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Author(s): Richard I. Yeaton
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A CYCLICAL RELATIONSHIP BETWEEN *LARREA TRIDENTATA* AND *OPUNTIA LEPTOCAULIS* IN THE NORTHERN CHIHUAHUAN DESERT

RICHARD I. YEATON

Department of Biology, University of Pennsylvania, Philadelphia, Pa 19104, *U.S.A.*

SUMMARY

(1) Analysis of the relationships and performance of *Larrea tridentata* and *Opuntia leptocaulis* in the Big Bend National Park, Texas (Chihuahuan Desert), indicated that the former serves as a site for establishment of the latter and is eventually replaced by it.

(2) Burrowing rodents and soil erosion damage the shallow roots of *O. leptocaulis* and, presumably, increase the mortality rate, while having little effect on *Larrea tridentata*. This leaves openings which are colonized by the prolific *L. tridentata*.

INTRODUCTION

Yeaton, Travis & Gilinsky (1977) demonstrated by nearest-neighbour analysis (Pielou 1960) that co-existence of two species in a simple community in the Sonoran Desert could be explained by vertical partitioning of the soil profile by their root systems. A similar approach to an association comprised of *Larrea tridentata* (DC.) Colville and *Opuntia leptocaulis* DC. in the northern Chihuahuan Desert, however, yielded little evidence of interspecific competition and partitioning of resources. The data presented below indicate that, rather than being spatially displaced from *Larrea tridentata*, individuals of *Opuntia leptocaulis* appear to establish directly under the canopy of the former. Dynamic relationships between species in arid habitats have hitherto received little attention, but this association seemed to afford evidence of a cyclical replacement sequence and is interpreted in that context in this paper.

DESCRIPTION OF SITE

The study site was located on flat alluvial plains in a small valley at an elevation of 600 m in Big Bend National Park, Texas (20°10′ N, 103° W). Anthony (1954) gives a general description of the area, which is a northern extension of the Chihuahuan Desert. Annual rainfall is *c.* 250 mm, falling chiefly during the months of July and August. The soils are derived from a mixture of limestone and grey shale (the Boquillas formation—West Texas Geological Society 1972).

The site is intersected by numerous small gullies, 1–10 dm deep. On the flats between these the vegetation is composed almost entirely of *Larrea tridentata* (the creosotebush, a shrub) and *Opuntia leptocaulis* (the Christmas tree cholla, a cylindro-opuntia cactus with

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twig-like branches). Both appear also in and at the edges of the gullies, along with *Prosopis* spp. (mesquite) and *Leucophyllum violaceum* Pennell (silverleaf).

*Larrea tridentata** and *Opuntia leptocaulis*, although variable, are both roughly hemispherical in shape in this habitat; hence the sizes of individuals can be indicated approximately by their diameters (where the outline was not circular, an average was calculated from two measurements, one along the longest axis and the second at right angles to this).

Data were gathered to answer the following questions.

(i) Is one species replacing another?

(ii) If so, what is the mechanism of replacement?

(iii) What prevents the association from becoming a pure stand of *O. leptocaulis?*

METHODS

Three 25 × 25 m quadrats were laid out randomly, and the numbers of individuals of each species in the quadrats were counted and records made of those individuals having either live individuals or dead remains of the other species beneath their canopy. The dead remains of the two species, consisting of stumps and partially buried stems, could be easily distinguished, because the wood of *Larrea tridentata* is solid and its stump composed of multiple stems, whereas the stems of *Opuntia leptocaulis* are hollow and the branches derive from a single main stem. Since *O. leptocaulis* is relatively scarce, the quadrat data were supplemented by examining every isolated individual of *O. leptocaulis* found in the areas around the quadrats until at least 100 had been sampled.

A comparison was then made of the performance of individuals of *Larrea tridentata* growing alone and with *Opuntia leptocaulis* under their canopy. Large individuals (defined as having diameters $>0{\cdot}5$ m) growing alone in quadrat 1 were scored according to the following classes of percentage of living stems: 76–100% alive, (4); 51–75% alive, (3); 26–50%, (2); 1–25%, (1). All individuals growing with *O. leptocaulis* were scored in this way in the quadrats and their surrounding areas. A 2 × 2 contingency table was constructed to test the association of *O. leptocaulis* with vigorous (score (3) or (4)) or non-vigorous (score (2) or (1)) *Larrea tridentata.*

Similarly, the performance of *Opuntia leptocaulis* was examined in relation to that of a sample of large *Larrea tridentata.* Data were obtained from several line transects through the site to provide a sample of at least fifty individuals of each species. Each individual of *O. leptocaulis* was divided along its long axis into four quadrants. Score (4) was allocated if live stems were present in all quadrants, (3) if live stems were present in three out of the four quadrants, etc. This approach was necessary, since a large part of each individual gives the impression of being extremely desiccated during the dry period of the year (the study was conducted in January 1976), although recovery is rapid when the rains fall.

RESULTS AND DISCUSSION

The density of all shrubs in the quadrats is given in Table 1. *Larrea tridentata* and *Opuntia leptocaulis* together accounted for between 93 and 97% of all individuals. Of the population of the latter, 57% (range 23–81%) occurred under the canopy of *Larrea tridentata*, suggesting preferential establishment in this situation. The seeds of *Opuntia leptocaulis* are contained in red fruits dispersed by birds and rodents which probably use *Larrea*

* See Fig. 3 in Yeaton, Travis & Gilinsky (1977), p. 592.

TABLE 1. Density (individuals m^{-2}) of live *Larrea tridentata*, *Opuntia leptocaulis* and other shrubs on three 25 × 25 m plots

Species	Quadrat 1	Quadrat 2	Quadrat 3	Average
Larrea tridentata	0·12	0·33	0·34	0·26
Opuntia leptocaulis	0·02	0·03	0·06	0·04
Other species	0·01	0·01	0·02	0·01
Total	0·15	0·37	0·42	0·31
Proportion of *O. leptocaulis* established under *L. tridentata*	0·23	0·81	0·58	0·57

TABLE 2. Association of *Larrea tridentata* and *Opuntia leptocaulis* with remains of the other species

	Larrea tridentata standing alone	*Opuntia leptocaulis* standing alone
Number of individuals with remains of the other species beneath	4	102
Number of individuals without remains of the other species beneath	495	23

$\chi^2 = 457{\cdot}06$, $P < 0{\cdot}005$.

tridentata as a perch or refuge. Furthermore, the multiple stems of the latter gather fine wind-blown particles which provide a more suitable seed bed for *Opuntia leptocaulis* than the hardened soils of the unvegetated flats (Muller 1953).

Table 2 indicates that 82% of the *O. leptocaulis* standing alone in the study site had the dead remains of *Larrea tridentata* beneath them. It is, however, difficult to determine whether *L. tridentata* is actively replaced by *Opuntia leptocaulis*. Large *Larrea tridentata* growing alone were more vigorous than individuals with *Opuntia leptocaulis* under their canopy (Table 3), while large *O. leptocaulis* individuals were associated with less vigorous *Larrea tridentata* (Table 4). These data and observations of the root systems of the two species suggest that the process involves more than a mere passive replacement of *L. tridentata* by *Opuntia leptocaulis* as the former dies of old age. The root system of *O. leptocaulis* is very shallow, occupying the top decimetre of the soil, and overlies that of *Larrea tridentata* which penetrates into the deeper subsurface layers (exceeding 1 m in depth in the largest individuals at the edges of gullies). When rainfall is in small amounts most of it will thus be intercepted by *Opuntia leptocaulis* roots.

The remaining question concerns the reasons why these processes do not lead to the formation of pure stands by *O. leptocaulis*. There appear to be two causes of reduced vigour in the population of this species. First, rodents burrow preferentially under the bushes and gnaw through some of their roots. Of those growing alone, 69% had one or more rodent burrows, as compared with 7% under *Larrea tridentata* (Table 5). A higher proportion (40%) of the larger individuals of *Opuntia leptocaulis* had burrows beneath them than of the smaller bushes (17%—Table 6). These observations suggest that the bushes (especially the larger ones), which are furnished with sharp spines, afford protection to the rodents (probably *Perognathus merrami gilvus* Osgood and *Dipodomys merrami ambiguus* Merriam (Borell & Bryant 1972)). Secondly, soil erosion by wind and water, although not so frequently observed, exposes the shallow roots of *Opuntia leptocaulis* and leads to breakage, affecting both large and small individuals equally.

These factors appear to have little or no effect on the deeper-rooting *Larrea tridentata*, but in *Opuntia leptocaulis*, where there was evidence of one or both influences at work, 60% of the individuals were scored as non-vigorous, as compared with 24% in their absence (Table 7). It is suggested that these factors increase the rate of mortality of

TABLE 3. Effect of *Opuntia leptocaulis* on the vigour of large individuals (>0·5 m diameter) of *Larrea tridentata*

	Vigorous	Non-vigorous
L. tridentata alone*	35	9
L. tridentata with *Opuntia leptocaulis*†	18	30

$\chi^2 = 14{\cdot}94$, $P < 0{\cdot}005$.

* For individuals in quadrat 1.

† For individuals in all three quadrats and surrounding areas (see text).

TABLE 4. The effect of size of *Opuntia leptocaulis* on the vigour of *Larrea tridentata*

		L. tridentata	
		Vigorous	Non-vigorous
Opuntia leptocaulis	Large*	5	20
	Small*	13	10

$\chi^2 = 5{\cdot}35$, $P < 0{\cdot}025$.

* Large—diameter > 0·5 m; small, < 0·5 m.

TABLE 5. Incidence of rodent burrows under large *Larrea tridentata* and *Opuntia leptocaulis* growing alone

	Larrea tridentata	*Opuntia leptocaulis*
Burrows	6	73
No burrows	80	33

$\chi^2 = 72{\cdot}83$, $P < 0{\cdot}005$.

TABLE 6. Incidence of burrows and soil erosion under large* and small* *Opuntia leptocaulis*

	Large*	Small*
Total sampled	65	60
Number vigorous	29	45
Number with burrows	26	10
Number eroded by wind and water	9	8

* Large—diameter > 0·5 m; small, < 0·5 m.

TABLE 7. Relationship between vigour of *Opuntia leptocaulis* (large and small) and occurrence of burrows and/or soil erosion

		Vigorous	Non-vigorous
Burrows and/or	absent	55	17
soil erosion	present	21	32

$\chi^2 = 15{\cdot}81$, $P < 0{\cdot}005$.

Opuntia leptocaulis without affecting that of *Larrea tridentata*. The locations of dead or dying *Opuntia leptocaulis* are open to colonization by either species. *Larrea tridentata*, however, is the more prolific seed producer of the two, and since establishment of *Opuntia leptocaulis* may be confined to the fine soils collected by the stems of *Larrea tridentata*,

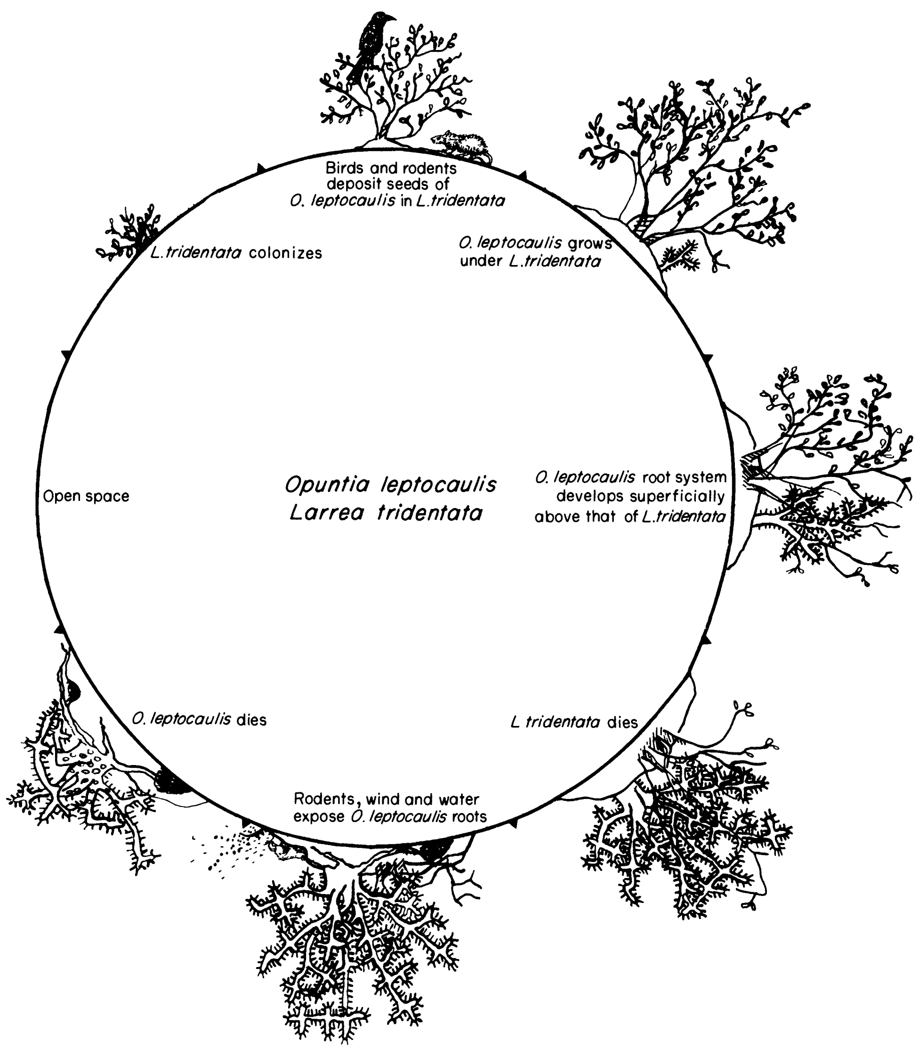

FIG. 1. Diagram of postulated cyclical replacement of *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert.

replacement of *Opuntia leptocaulis* by *Larrea tridentata* is probable. In the light of this it seems possible that a cyclical process is taking place (Fig. 1).

If this is a correct interpretation, the cyclical process may in fact provide the opportunity for the two species to be associated in a habitat where water supply is so limiting as otherwise (perhaps) to support only one. The plant associations quickly become more diverse along the altitudinal gradient from the Rio Grande Valley to the Chisos Mountains (Anthony 1954), indicating that with greater water availability, resource partitioning comes into play rather than cyclical change.

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