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Stem demography of *Prosopis glandulosa* var. *torreyana* in vegetation arcs and associated bare areas

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Abstract. Vegetation arcs are characterized by dense patches of up to 100 % plant cover surrounded by bare areas where cover is around 5 %. These patterns of contracted vegetation have been reported mainly in alluvial fans of arid and semiarid zones (known as *bajadas*) with gentle slopes (0.2 - 2 %), summer rainfall, and heavy showers that run as sheet-flow. It has been suggested that run-off water from bare areas is stopped at the front of the arcs and, depending on the amount of rainfall, may advance superficially into the arc, reaching the downslope limit less often. These dynamics would imply a gradient of water availability inside the arc, higher at the upper edge. We termed this the *moisture gradient hypothesis*. We indirectly tested this hypothesis by following the demography of a cohort of stems of the honey mesquite *Prosopis glandulosa* var. *torreyana* in three vegetation arcs and their corresponding bare areas during a yearly cycle at the Bolsón de Mapimí in the Chihuahuan Desert. We selectively removed different plant life-forms (trees, shrubs and herbs) in three positions within the arcs; no manipulation was possible in the bare areas due to low plant cover. The results suggested that removal of other plant life-forms, mainly grasses, affected growth and survival of mesquite low (but not high) stems, making them accessible to medium-sized mammal browsers (jackrabbits and packrats). These results suggest that, at least for the honey mesquite, water availability in vegetation arcs was not the most strongly limiting factor for shoot performance and demography, and that browsing damage, a biotic constraint, took precedence over resource limitation.

Keywords: Chihuahuan desert; Contracted-vegetation pattern; Herbivory; Life form; Mexico; Removal experiment.

Nomenclature: Correl & Johnston (1979).

Introduction

Vegetation arcs or stripes alternating with bare areas have been reported for arid and semiarid regions of the world (White 1970; Mabbut & Fanning 1987; Tongway & Ludwig 1990). These localities share common characteristics, namely, summer rainstorms of high intensity in short periods of time, low slopes (0.2 - 2 %), and mostly fine-textured soils. The pattern of rainfall favors

runoff over infiltration and, due to the low slopes, water tends to run as sheet-flow. In the bare zones, water does not infiltrate readily due to the existence of an impervious layer which derives from sorting of fine soil particles caused by rainsplash. As a consequence, water from these zones runs downslope and may be stopped by, or pass through, vegetation arcs, depending on the amount of rain.

Greig-Smith (1979), based on work by Boaler & Hodge (1964), Hemming (1965) and White (1971), suggested that vegetation arcs may be formed by the lateral extension of the downslope edge of bare patches which are formed randomly on a completely vegetated surface or, alternatively, on bare areas, from lateral spread of vegetation patches located initially over physical obstacles that impede sheet flow. He also suggested that run-off water from bare areas is stopped at the front of the arcs and, depending on the amount of rainfall, may advance superficially into the arc, reaching the downslope limit less frequently. Such dynamics would imply a gradient of water infiltration and availability, higher in the upslope (front) than in the downslope (back) part of the arcs. We termed this the *moisture gradient hypothesis*. This hypothesis would also imply that water availability is much lower at the downslope ecotone (vegetation arc - bare area) than in the zone where the upslope bare area and the front of the arc meet. Cornet et al. (1992) reported that the range of water storage capacity during five characteristic rain events was 2.2 - 5.3 × the rainfall in the upslope part of the vegetation arc against 1.7 - 1.8 × at the downslope part. These ranges contrast with those of the bare areas corresponding to the arc: 0.2 - 0.5 × the rainfall. Since it is reasonable to assume that plant growth and development respond to the humidity gradient along the vegetation arc, we hypothesize that plants should grow less as we move from the front to the back of any arc.

An approach used to measure the growth of woody plants in relation to environmental or experimental factors is module demography – a module being any constructional unit that is iterated as the plant develops (Bell 1991). Using this approach, Mailette (1987) found

in a tundra in Quebec that bud damage in *Betula cordifolia* was higher in areas exposed to higher winds and lower temperatures, which explained the differences in shape of trees growing in exposed sites when compared to protected sites. Jones & Harper (1987a, b) found a significant relationship between bud survival and growth, and the interference zone between neighboring *Betula pendula* trees. In an arid zone, Flores-Martínez et al. (1994) found that module, inflorescence and fruit production of large *Mimosa luisiana* shrubs, a nurse plant, were affected if associated with the (nursed) cactus *Neobuxbaumia tetetzo*.

The branching process through growth of new shoots and bud suppression has been considered by Bell (1984) as a “system locating functional sites (nodes) at discrete intervals by the interposition of spacers (internodes)”. However, (1) shoot growth may interfere with other shoots by overshadowing them (Harper 1985); (2) new shoots may demand water or nutrients, which implies their redistribution in the plant and/or growth of new roots to satisfy this demand; and (3) at the plant level, resources in demand can be limited (Caldwell et al. 1991) and thus competed upon by individuals of similar or different life forms (Fonteyn & Mahall 1981; Fowler 1986; Eissenstat & Caldwell 1988; Belsky 1994).

In this paper we indirectly tested the moisture gradient hypothesis through a modular approach, considering the three aspects mentioned above. We studied the demography of a cohort of stems of the large shrub/small tree *Prosopis glandulosa* var. *torreyana* (Mimosoideae), in three vegetation arcs. We sought to answer these questions: Is module survival and development similar at different heights within the tree? Is it related to the location of the tree within and outside vegetation arcs? Does the exclusion of potential competitors affect it? Finally, which are the causes of module mortality?

Methods

Study site

The study site (103° 44' W, 26° 41' N, 1170 m altitude) is located in a lower bajada, that is the lower part of alluvial fans in arid and semiarid zones (Summerfield 1991); at the Bolsón de Mapimí, a closed basin within the Chihuahuan Desert. Average annual rainfall is 264 mm, 71 % of which comes in summer showers of short duration. 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). The vegetation is a xerophytic scrub (Rzedowski 1978) or Chihuahuan Desert scrub (Brown 1982). Soils are haplic Yermosols and their texture is predominantly clay loam. The vegetation arcs

under study are located on the lower bajada surrounding an inselberg called Cerro de San Ignacio (Fig. 1). Here, vegetation arcs consist of an undifferentiated (*sensu* Boaler & Hodge 1964) mixture of grasses, mainly *Hilaria mutica* and woody species, mainly *P. glandulosa* var. *torreyana*. Other woody species are *Flourensia cernua*, *Ziziphus obtusifolia*, *Castela texana* and *Koeberlinia spinosa* (Mauchamp et al. 1993). For a list of plant species in vegetation arcs see Cornet et al. (1988).

Species

The honey mesquite, *Prosopis glandulosa* var. *torreyana*, is a long-lived woody species, which is common inside vegetation arcs and – albeit with a much lower density – in bare areas. This and other species of *Prosopis* are considered as phreatophytes (MacMahon & Schimpf 1981) or, more precisely, facultative phreatophytes, i.e. with roots that can take water from shallow and deep soil horizons (Simpson & Solbrig 1977; Heitschmidt et al. 1988; Ansley et al. 1990). They appear to be sensitive to diurnal changes in soil water availability (Hanson & Dye 1980; Brown & Archer 1990) as well as to seasonal changes (Cable 1977; Mooney et al. 1977; Brown & Archer 1989). Honey mesquites have responded to experimental irrigation and superficial root severing (Ansley et al. 1988, but see Montaña et al. 1995), and to the exclusion of grasses and fertilization (Cornejo-Oviedo et al. 1992).

The buds from a mesquite shoot may produce leaves, shoots, spines or inflorescences. Each new shoot may

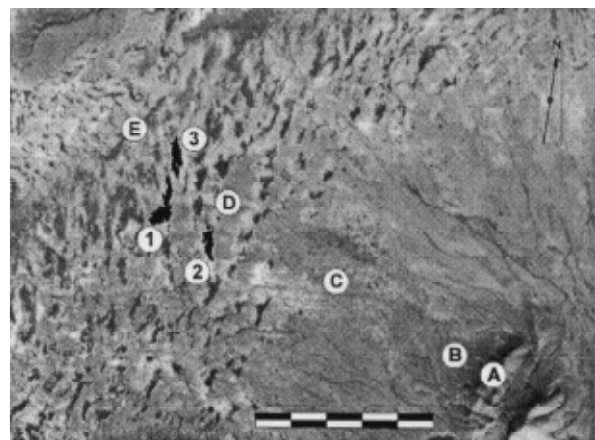


Fig. 1. The study site, with Cerro San Ignacio is at the lower right margin. Numbers in circles indicate the location of the three vegetation arcs under study. Landforms are: rocky outcrops at the hillsides (A), Piedmont (B), upper Bajada (C), lower Bajada where the vegetation arcs are found (D), and valley bottom (E).

consist 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 were recorded mainly from March through May, although shoot growth can continue (decreasingly) until September; mesquites lost their leaves completely in January. We found no evidence of a second peak of growth as reported by Nilsen et al. (1987) for the same variety in the Sonoran Desert, where winter rainfall is more common. New tissue production precedes the season with highest probability of rainfall. Shoots produced in a recent growing period are easily distinguishable from former shoots, since spines (modified shoots, Mooney et al. 1977) are flexible, a characteristic that can be used to select a cohort of shoots. Spine flexibility is lost within the first months after shoot expansion.

Selection of vegetation arcs and positions within arcs

We selected three vegetation arcs at the lower bajada of Cerro San Ignacio (1 - 3 in Fig. 1). Vegetation arcs 1 and 3 are contiguous and on similar contour lines, while vegetation arc 2 is found upslope of vegetation arc 3. Each vegetation arc can be divided in two main axes: one parallel and one perpendicular to the slope. Under the water gradient hypothesis, positions along a line perpendicular to the slope share similar water availability while positions along lines parallel to the slope differ in water availability. Thus, the central part of each arc was subdivided into three parts (front, middle and back of arc). Four 5 m × 10 m plots, separated by a zone of 3 m width, were traced in each of the three positions, the axis perpendicular to the slope. There was a total of 12 plots in each vegetation arc. The dimensions of the three arcs are 300 m × 90 m, 174 m × 44 m and 250 m × 54 m. The distance to the nearest arc on the direction of the slope is 123, 156 and 89 m for arcs 1 through 3, respectively.

Removal of plant life forms

We used a target method (cf. Aarsen & Epp 1990) to test the effect of the removal of plant life forms on mesquite growth. Four treatments were carried out in each position: control, *C*, no removal, removal of herbs, *-G*, mainly grasses, woody plant removal, *-W*, and herb and woody plant removal, *-G -W*. The treatment for each plot was randomly assigned. When indicated by treatment, herbs or woody plants were cut off at ground level. Sprouts of the removed life forms were pruned during each field visit.

Selection of individuals

Two mesquite plants were selected within each plot. To track differences between growth in relation to shoot height within the tree, 10 recent shoots were marked in the uppermost, and 10 on the lowermost, part of each selected individual. If sufficient shoots were available they were randomly selected, otherwise all were sampled.

Selected shoots were marked at their base by means of an aluminum tag attached to a plastic-coated copper wire (Fig. 2).

Due to the lack of recent shoots in four of the 36 plots (one in vegetation arc 2 and three in vegetation arc 3), an additional tree was used in two plots, three in one plot and six (30 - 60 cm high individuals) in the last plot. The peculiarities of this sampling were due to the *a priori* decision to consider only trees within plots.

To compare shoot demography of mesquite individuals within and outside vegetation arcs, two individuals were selected in each of the bare areas associated with vegetation arcs. As a result of the whole sampling design, we marked a cohort of 1560 shoots distributed in 89 trees.

Response variables

Our modular unit of measurement was the shoot. The measurement of each module was made on a bi-monthly basis from May 1988 through May 1989. We measured the length, number of nodes, leaf number, and, during flowering and regrowth, number of inflorescences (later number of pods), node number of new (secondary or higher level) shoots, and leaves in the initial module cohort. In each measurement the cause of dieback or death of any shoot (water deficit, browsing by the black-tailed jackrabbit *Lepus californicus* or the packrat *Neotoma albigula*, or by bostrichid beetles) was noted. Browsing was determined by the evidence of the cut; we considered the nodes or shoots to have died as a consequence of water deficit if there was no external sign of perturbation.

Statistical analysis

We calculated two rates: the survival rate of the initial cohort of modules and the rate of change of the initial cohort and the modules derived from it.

We define the survival rate (s_t) as the difference between the natural logarithm of the number of live nodes of the initial cohort surviving at a given interval (n_t) and the natural logarithm of the initial number of nodes per module (n_0):



Fig. 2. Honey mesquite shoot with a derived regrowth. Numbers indicate nodes counted when there was dieback in the original shoot.

$$s_t = \log(n_t + 1) - \log(n_0 + 1) \quad (1)$$

The rate of change, c_t is the difference between the natural logarithm of the number of nodes, n_t , of the initial cohort surviving at a given interval t , plus the number of nodes of secondary modules, m_t , produced after initiation and surviving at a given interval t , and the natural logarithm of the initial number of nodes per module, n_0 :

$$c_t = \log(n_t + m_t + 1) - \log(n_0 + 1) \quad (2)$$

We chose the logarithmic transformation of the original data to compare between rates of different orders of magnitude (Begon et al. 1986), and added unity to the number of nodes to be transformed to avoid indeterminacy in case there was a complete loss of the module (Zar 1984).

To test the effect of each factor and their interaction on the differences in both rates, we used the BMDP procedure 8V (General Mixed Model Analysis of Variance with equal sample sizes, Jennrich & Sampson 1979) for a nested analysis of variance with repeated measures. Due to the equal sample size requirement, vegetation arcs were analyzed separately from bare areas. In vegetation arcs we considered the vegetation arc, M ; position within the arc, P ; treatment, T ; measurement date, F ; height of module, H ; and plant, A , as fixed factors. The nested variables were the plant – A on M , P

and T , and the module – B on M , P , T , A and H –, which we considered as random. The general mixed ANOVA model for survival rate and rate of change, y , with nested factors inside parentheses is:

$$y = M + P + T + H + F + A(MPT) + B(MPTAH) \quad (3)$$

plus their interactions. For the bare-area mesquites, the factors under consideration were the same as in vegetation arcs and with similar characteristics, but there were no treatment or position factors. The general mixed ANOVA model for survival rate or rate of change (y) in bare areas, with nested factors inside parentheses is:

$$y = M + H + F + A(M) + B(MAH) \quad (4)$$

plus their interactions. Since the BMDP 8V routine used in the analyses requires equal cell sizes, we excluded the trees with less than 20 tagged modules. Missing data corresponding to 120 modules (8.3 % of the sample) were estimated as the average for each combination of the pertinent factors (Zar 1984). The individuals excluded from these analyses are considered elsewhere (López-Portillo & Montaña unpubl.).

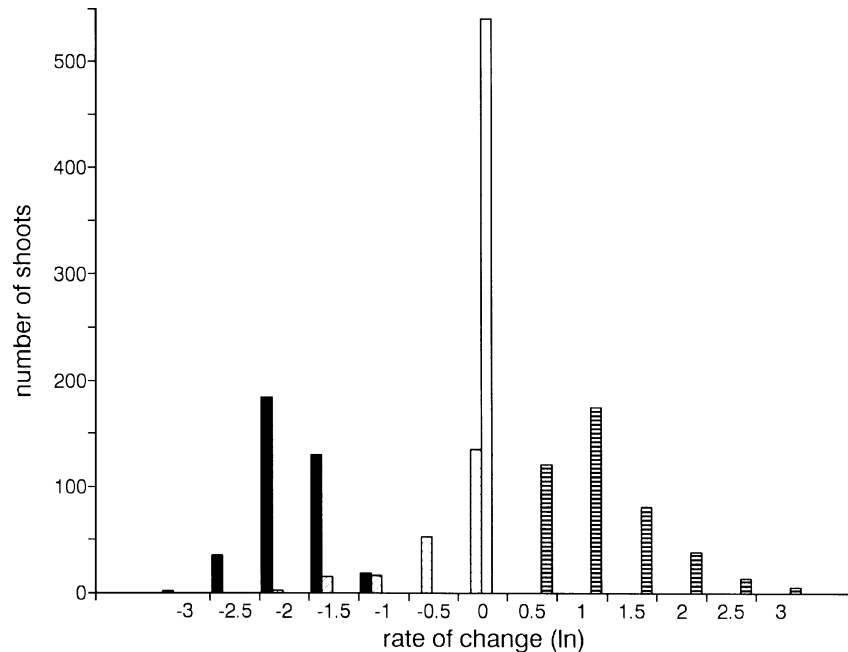
Since we found significant differences between treatment and factor levels in all ANOVAs, we used Newman-Keuls multiple comparisons for nested ANOVAs to assess differences between levels of the significant factors and factor interactions (Zar 1984). If any two or more combinations of factors were not significantly different, we merged their corresponding data to calculate new means and 95% confidence intervals (Zar 1984, pp. 259 - 260).

Results

Frequency distribution of response variables

The frequency distribution of the response variables in vegetation arcs and bare areas was not Normal ($P < 0.01$, Kolmogorov-Smirnov test, Zar 1984). For rates of survival, it is the outcome of three different processes: dormancy (zero, no gain or loss of nodes), dieback (negative values, death of nodes within shoots) and death of whole shoots (also negative values); values are bounded on zero and unbounded for negative values (since s_t depends on the initial number of nodes, values would be more negative if more nodes were found in a given stem and if all were dead at a given interval). For rates of change, it is the outcome of four processes (Fig. 3): growth (positive values; node increment by growth of secondary or higher-order shoots), dormancy, dieback, and death of shoots. However, we decided to analyze our data through ANOVA since we found no other way to consider the nested variables and repeated

Fig. 3. Frequency distribution of the rate of change in six bimonthly measurements of 1560 shoots belonging to 89 trees from tree vegetation arcs and their associated bare areas. The frequency distribution is the outcome of four different processes characterized by the fate of the shoots: dormant (empty bars); dead (filled bars); with dieback (diagonally-filled bars); and grown (horizontally-filled bars).



measures of the experimental design. We are aware that results should be interpreted with caution, trusting on the robustness of the ANOVA and on the degrees of freedom of our data sets (Zar 1984, p. 170).

Survival rates and rates of change in vegetation arcs

The ANOVA model for survival rates containing all significant terms and interactions accounted for 17.2 % of total variation (TV, the total sum of squares) in the data. There were significant differences between treatments, height of modules and sampling dates simultaneously, as indicated by their interaction. The main effects and their interactions accounted for 9.3 % of the TV. Other significant interactions involved the effect of the vegetation arc or experimental block (0.6 % of TV). Variability due to differences between individual trees accounted for 7.3 % of TV, and the highest percentage (76.2 %) corresponded to variability between modules. There were no significant differences associated with the position within vegetation arcs.

A Newman-Keuls multiple comparisons test for nested ANOVAs (Zar 1984) averaging over module height, treatments and sampling dates allowed for the formation of three significantly different groups (SDG; $P < 0.05$): (1) lower modules in treatments where woody plants were excluded (-W) and in controls (C); (2) lower modules in trees from plots subjected to the exclusion of grasses (-G) and of woody plants and grasses (-W-G);

and (3) upper modules in all treatments. These results indicate that (a) survival rates do not differ between modules at the higher part of trees regardless of the treatment or the position within the vegetation arc, and (b) there are significant differences in the lower modules which seem to depend mainly on the exclusion of grass cover, since there were no differences between the controls and the plots where only woody plants were excluded.

Fig. 4a shows the change in time of average percent survival rates ($s' = 100 * \exp(s)$) in the three SDG. The lowest rates were found in lower modules of trees under treatments -G and -G -W and the highest survival corresponded to modules in the upper part of trees regardless of treatment or position. With respect to time, lower modules in the C and -W treatments differed significantly from the former 310 days after the experiment began.

The ANOVA model for rates of change containing all significant terms and interactions accounted for 12.7 % of TV in the data. As in survival rates, there was a significant interaction between treatments, height of modules and sampling dates: $T \times H \times F$. The main effects and their interactions accounted for 4.5 % of TV. Other significant interactions involved the differential effect of the vegetation arcs on treatments, height of shoots, and date (1.4 % of TV). Differences between trees accounted for 6.9 % of TV, and the highest percentage (76.7 %) corresponded to variability between modules.

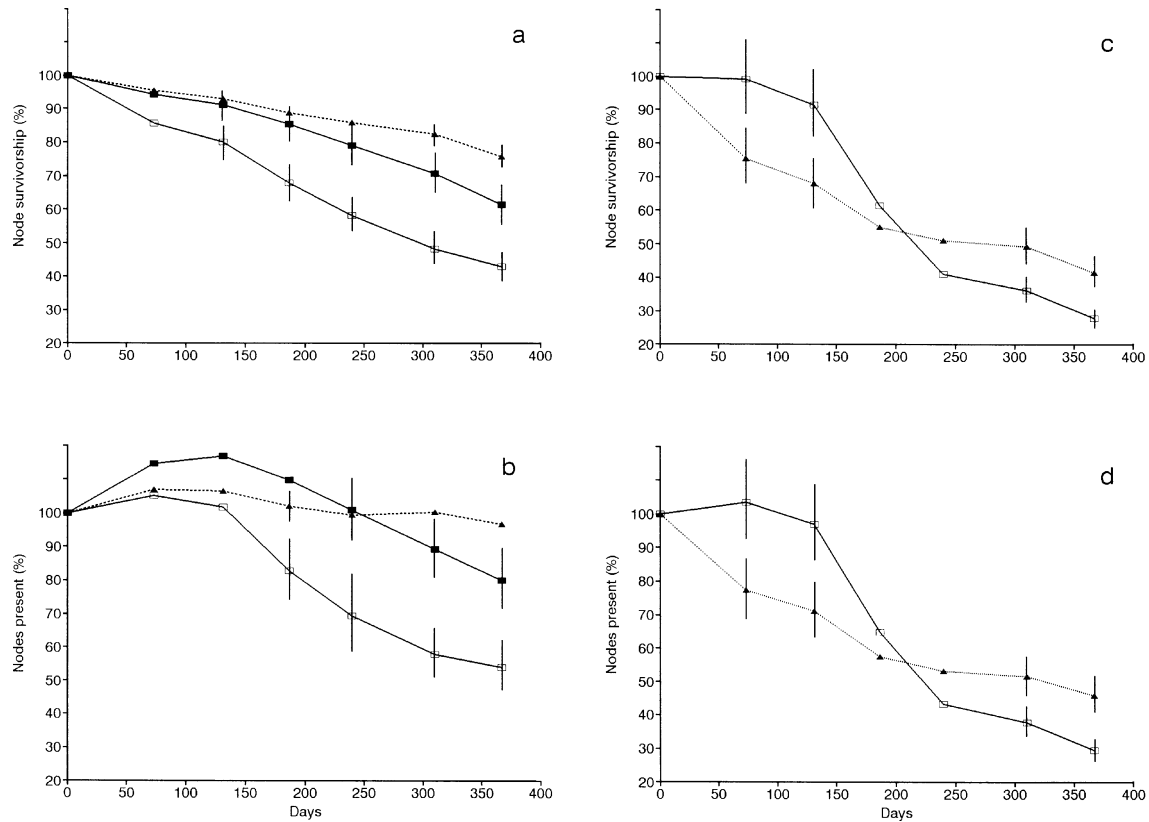


Fig. 4. Evolution in time of the survival rate (*a, c*) and the rate of change (*b, d*) expressed as percentages of the number of initial live nodes in three shoot groups from vegetation arcs (*a, b*) and two from bare areas (*c, d*): upper part of trees (triangles); lower shoots in the woody plant removal and control treatments (filled squares); and lower shoots in the herb and herb-woody plants removal treatments in vegetation arcs, and on bare areas (empty squares). Vertical lines indicate 95% confidence intervals when significant differences between groups were found.

Also, as in survival rates, there were no significant differences associated to the position within arcs. The corresponding multiple comparisons suggested two significantly different groups: (a) upper modules in all treatments and the lower modules of trees subjected to *C* and *-W* treatments; and (b) lower modules of the trees subjected to *-G* and *-G -W* treatments.

Fig. 4b shows the average percent rates of change, $c' = 100 * \exp(c)$, in the SDG and in relation to time. The two groups are significantly different 187 days after the beginning of the experiment. We preserved the three significantly different groups (SDG) found when analyzing the survival rates (i.e. separated upper from lower modules in the group (a) above) since we suspected that module dynamics depended on their height. Results indicated that the average rates of change were relatively lower in low modules when herbs were excluded. There was no net average module growth in any group.

Survival rates and rates of change in bare areas

The ANOVA model for survival rates containing all significant terms and interactions accounted for 19% of TV in the data. There were significant differences between height of modules and sampling dates simultaneously, as indicated by the interaction term ($H \times F$). The main effects and their interactions accounted for 14.7% of the TV, and the remaining 4.4% corresponded to the interactions of the bare areas and height or date. There were no significant differences associated with trees, and the highest percentage of TV (66.5%) corresponded to variability between modules. The multiple comparisons test indicated differences between high and low modules (Fig. 4c): survival rates (s') of upper modules was (a) significantly lower in the second and third dates of measurement, and (b) significantly higher in the two last dates of measurement. The results for the ANOVA model for rates of change (c') were similar to those found for survival rates (Fig. 4d).

Table 1. Percent of shoots in relation to their fate or development in the significantly different groups found in vegetation arcs (A-C) and bare areas (D-E). Groups are, in vegetation arcs, lower shoots in woody-plant removal and control treatments (A); lower shoots in herb and woody-plant+herb removal treatments (B); and upper shoots (C); in bare areas, lower (D) and upper (E) shoots. Same letters in a row indicate no significant differences between groups ($P > 0.05$).

Cause of death	Vegetation Arc			Bare zone		χ^2	P
	A	B	C	D	E		
Bostrichids	0	0	0.007	0	0.033	-	-
Lagomorphs and rodents	0.14 b	0.32 c	0.07 a	0.50 d	0.33 c	160	< 0.001
Water deficit	0.05 a	0.04 a	0.04 a	0.12 b	0.02 a	9.75	0.04
Dieback	0.15	0.16	0.13	0.12	0.08	4.43	0.35
Dormant	0.33 b	0.23 a	0.47 c	0.15 a	0.42 c	75.78	< 0.001
Grown	0.34 c	0.25 b	0.29 b	0.12 a	0.12 a	22.76	< 0.001
n	320	350	670	60	60		

Module fates

To explore the causal agents of dieback (i.e. death of nodes) or of module death, negative rates of change from the first to the last sampling dates were related with the type of damage. Our field data indicated two causes for module dieback or death (water deficit and browsing by the jackrabbit *Lepus californicus* or the packrat *Neotoma albigula*). A third cause, death of shoots by wood-boring bostrichids, killed only seven shoots concentrated in three of the 89 individuals under study. Since each SDG differs in number of modules, we used the normal approximation for comparing more than two proportions on each of the causes of dieback or death (Zar 1984). We found significant differences on most cases ($P < 0.05$), and thus used the multiple comparisons for proportions procedure (Zar 1984) to distinguish between groups. A similar procedure was used to compare between SDG regarding the proportion of dormant and grown modules.

The relationship between the SDG and module fates are shown in Table 1. Death of modules due to browsing was high in the lower and upper modules in bare areas and in the lower modules of trees subjected to $-G$ and $-G - W$ treatments in vegetation arcs (D, E and B, respectively). Death due to water deficit was similar in all but one of the SDG (D in Table 1). There were no significant differences between SDG regarding module dieback. These results suggest that plants most exposed to browsers due to natural or experimental absence of grasses were the most affected, and that biomass removal did not ameliorate the effects of water deficit, as could be expected if mesquites competed with removed plants for water.

More than 40 % of the upper modules of trees in vegetation arcs and bare areas remained dormant during the yearly cycle (Table 1), 33 % of the lower modules in plants subjected to C and $-L$ treatments in vegetation arcs also remained dormant, and the lowest proportions

were found in the treatments most affected by browsers (B and D in Table 1). Finally, more lower modules in treatments C and $-W$ grew (A in Table 1) than in any other SDG.

Discussion

Module survival and growth and the moisture gradient hypothesis

In this experiment we indirectly tested the hypothesis of a water availability gradient in vegetation arcs. Since water could be a limiting resource we combined the effect of exclusion of life forms in the survival and growth of mesquite modules. Thus, the experimental design included the test for the effects of three factors: the location inside vegetation arcs and in bare areas, the effect of the exclusion of life forms, and the effect of module height. However, we did not measure water availability; results of previous works (Ansley et al. 1988, 1990) suggest that the plant would be sensitive to this resource. The vegetation arcs and their associated bare areas were considered as the treatment blocks.

There were no effects of tree position on the growth of modules. If mesquite is sensitive to water availability, this result would not support the moisture gradient hypothesis, and would suggest that during the annual cycle under study, water availability for mesquites was homogeneous within vegetation arcs or that water was not limiting in these locations. It could be argued that the plant under study is a phreatophyte (MacMahon & Schimpf 1981) and deep roots may be in contact with an unknown water source which is independent of the position in vegetation arcs. However, it has been demonstrated that mesquites are in fact facultative phreatophytes which develop superficial as well as deep roots (Heitschmidt et al. 1988; Montaña et al. 1995) and that the severing of superficial roots affect their water

potentials (Ansley et al. 1990). On the other hand, roots in our locality may not grow deeper than 2 m, where the basal rock is found, and water at this depth is related to the presence of vegetation arcs (Cornet et al. 1992).

Another argument to explain the lack of relation between module survival and growth and tree position in vegetation arcs is that the response of plants may depend on the interannual variability of available water (Wondzell & Ludwig 1995). As stated before, module growth and inflorescence production precedes the season with highest probability of rainfall. For this reason, Antoine Cornet and Carlos Montaña (pers. comm.) suggested that new tissue is produced at the expense of the residual substrate water corresponding to the previous year. From this point of view, mesquite vegetative and reproductive parts in 1988 (the year this study began) responded to rainfall in 1987 (324 mm) which was 1.6× higher than in 1988 and almost twice the rainfall in 1989.

Based on data from a tropical savanna in South Africa where the shrub or tree *Acacia tortilis* and the grass *Cenchrus ciliaris* are the common species, Knoop & Walker (1985) suggested that competition between these two species is more intense during the years with average rainfall values; reversely, Weltzin & Coughenour (1990) described a beneficial effect of *A. tortilis* over *C. ciliaris* when the grass is under the shadow cast of the tree canopy. Since mean average rainfall at our study site is 264 mm, 1987 was above and 1988 below this value. Thus, Knoop and Walker's condition was not met; however, although there was a transition from a wet (above average rainfall) to a dry year (below average), the development of shoots at the beginning of the experiment and loss, dieback and regrowth during the successive sampling dates were never related to the position of trees within vegetation arcs.

If mesquite competed with other plant life forms for water or nutrients, the exclusion of these would result in a growth proportional to the biomass removed from the area (Cornejo-Oviedo et al. 1992). However, average growth of mesquite modules was opposite to that expected trend, since the most affected modules belonged to the treatments where more biomass was excluded. There were other causal agents which took precedence to water availability and to the possible effect of competition between plant life forms.

Browsing

Shoot dieback and death were higher in natural bare areas and in the experimentally-exposed sites and were mainly related to jackrabbit and packrat browsing. This implies that vegetation surrounding mesquites is an obstacle to browsers, a result analogous to that obtained

by McAuliffe (1986), who found that survival probability of saplings of the leguminous shrub *Cercidium microphyllum* was higher inside the refugia provided by perennials. Browsing is also the predominant factor in low as well as in high-positioned shoots of the trees sampled in the bare areas.

Vorhies & Taylor (1933 in Mares et al. 1977) found that mesquite parts accounted for 56% of the diet in *Lepus californicus* in Arizona and Nilsen et al. (1987) estimated that, in the Sonoran Desert in California, 35% of shoots of the same species variety we studied were lost to rodents and jackrabbits. It has been suggested that mesquite is an alternative diet for medium-sized herbivores during the dry periods when herbs associated with a higher water availability are less frequent (Mares et al. 1977). In our study site, rainfall in 1988 was registered from April to September, when a higher herb cover could be developed. By the end of summer this resource was substantially diminished and mesquite could have been the main source of food and density of browsers was unchanged. Mortality of lower shoots should have been higher during the driest and hottest season (i.e. end of summer through autumn) if mesquite was the alternative food source. However, an analysis made to explore the shape of the survival curves in vegetation arcs and in the bare areas indicated that the quadratic term was not significant in any treatment ($P > 0.05$), which suggests a Deevey-type II survival curve (Harper 1977) of constant mortality through time. Thus, mesquite seems to be a source continuously used by browsers.

Residual variability

A high proportion of the sum of squares (SS) in our ANOVAs corresponded to the experimental error: 76% and 67% in mortality and growth rates in vegetation arcs and bare areas, respectively. At the end of the experiment on interference between tree crowns carried out on *Betula pendula* by Jones & Harper (1987a) the sources of variation of the ANOVA (tree, age and interference zone) left 71% of the SS unexplained. By the third year, the SS explained by the significant factors did not change, but the interference zone between *Betula* crowns had a significant effect on buds ($P < 0.05$); however, this effect explained only 1-2% of total SS. Even though the experiments on *Betula pendula* and *Prosopis glandulosa* are very different, the residual variability is similar. Jones & Harper (1987a) suggested that this variability had two sources: (a) causes attributable to the indeterminate type of growth in buds, and (b) causes attributable to the analyses, which implied grouping a high quantity of data 'with consequent loss of detail'. They also considered the effect of factor level

selection and the lack of specific information on the characteristics of every part of the crown. In our results some reasons for the unexplained variability could be also proposed: those related to site and experimental unit selection, and those characteristic of module phenology and the interactions with herbivores.

Although more studies of demography at the modular level are needed, we suggest that the unexplained variability in modular demography is a consequence of the different fates of modules, which in turn condition the statistical distribution of the error. Even though transformations of original data before analysis are made to normalize error distribution (Jones & Harper 1987a, b; Mailette 1987), only Mailette (1992), in a study concerning the modular demography of the herbaceous perennial *Potentilla anserina*, indicated that the distribution of transformed values is not significantly different from the Normal. The problem of high unexplained variability seems unavoidable, given the different alternatives in module development and the possibility that it is affected by intrinsic (e.g. dormancy) and extrinsic (e.g. browsing) phenomena.

From this discussion we conclude that:

1. We could not find a relationship between tree position in vegetation arcs and module growth which could suggest that water availability for mesquites was homogeneous along these patches, a result that would not support the moisture gradient hypothesis. However, it could also suggest that while water availability varies considerably, it was not the most strongly limiting factor for shoot performance and demography. Both hypotheses could be tested if stem demography and water availability were measured simultaneously.

2. Since the removal of plant life forms (mainly grasses) affected the survival of low stems of mesquite, it can be suggested that such association was beneficial enough to override any possible intraspecific competence.

3. Module mortality was associated mainly with the herbivory of medium-sized mammals (jackrabbits and packrats).

4. The unexplained variability in modular demography of woody plants may be a consequence of their differences in phenology and the activity of herbivores.

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References

- Aarsen, L.W. & Epp, G.A. 1990. Neighbour manipulations in natural vegetation: a review. *J. Veg. Sci.* 1: 13-30.
- Ansley, R.J., Jacoby, P.W. & Cuomo, G.J. 1990. Water relations of honey mesquite following severing of lateral roots: influence of location of subsurface water. *J. Range Manage.* 43: 436-442.
- Ansley, R.J., Jacoby, P.W. & Lawrence, B.K. 1988. Influence of stress history on water use patterns of honey mesquite. In: Wallace, A., Durant, E. & Haferkamp, M.R. (eds.) *Proceedings of the symposium on shrub ecophysiology and biotechnology*, pp. 75-82. USDA, Forest Service, General Technical Report-INT. 256, Logan, UT.
- Begon, M., Harper, J.L. & Townsend, C.R. 1986. *Ecology. Individuals, populations and communities*. Sinauer Ass. Inc., Sunderland, MA.
- Bell, A.D. 1984. Dynamic morphology: a contribution to plant population ecology. In: Dirzo, R. & Sarukhán, J. (eds.) *Perspectives on plant population ecology*, pp. 48-65. Sinauer Ass. Inc., Sunderland, MA.
- Bell, A.D. 1991. *Plant form*. Oxford University Press, Oxford.
- Belsky, A.J. 1994. Influences of trees on savanna productivity: tests of shade, nutrients, and tree-grass competition. *Ecology* 75: 922-932.
- Boaler, S.B. & Hodge, C.A. 1964. Observations on vegetation arcs in the Northern region, Somali Republic. *J. Ecol.* 52: 511-544.
- Brown, D.E. 1982. Biotic communities of the American Southwest United States and Mexico Chihuahuan Desert-scrub. *Desert Plants* 4: 169-179.
- Brown, J.R. & Archer, S. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. *Oecologia (Berl.)* 80: 19-26.
- Brown, J.R. & Archer, S. 1990. Water relations of perennial grass and seedling vs. adult woody plants in a subtropical savanna, Texas. *Oikos* 57: 366-374.
- Cable, D.R. 1977. Seasonal use of soil water by mature velvet mesquite. *J. Range Manage.* 30: 4-11.
- Caldwell, M.M., Manwaring, J.H. & Durham, S.J. 1991. The microscale distribution of neighbouring plant roots in fertile soil microsites. *Funct. Ecol.* 5: 765-772.
- Cornejo-Oviedo, E., Gronski, S. & Felker, P. 1992. Mature mesquite (*Prosopis glandulosa* var. *glandulosa*) stand description and preliminary effects of understory removal and fertilization on growth. *J. Arid Environ.* 4: 339-351.
- Cornet, A. 1988. Principales características climáticas. In: Montaña, C. (ed.) *Estudio integrado de los recursos vegetación, suelo y agua en la Reserva de la Biosfera de Mapimí*, pp. 45-76. Instituto de Ecología, México, D.F.
- Cornet, A.F., Delhoume, J.P. & Montaña, C. 1988. Dynamics of striped vegetation patterns and water balance in the Chihuahuan desert. In: Daring, H.J., Werger, M.J.A. & Willems, J.H. (eds.) *Diversity and pattern in plant communities*, pp. 221-231. SPB Academic Publ., The Hague.
- Cornet, A.F., Delhoume, J.P., Montaña, C. & López-Portillo, J. 1992. Water flows and the dynamics of desert vegetation

- stripes. In: Hansen, A.J. & Di Castri, F. (eds.) *Landscape boundaries. Consequences for biotic diversity and ecological flows*, pp. 327-345. Ecological Studies 92. Springer Verlag, Berlin.
- Correl, D.S. & Johnston, M.C. 1979. *Manual of the vascular plants of Texas*. University of Texas, Dallas, TX.
- Eissenstat, D.M. & Caldwell, M.M. 1988. Competitive ability is linked to rates of water extraction. *Oecologia (Berl.)* 75: 1-7.
- Flores-Martínez, A., Ezcurra, E. & Sánchez-Colón, S. 1994. Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisiana*. *J. Ecol.* 82: 325-330.
- Fonteyn, P.J. & Mahall, B.E. 1981. An experimental analysis of structure in a desert plant community. *J. Ecol.* 69: 883-896.
- Fowler, N. 1986. The role of competition in plant communities in arid and semiarid regions. *Annu. Rev. Ecol. Syst.* 17: 89-110.
- Greig-Smith, P. 1979. Pattern in vegetation. *J. Ecol.* 67: 755-779.
- Hanson, J.D. & Dye, A.J. 1980. Diurnal and seasonal patterns of photosynthesis of honey mesquite. *Photosynthetica* 1: 1-7.
- Harper, J.L. 1977. *Population biology of plants*. Academic Press, London.
- Harper, J.L. 1985. Modules, branches, and the capture of resources. In: Jackson, J.B.C., Buss, L.W. & Cook, R.E. (eds.) *Population biology and evolution of clonal organisms*, pp. 1-33. Yale University Press, New Haven and London.
- Heitschmidt, R.K., Ansley, R.J., Dowhower, S.L., Jacoby, P.W. & Price, D.L. 1988. Some observations from the excavation of honey mesquite root systems. *J. Range Manage.* 41: 227-231.
- Hemming, C.E. 1965. Vegetation arcs in Somaliland. *J. Ecol.* 53: 57-68.
- Jennrich, R. & Sampson, P. 1979. Analysis of variance and covariance including repeated measures (BMDP 8V). In: Dixon, W.J. & Brown, M.B. (eds.) *Biomedical computer programs, P-Series*, pp. 540-580. University of California Press, Berkeley, CA.
- Jones, M. & Harper, J.L. 1987a. The influence of neighbours on the growth of trees. I. The demography of buds in *Betula pendula*. *Proc. R. Soc. London B232*: 1-18.
- Jones, M. & Harper, J.L. 1987b. The influence of neighbours on the growth of trees. II. The fate of buds on long and short shoots in *Betula pendula*. *Proc. R. Soc. London B232*: 19-33.
- Knoop, W.T. & Walker, B.H. 1985. Interactions of woody species and herbaceous vegetation in a Southern African savanna. *J. Ecol.* 73: 235-253.
- Mabbutt, J.A. & Fanning, P.C. 1987. Vegetation banding in arid Western Australia. *J. Arid Environ.* 12: 41-59.
- MacMahon, J.A. & Schimpf, D.J. 1981. Water as a factor in the biology of the North American desert plants. In: Evans, D.D. & Thames, J.L. (eds.) *Water in desert ecosystems*, pp. 114-171. IBP. Dowden, Hutchinson & Ross Inc. Stroudsburg, PA.
- Mailette, L. 1987. Effects of bud demography and elongation patterns on *Betula cordifolia* near the tree line. *Ecology* 68: 1251-1261.
- Mailette, L. 1992. Plasticity of modular reiteration in *Potentilla anserina*. *J. Ecol.* 80: 231-239.
- Mares, M.A., Enders, F.A., Kingsolver, J.M., Neff, J.L. & Simpson, B.B. 1977. *Prosopis* as a niche component. In: Simpson, B.B. (ed.) *Mesquite. Its biology in two desert scrub ecosystems*, pp. 123-149. Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Mauchamp, A., Montaña, C., Lepart, J. & Rambal, S. 1993. Ecotone dependent recruitment of a desert shrub, *Flourensia cernua*, in vegetation stripes. *Oikos* 68: 107-116.
- McAuliffe, J.R. 1986. Herbivore-limited establishment of a Sonoran desert tree, *Cercidium microphyllum*. *Ecology* 67: 276-280.
- Montaña, C., Cavagnaro, B. & Briones, O. 1995. Soil water use by co-existing shrubs and grasses in the Southern Chihuahuan Desert. *J. Arid Environ.* 31: 1-13.
- Mooney, H.A., Simpson, B.B. & Solbrig, O.T. 1977. Phenology, morphology, physiology. In: Simpson, B.B. (ed.) *Mesquite. Its biology in two desert scrub ecosystems*, pp. 26-43. Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Nilsen, E.T., Sharifi, M.R. & Rundel, P.W. 1987. Leaf dynamics in an evergreen and a deciduous species with even-aged leaf cohorts from different environments. *Am. Midl. Nat.* 118: 48-55.
- Rzedowski, J. 1978. *Vegetación de México*. Limusa, Mexico City.
- Simpson, B.B. & Solbrig, O.T. 1977. Introduction. In: Simpson, B.B. (ed.) *Mesquite. Its biology in two desert scrub ecosystems*, pp. 1-25. Dowden, Hutchinson & Ross, Stroudsburg, PA.
- Summerfield, M.A. 1991. *Global geomorphology*. Longman Scientific & Technical, Harlow.
- Tongway, D.J. & Ludwig, J.A. 1990. Vegetation and soil patterning in semi-arid mulga lands of Eastern Australia. *Aust. J. Ecol.* 15: 23-34.
- Weltzin, J.F. & Coughenour, M.B. 1990. Savanna tree influence on understory vegetation and soil nutrients in northwestern Kenya. *J. Veg. Sci.* 1: 325-334.
- White, L.P. 1970. *Brousse tigrée* patterns in southern Niger. *J. Ecol.* 58: 549-553.
- White, L.P. 1971. Vegetation stripes on sheet wash surfaces. *J. Ecol.* 59: 615-622.
- Wondzell, S. & Ludwig, J.A. 1995. Community dynamics of desert grasslands: influences on climate, landforms, and soils. *J. Veg. Sci.* 6: 377-390.
- Zar, J.H. 1984. *Biostatistical analysis*. 2nd ed. Prentice-Hall, Englewood Cliffs, NJ.

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