56**	**0·51**
July 1998	**0·66**	**0·68**	**0·81**	–	**0·74**	**0·56**
July 1999	0·23	**0·46**	**0·59**	**0·66**	–	**0·78**
Nov. 2000	0·27	**0·51**	**0·55**	**0·66**	**0·64**	–

All correlations in bold are significant ($P < 0{\cdot}02$) after sequential Bonferroni correction; $n = 30$, except correlations with November 2000 ($n = 27$).

TABLE 2. *Spearman rank correlation coefficients of the number of bitten* vs. *the number of current shoots per stem for six sampling dates in naturally established mesquites exposed to jackrabbit browsing*

		Current shoots					
		Dec. 1996	July 1997	Dec. 1997	July 1998	July 1999	Nov. 2000
Bitten shoots	Dec. 1996	0·17	0·06	0·28	0·11	0·22	0·05
	July 1997	0·08	0·11	0·07	0·01	-0·26	-0·18
	Dec. 1997	0·17	0·22	0·13	0·34	0·33	0·21
	July 1998	0·08	0·23	0·04	0·23	0·19	0·42
	July 1999	0·52	0·42	0·51	**0·68**	**0·66**	0·43
	Nov. 2000	0·13	0·15	0·29	0·37	0·42	**0·78**

All correlations are non-significant ($P > 0{\cdot}05$) except for three shown in bold, where $P < 0{\cdot}0001$ after sequential Bonferroni correction; $n = 30$, except correlations with November 2000 ($n = 27$).

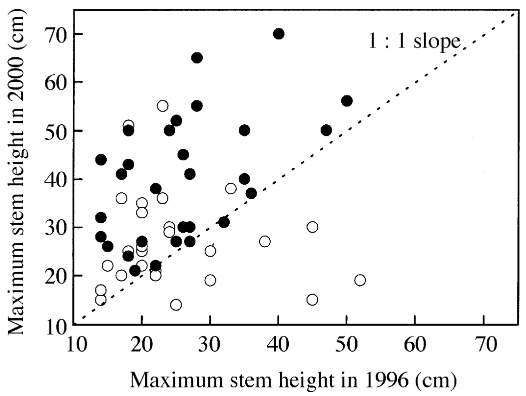

FIG. 4. Maximum stem height in the year 2000 vs. maximum stem height in 1996 for naturally established small mesquites excluded (filled circles) or exposed (open circles) to jackrabbit browsing in a Northern Chihuahuan desert scrubland. The diagonal line indicates the 1 : 1 slope.

previous shoot production in both control and exposed plants, as indicated by the highly significant and positive Spearman rank correlation coefficients after sequential Bonferroni corrections (Table 1). Correlation coefficient values were similar in control and exposed plants (paired *t*-test, $P = 0{\cdot}6$; Zar, 1999) and tended to increase as measurement dates became closer in time. The five non-significant correlations in both treatments corresponded to the measurements most distant in time.

The correlation coefficients of the number of bitten *vs.* current shoots were non-significant in 33 out of 36 cases (Table 2), and did not tend to increase as dates were nearer in time as observed above. The three significant and positive correlations were obtained when correlating the number of bitten shoots in the July 1999 with the number of current shoots for that date and the previous one (July 1998), and the number of bitten *vs.* current shoots in November 2000. There were no significant Spearman rank correlations even before sequential Bonferroni corrections in the number of bitten shoots among sampling dates (r_s range: –0·19–0·36, $P > 0{\cdot}05$, $n = 30$ except for November, when $n = 27$), suggesting that there was no selective browsing among plants. There was also no consistent increase in the value of the correlation coefficients as dates became closer in time.

DISCUSSION

Plant survival, nodes and meristems, and inflorescence production

Weltzin *et al.* (1997) found that the chances of survival of 1-year-old *Prosopis glandulosa* var. *glandulosa* seedlings were reduced by 50 % after 3 months of exposure to prairie dogs, and concluded that these herbivores 'suppressed rather than eliminated' *Prosopis* from the colony site. By analogy, the emphasis on the discussion of the results presented here is on how the surviving mesquites were able to tolerate jackrabbit browsing pressure. The experiment concerning transplants suggests that browsing of 2-year-old (in the case described here) mesquite saplings may result in their death, especially if they consist of one or two basal stems that may be cut below or very near the most basal internode. If the internodes were below ground or were not cut, further regrowth by branching near the base would protect the stem–root connection and the plant may survive (cf. Van Auken and Bush, 1989; Weltzin *et al.*, 1998). In this way, browsers such as jackrabbits modulate plant size and architecture at early stages of growth.

The architecture of naturally established mesquites is considered a response to continuous browsing; when a small stem is browsed, the remaining segment may develop new shoots whose density will not allow or deter jackrabbit access to basal stem parts, a reason why mortality was very low. Mesquites are able to survive browsers by augmenting, even under strong browsing pressure, a reserve of meristems that allow them to develop an architecture that protects the vital root–shoot connection. On a unit stem length basis, the meristem reserves are greater in small (approx. 60 cm height) than tall (approx. 2–3 m height) trees: small mesquites produce a median of 1·1 nodes cm^{-1} while taller mesquites produce half as much (0·6 nodes cm^{-1}) ($P <$ 0·001, Mann–Whitney rank test, $n = 50$ stems distributed in 50 plants per size; A. J. Martínez, unpubl. res.). In this way, a 30-cm-long stem in a small plant would have 33 nodes (each with up to three meristems), while a similar stem in a tall plant would have only 18 nodes. Such characteristics are advantageous for the plant under constant browsing pressure, especially if spines constitute mechanical defences (Cooper and Owen-Smith, 1986). In the studied species, spines are shorter in small than in mature plants (1·2 ± 0·03 cm *vs*. 2·3 ± 0·09; A. J. Martínez, unpubl. res.).

Eighteen per cent of naturally established mesquites produced inflorescences nearly 5 years after exclusion, indicating that browsing delays sexual reproduction, as has been reported for other species (Whitham *et al.*, 1991). None of the transplanted mesquites within enclosures produced inflorescences, probably a consequence of their smaller dimensions when compared with naturally established plants.

Plant size, shoot size and browsing

The average dimensions of naturally established and transplanted mesquites exposed to browsers remained the same during the experiment (i.e. there was no significant net growth) because the new tissue produced every season only replaced that lost by browsing. When comparing exposed plants with controls, it was found that small mesquites in the two study groups definitely under-compensated for jackrabbit browsing. Further, by comparing current shoot production with bitten shoots, it was estimated that jackrabbits affect more than half of the newly produced shoots. It is important to consider that even though there was an initial dieback due to transplant stress in the 2-year-old transplanted saplings, all size-related attributes were greater in the plants excluded from jackrabbits, showing that browsing definitely adds to dieback.

It was expected that jackrabbit browsing would break apical dominance of small mesquite plants and cause them to branch more than controls, as has been reported for other browsers and plant species (Maschinski and Whitham, 1989; Seen and Haukioja, 1994; Tuomi *et al.*, 1994; McLaren, 1996). However, although stem length was shorter in exposed plants, the number of current season shoots per stem was similar to that produced in the controls, which contrasts with the results reported on two species of birch (Danell *et al.*, 1985) in which the number of shoots and the frequency of terminal bud abortion decreased following browsing by moose. It is possible that browsing-induced branching prior to the start of experiments continued after 4 years following the establishment of exclosures (Gadd *et al.*, 2001). It may also be possible that it is a consequence of a high node/meristem density, weak apical dominance (Haukioja, 1991) and reduced competition among shoots (Du Toit *et al.*, 1990). Nevertheless, the result is a higher stem density per unit area in exposed plants (cf. Massei *et al.*, 2000). It is not only the amount of spines per unit length of stem that is important as a browser deterrent, but also the tri-dimensional arrangement among stems, as can be inferred from the feeding behaviour of browsers (Cooper and Owen-Smith, 1986; Coe and Coe, 1987; Cooper and Ginnett, 1998; Pisani *et al.*, 2000).

Correlations within and among dates in shoot production and browsing

From the results related to Spearman rank correlations, three aspects emerge. (1) The significant and positive correlation coefficients between current and previous shoot production indicated consistency among plants (i.e. that plants that produced more shoots always did). Also, since there were no significant differences in the Spearman coefficient values between treatments, there seems to be no browsing-induced response in this case. (2) When comparing the number of current shoots with the number of bitten shoots, it was found that in 33 out of 36 cases the correlations were not statistically different from zero. This indicates that browsers do not have a clear tendency to select the stems/plants that produce more shoots. (3) There were no within-plant correlations in the number of bitten shoots at the different sampling dates. Such a correlation (indicating that some mesquites are consistently browsed while others are not) would be expected if there were an induced resistance, as Ernest (1994) observed in *Larrea tridentata*.

Little literature concerning chemical defences against herbivores in *Prosopis* species was found. Cates and Rhoades (1977) found more alkaloids in younger than older *Prosopis* leaves and that these compounds seemed to be effective as defences against generalist species (which preferred older leaves), but not against mono- or oligophagous species, which preferred younger leaves due to their higher nitrogen content. Species considered by Cates and Rhoades (1977) were in the Lepidotera and Hymenoptera. Other compounds involve gums (Bemiller, 1989), but these monosaccharides may act as mechanical defences against xylophagous Coleoptera. Although a thorough analysis of secondary compounds is wanting, it appears that honey mesquites depend exclusively on their spines for protection against small browsers; this may not be so for other species of *Prosopis* (Pisani *et al.*, 2000).

Plant architecture

Browser pressure was so pervasive that, by the end of the experiment, the general appearance of exposed mesquites was different from the controls in both naturally established and transplanted mesquites. Stems and current shoots of exposed plants were shorter, giving them a more compact appearance, armed with spines. Further, the prostrate, multistemmed growth of exposed plants gave them a carpet-like appearance (Fig. 1) analogous to a grazing lawn (McNaughton, 1984), as Du Toit *et al.* (1990) also found for two species of *Acacia* in Africa. However, while grazed (as compared with ungrazed) lawns have a higher biomass per unit area because more individuals and species are packed as a consequence of the reduction in plant height and interindividual competition, jackrabbit browsing did not increase any of the individual mesquite biomass indicators we used. On the other hand, the architecture of protected plants changed from a concentrated, compact form to a more extended and dispersed one when compared with browsed plants. This is similar with what Vourc'h *et al.*, (2002) found in young *Thuja plicata* trees browsed by the Sitka black-tailed deer (*Odocoileus hemionus sitkensis*). Heavily browsed trees were stunted and branched at the base, whereas lightly browsed trees were taller and had one basal stem.

The differences in plant architecture may have consequences on photosynthetic efficiency (Valladares and Pugnaire, 1999). By producing many stems, the plant may generate a microhabitat in which self-shading reduces photoinhibition. Transpiration may also be reduced due to the decrease in radiation input and to the creation of a relatively homogeneous boundary layer around the plant. A trade-off would then result; the compact growth form may be beneficial to the plant in terms of structural photoprotection, but vertical growth would be more efficient as a means to escape jackrabbit browsing and of increasing the likelihood of sexual reproduction by growing to the dimensions needed to produce flowers.

Shoot escape from browsing

Jackrabbit browsing equalled average vegetative growth as indicated by the null net positive growth of exposed plants. However, we could expect a threshold beyond which jackrabbit browsing stopped if there is a trade-off between handling time, which increases with spine density (Cooper and Owen-Smith, 1986; Gowda 1997; Cooper and Ginnett, 1998) and predation risk (Nilsen *et al.*, 1987; Lagos *et al.*, 1995). For this reason, browsers may miss one or more stems and the relative independence of these intact stems would result in their greater growth when compared with browsed stems (Milewski *et al.*, 1991; Myers and Bazely, 1991), a view which rests on the source–sink hypothesis of Haukioja (1991). If this process continues, stems may reach a size greater than that which can be severed by jackrabbits and, in this way, escape browsing. Twenty-two per cent of the small (<0·6 m in height) mesquites within our 1-ha site had one or two tall stems surrounded by a lower and denser crown and, within our study period, the stems of some of the exposed naturally established individuals increased their height at rates similar to the controls. If this is the case, there would be no need for an induced chemical response to avoid browser damage, contrary to what Ernest (1994) found in *Larrea tridentata* (a spineless species), in which susceptibility to jackrabbits was variable among, but consistent within, plants.

Only the juvenile phase of the plant life cycle was included in the present study and these data provide little information on the effect of browsers in plant sexual reproduction and ultimately plant fitness (Crawley, 1987). The effect of grazers and other herbivores on long-lived plants is limited to the height they can reach and the tissues they consume and/or damage (Milewski *et al.*, 1991; Haukioja and Honkanen, 1997). Heavy pruning, either experimental or due to browsing, has been long shown to cause the reversal of reproductive woody plants to a juvenile, non-reproductive phase which would be more resistant to browsing (Moorby and Wareing, 1963; Kozlowski, 1971; Bryant *et al.*, 1983; White 1988).

By experiment, it is documented here that, even under continuous browsing and even if plants under-compensate for browser damage, mesquites are able to grow a few stems that will eventually reproduce. There may be many examples in other parts of the world of such browser-related changes in plant architecture. For example, Coe and Coe (1987) made several observations related to the response of African acacias to big and small mammalian browsers, such as 'hour-glass' and 'flattened shapes with vigorous adventitious growth in many species, where foliage is dense and flowering suppressed'. In other cases, flowering and fruit production 'are concentrated on the upper canopy, where the plant has 'escaped' beyond the reach of browsers'. An extreme example provided by Coe and Coe (1987) is the Kenyan endemic *A. thomasii*, 'which seems to concentrate its leaf growth naturally on the lower levels, with flowering limited to the tips of one or two long branches that arise from the centre of the bush and elongate 7–10 m, out of the reach of browsers'.

The exclosures employed in this experiment were semipermeable in the sense that jackrabbits were the only browsers excluded from the honey mesquite. However, browsing in controls was negligible and thus the observed effects on plant growth suggest that jackrabbits are the key mesquite browsers during the first stages of establishment and growth. It is suggested that shoot production and the resulting architecture of mesquites after browser damage may be of adaptive value, since it increases the probability of survival of small mesquites and also the probability of growth (albeit at a slower rate) and future reproduction.

In conclusion, several characteristics make small honey mesquites especially tolerant to browsing and possibly to other environmental factors such as radiation and water stress: (1) they have a high reserve of meristems even under browsing pressure; (2) under such pressure, the distribution of many short and spiny stems at a similar height would tend to form a compact structure that protects the root crown and thus genet survival; and (3) even if mesquites under-compensate for browsing damage, some develop at least one stem that grows tall enough to effectively escape jackrabbit browsing, thus increasing their chances to reproduce sexually. Since large browsers are absent in North and South American deserts, other small and medium-sized browsers, ranging from insects such as the twig-girdling cerambycids (A. J. Martínez, A. Eben, J. López- Portillo, unpubl. res.) to deer may be important for survival, growth, architecture and reproduction of the taller mesquites.

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