

## Do Cholla Cacti (*Opuntia* spp., Subgenus *Cylindropuntia*) use or need nurse plants in the Mojave Desert?

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(1) Three species of *Cylindropuntia* cacti, or chollas, occur in the Mojave Desert of southern California: *Opuntia echinocarpa*, *O. ramosissima*, and *O. acanthocarpa*. The spatial distributions of chollas of different sizes, and presumably ages, were examined at three sites of similar elevation, soils and uniform topography, but at which the densities of the different chollas and of certain other shrubby plants are different.

(2) The youngest chollas are strongly associated with particular nurse plant species (especially the perennial grass *Hilaria rigida*), but differentially among cholla species and between sites with different composition of potential nurses.

(3) Nurse plants are generally replaced by the growing chollas, but some nurse species recur with, and are nursed by, adult chollas. Other shrub species have no importance as cholla nurses, but occur as cholla protegés.

(4) Data are reported on the potential for fruit trapping and herbivore protection by the nurse plants, and for light and water competition between chollas of different ages and other species in the vegetation. The roles of such processes in the dynamics of the cholla populations, and alternative explanations for the nurse plant phenomenon, are discussed.

### Introduction

Recent literature on desert vegetation has emphasized that the spatial disposition of different plant species is by no means random. Some species, often the larger co-dominants, are uniformly spaced, while smaller species might be clumped in their interstices (e.g. Cody, 1986a). A more subtle pattern of considerable ecological interest is the occurrence of some species more or less often than expected by chance as each others' near neighbors (Fonteyn & Mahall, 1981; Cody, 1986a,b,c). When such nonrandom associations are between adults of one species and the juveniles of other, the concept of a nurse plant arises. The nurse plant idea has been discussed particularly for columnar and other cacti species. The basic notion is that a given plant species, the 'nurse', provides appropriate conditions for the establishment of a second plant species, the 'protegé', seedlings of which are thus found disproportionately often in close association with the supposed nurse species.

In most studies it is unclear as to which specific factors the association of the protegé with its nurse species is owed. Possibly specific germination or early growth conditions are provided by the nurse in its modification of the abiotic environment (e.g. increased shade, decreased evaporation). Alternatively the biotic conditions might be particularly favorable, such as complementary rather than competing root systems between nurse and protegé, or a safe haven from herbivores or other sorts of predators. In fact a combination

of these potential advantages to the protégé, rather than a single one, may explain the association. For example, the widely recognized nurse-protégé association of the columnar cactus *Carnegiea gigantea* (Engelm.) Britton & Rose with leguminous trees such as *Cercidium microphyllum* (Torrey) Rose & I.M. Johnston in the Sonoran Desert (Steenburgh & Lowe, 1977) has been attributed to shading effects of the nurse tree (Turner *et al.*, 1966; Despain, 1974) and to frost protection of the young plants (Nobel, 1980).

The association between nurse and protégé species may not be mutually beneficial, as the protégé can cause die-back in the nurse (as does *Carnegiea* in *Cercidium*; McAuliffe, 1984a) and eventually may take over the space from its nurse. This makes the interaction one akin to parasitism or predation (+/-) rather than symbiosis (+/+) or commensalism (+/0); hence nurse and protégé may undergo population cycles in the classical predator-prey fashion, as suggested by Vandermeer (1980) for *Carnegiea* and *Cercidium*. A further example of nurse plant associations between columnar cacti and leguminous trees is that of *Neobuxbaumia tetetzo* (R. Weber ex. K. Schum.) Backeb. with *Mimosa luisana* Brandege in subtropical deciduous woodland in central México (Valiente-Banuet, Vite & Zavala-Hurtado *et al.*, 1991), and other cactus examples are provided by *Mammillaria* and *Echinocereus* spp. under *Opuntia fulgida* Engelm. (McAuliffe, 1984b) and by *Mammillaria* under various shrubby nurses in Baja California (Shainsky, 1978). Protection of the protégé from browsing jackrabbits (*Lepus* spp.) has been implicated in the latter examples.

A corollary of the concept of nurse-protégé plants is that in some circumstances pairs of plant species may serve reciprocally as nurses of each others' juveniles (in a symbiotic, +/+, interaction), leading possibly to a local (patchwise) cyclical succession. For example, Hutto *et al.* (1986) showed that seedling saguaros will become established preferentially under the small shrub *Ambrosia deltoidea* (Torrey) Payne, which in turn occurs in higher density under adult saguaros. With or without reciprocal nursing, in certain arid vegetation types where two species are particularly conspicuous, even co-dominant, a cyclical succession may help to explain plant coexistence and co-dominance. An example is provided by work on *Larrea divaricata*-*Opuntia leptocaulis* in the Chihuahuan Desert (Yeaton, 1978), where the former fosters juveniles of the latter, is eventually outcompeted by the *O. leptocaulis* DC., but becomes re-established in the open space vacated by the *O. leptocaulis* that are dead or dying from the effects of erosion and rodent burrowing on their shallower roots. A similar sequential and alternate occupation of space by different species characterizes the *Acacia schaffneri*-*Opuntia streptacantha* vegetation in central México (Yeaton & Romero Manzanares, 1986).

In the Mojave Desert of southwestern California, three species of cholla cacti (*Opuntia*; subgenus *Cylindropuntia*) occur: *O. acanthocarpa*, *O. echinocarpa*, and *O. ramosissima*. This paper documents the associations of juvenile cholla cacti with other plant species at several sites in the Mojave Desert, and discuss alternative explanations for the patterns of association in relation to the nurse plant and cyclical succession theories.

## Methods

Data on the spatial disposition of cholla cacti were collected at three sites in the Mojave Desert. Two are located in the central Mojave Desert, at the Granite Mountains (GM: 34°48'N, 115°38'W; 1227 m a.s.l.) and the Mid Hills (MH: 35°06'N, 115° 29' W; 1288 m a.s.l.) where all three species occur (*O. acanthocarpa*, *O. echinocarpa*, *O. ramosissima*). These sites were described in detail in Cody (1986a) as GNE and MHE respectively. The third is in the southwestern part of the desert, near Yucca Valley on the west side of Old Woman Springs Road (YV: 34°08'N, 116°25'W; 1100 m a.s.l.), where only the first two species are present. All three sites are located in areas that are topographically extremely uniform, on near-level alluvial bajadas unbroken by washes, drainage channels or surface rocks, with coarse gravelly substrates of decomposed granite.

Plants were surveyed in 0.25 ha at the Granite Mountains and Yucca Valley sites, in 0.28 ha at the Mid Hills for *O. ramosissima*, and in 0.5 ha at this site for *O. acanthocarpa* and

*O. echinocarpa* (which occurred here at lower densities than those of the other cholla). Plant data were recorded (1986–1989) in contiguous 10 m × 10 m quadrats (numbering, e.g., 25 at the GM site) that were counted consecutively at each site.

In each quadrat the numbers of individuals of all plant species > 10 cm high were counted, and quadrats searched for young chollas (regardless of size). Each cholla located was measured (height  $H$ , maximum width  $W$ , and the number of terminal joints  $T$ , thereby providing a good index of overall plant size and photosynthetic area. The distance to stem and canopy of its first and second near-neighbour were also measured. The identities, heights and widths of these near-neighbours were then recorded. Further, 250 quasi-random points were located in each site, from which the total plant cover, and the relative cover values of each plant species present, were calculated. Note that, in this open and sparse vegetation, such points are nearly always located within the cover of a single plant individual, or else in the open. There is, in general, very little shading of one species by another, with two sorts of exceptions; some smaller shrubs are found partially or wholly within the (vertically projected) canopy of certain larger and open-canopied plants, and young chollas, single-stemmed or scarcely branched, are often found within or emerging from the cover of low-spreading potential nurse species. Thus point-counts nearly always record but a single plant species.

At YV the ground was searched for *O. echinocarpa* fruits, and their locations noted. At this site and at GM the shading characteristics of potential nurse shrubs were measured in terms of the proportion of the ground shaded at noon beneath the plant canopy (in February, YV, and in June, GM). Both horizontal and vertical density profiles were made of a selection of plant species at both of these sites, and the proportion of the foliage of a plant that is within 5 cm of the ground, an index of ground-level vegetation for that species, is used as a measure of fruit-trapping potential.

Lastly, what light (if any) stability theory might shed on nurse-protégé populations and reciprocal nursing was also examined. Appendix A contains a loop analysis (Levins, 1975; Puccia and Levins, 1985) of reciprocal nursing in two plant species  $X$  and  $Y$ , and the results of this analysis are discussed below.

## Results

### *General Site Characteristics*

The overall characteristics of the three sites are given in Table 1. Total plant cover and overall plant density vary about 2-fold among sites, although plant species number (24 to 28) is relatively similar. The densities of the three cholla species vary widely among sites, but the proportion of the total plant numbers that is comprised of chollas remains nearly constant at 9–11%. The relative cover and density values of all perennial plants counted at the sites are shown in Table 2. The reduced total cover in GM is associated with the high densities there of the larger shrubs *Yucca schidigera*, *Larrea divaricata* and *O. acanthocarpa*, and the overall higher plant density at YV is owed chiefly to an abundance of the perennial grass *Hilaria rigida*, and of several smaller shrubs (*Krameria*, *Gutierrezia*, and *Salazaria*).

### *Yucca Valley*

At the YV site *O. echinocarpa* is the most conspicuous cholla; the 0.25-ha census yielded 196 *O. echinocarpa* individuals, of which 149 were rooted within the vertical projections of other plant canopies, and 47 were rooted in the open;  $p < 0.001$  that this might occur by chance (Chi. sq. = 39.2, df. = 1). But the youngest *O. echinocarpa* are small compared to most shrubs, and their association with larger shrubs indicates a potential nurse plant effect. On the other hand, adult *O. echinocarpa* reach considerably larger sizes (> 1.5 m tall) than do most other shrubs present (< 1 m), and the association of these large cacti with

**Table 1.** General site characteristics for three *Opuntia* (*cholla*) and nurse plant study areas in the Mojave Desert. YV = Yucca Valley (Old Woman Springs Road); GM = Granite Mountains (Northeast); MH = Mid Hills (East of Chicken Water Spring)

Variable:	Site:	YV	GM	MH
No. of perennial plant species		24	28	28
No. of plants > 10 cm high ha <sup>-1</sup>		14,876	6382	7868
Total plant cover*		53%	26%	55%
No. of plants ha <sup>-1</sup> of				
<i>O. ramosissima</i> Engelm.		760	300	493
<i>O. echinocarpa</i> Engelm. & Bigelow		784	56	82
<i>O. acanthocarpa</i> Engelm. & Bigelow		0	356	148
Total <i>cylindropuntias</i> ha <sup>-1</sup>		1544	712	723
Prop. of all peren. plant individuals		0.104	0.112	0.092

\* % of ground that is below the living plant canopies; the remainder is open ground.

**Table 2.** Plant densities and cover values at three sites in the Mojave Desert. 'Cover' means relative cover; the proportion of total plant cover that is made up by each plant species respectively; 'f' indicates a species' frequency in the total plant count, or its density relative to all plants at the site

Plant species:	Site:	YV		GM		MH	
		Cover	f	Cover	f	Cover	f
<i>Hilaria rigid</i> : (Thurb.) Benth.		0.296	0.372	—	—	0.145	0.329
<i>Coleogyne ramosissima</i> Torrey		0.229	0.095	0.081	0.086	0.0008	0.0005
<i>Eriogonum fasciculatus</i> Benth.		0.063	0.066	0.017	0.061	0.0012	0.003
<i>Ephedra nevadensis</i> S. Wats.		0.058	0.046	0.014	0.033	0.079	0.035
<i>Opuntia ramosissima</i> Engelm.		0.050	0.051	0.025	0.028	0.112	0.038
<i>Opuntia echinocarpa</i> Engelm. & Bigelow		0.038	0.059	0.004	0.021	0.0008	0.006
<i>Acamptopappus sphaerocephalus</i> (Harv. & A. Gray) A. Gray		0.036	0.038	0.007	0.034	0.045	0.076
<i>Senna arnata</i> (S. Wats) Irwin & Barneby		0.033	0.027	—	—	0.069	0.049
<i>Yucca schidigera</i> Roel. ex Ortgies		0.029	0.026	0.178	0.034	0.007	0.001
<i>Hymenoclea salsola</i> Torrey & A. Gray		0.025	0.027	0.077	0.080	0.149	0.069
<i>Tetradymia spinosa</i> Hook. & Arn		0.025	0.006	0.062	0.098	0.012	0.009
<i>Yucca brevifolia</i> Engelm.		0.023	0.016	—	—	0.039	0.008
<i>Gutierrezia microcephala</i> (DC.) A. Gray		0.021	0.038	0.0007	0.003	0.006	0.010
<i>Krameria parvifolia</i> Benth.		0.017	0.030	0.0001	0.0006	—	—
<i>Salazaria mexicana</i> Torrey		0.017	0.050	0.006	0.032	0.007	0.008
<i>Larrea divaricata</i> Cav.		0.017	0.003	0.190	0.018	0.003	0.0003
<i>Yucca baccata</i> Torrey		0.011	0.009	—	—	0.006	0.0009
<i>Haplopappus cooperi</i> (Gray) Hall		0.005	0.019	0.048	0.202	0.161	0.179
<i>Echinocereus engelmannii</i> (Parry) Lemaire		0.004	0.009	0.003	0.010	0.0004	0.002
<i>Opuntia basilaris</i> Engelm. & Bigelow		0.002	0.007	0.001	0.004	—	—
<i>Stipa speciosa</i> Trin. & Rupr.		0.0009	0.004	0.0004	0.003	0.0011	0.010

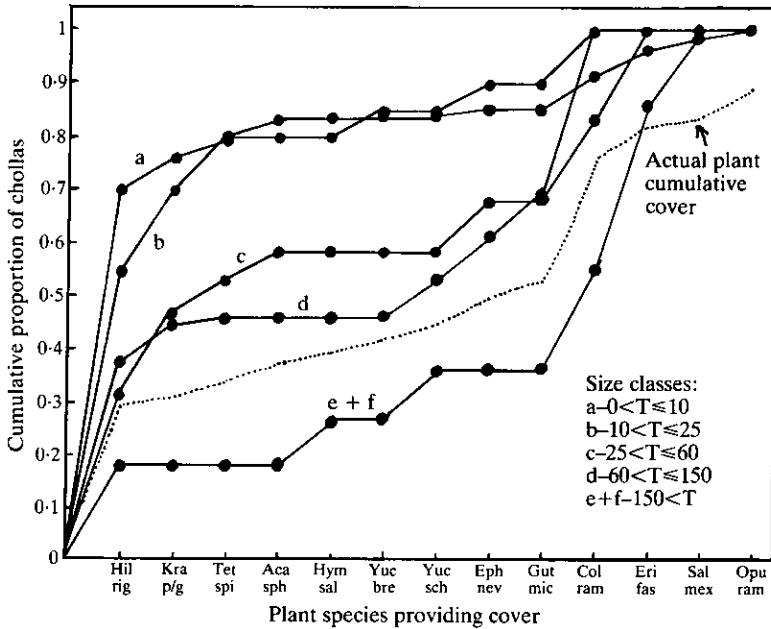
Table 2. *Continued*

Plant species:	Site:	YV		GM		MH	
		Cover	f	Cover	f	Cover	f
<i>Stephanomeria pauciflora</i> (Torrey) A. Nels		0.0006	0.002	0.0006	0.005	—	—
<i>Krameria grayi</i> Rose & Painter		0.0005	0.0005	—	—	—	—
<i>Opuntia phaeacantha</i> Engelm. & Bigelow		0.0001	0.0003	—	—	—	—
<i>Opuntia acanthocarpa</i> Engelm. & Bigelow		—	—	0.204	0.053	0.023	0.009
<i>Haplopappus linearifolius</i> DC.		—	—	—	—	0.008	0.005
<i>Thamnosma montana</i> Torrey & Frém.		—	—	0.040	0.076	0.111	0.084
<i>Menodora spinsecens</i> A. Gray		—	—	0.022	0.099	0.002	0.003
<i>Salvia dorrii</i> (Kell.) Abrams		—	—	—	—	0.004	0.058
<i>Muhlenbergia porteri</i> Scribn.		—	—	—	—	0.007	0.058
<i>Ferocactus acanthodes</i> (Lemaire) Britton & Rose		—	—	—	—	0.0001	0.0001
<i>Acacia greggii</i> A. Gray		—	—	0.008	0.002	0.0011	0.0004
<i>Coryphantha vivipera</i> (Nutt.) Britton & Rose <i>desertii</i> (Engelm.) T. W. Marshall		—	—	—	—	0.00001	0.00003
<i>Dalea fremontii</i> Torrey		—	—	0.0016	0.0007	—	—
<i>Lycium andersonii</i> A. Gray		—	—	0.005	0.003	—	—
<i>Lycium cooperi</i> A. Gray		—	—	0.004	0.002	—	—
<i>Mammillaria tretrancistra</i> Engelm.		—	—	0.00004	0.0011	—	—
<i>Porophyllum gracile</i> Benth.		—	—	0.00003	0.002	—	—
<i>Viguiera deltoides</i> A. Gray		—	—	0.001	0.0007	—	—

other (smaller) shrubs is more likely to reflect the invasion of their canopy areas with *O. echinocarpa* as nurse rather than as protégé.

Subdivision of the *O. echinocarpa* population into size classes makes this distinction clear; the use of  $T$  (= number of terminal joints) is a better indication of plant size, since it is more directly related to plant photosynthetic area and shrub volume than is either  $H$  (height) or  $W$  (width). Five size classes of *O. echinocarpa* show differences in their cumulative proportions with which they are rooted within the canopies of other plant species (Fig. 1). These other plants are ranked along the abscissa successively, from those showing strong associations with the smallest cacti at the left to those showing strongest associations with the largest cacti to the right (see Fig. 1). Note that 70% of the 86 individuals in the smallest size class are rooted within the perennial grass *Hilaria rigida*; this percentage drops in successively larger size classes to 55%, 32%, 38% and to 18% in the largest cacti. Likewise two species of *Krameria*, *K. parvifolia* and *K. grayii*, appear to act as nurse plants for the youngest cacti, and are associated especially strongly with the 'a' and 'b' size classes ( $T \leq 25$ ). On the other hand, some shrub species, particularly *Eriogonum fasciculatum* and *Salazaria mexicana*, associate with the largest cacti but not at all with the youngest, indicating that they establish preferentially within the shelter of the largest *O. echinocarpa*. The cumulative frequency of plant cover long the abscissa is shown as a dotted line in the figure.

Another view of these interactions is given in Fig. 2, where chi-square (ordinate) is used to compare the expected (E) to observed (O) numbers of cacti in different size classes within the cover of various shrubs. The association of the youngest cacti with *H. rigida* declines to insignificance with increasing cholla size (and presumably, age), indicating a

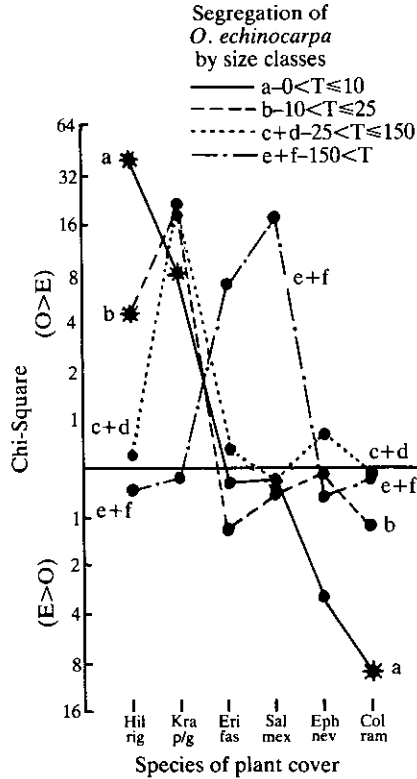


**Figure 1.** Five different size classes of *Opuntia echinocarpa* at Yucca Valley, Mojave Desert, measured in terms of numbers of terminal joints  $T$  and increasing from  $a$  through  $e + f$ , are shown as functions of the cumulative proportions of individuals in each size class (ordinate) vs. the (rank ordered) plant species with which they are closely associated. These plant species are ranked on the abscissa from those to the left which are strongly favored by the smallest *O. echinocarpa* individuals, to those at the right which are associated preferentially with the largest chollas. The dotted curve represents the cumulative relative cover at the site of the plant species ranked on the abscissa.

replacement of the grass by the cactus. There are also significant nurse effects with *Krameria*, with perhaps better survival of protégés associated with *Krameria* than with *Hilaria*, as indicated by stronger positive associations in size classes 'b' and 'c' than in class 'a'. *Coleogyne ramosissima* is significantly avoided by the smallest cacti, but no such effect is detectable with the larger cacti ( $T \geq 150$ ), which however do show a tendency to be positively associated with *Eriogonum* and *Salazaria*, presumably by acting in their turn as nurse plants. While 8.8% of the total plant cover at the site (see Table 2) was provided by *Opuntia echinocarpa* and *O. ramosissima*, the observed number of cacti within *Opuntia* cover is significantly less than what is expected by chance ( $O = 1$ ;  $E = 13.1$ ;  $\text{chi-sq.} = 11.2$ ,  $p < 0.01$ ).

### Mid Hills

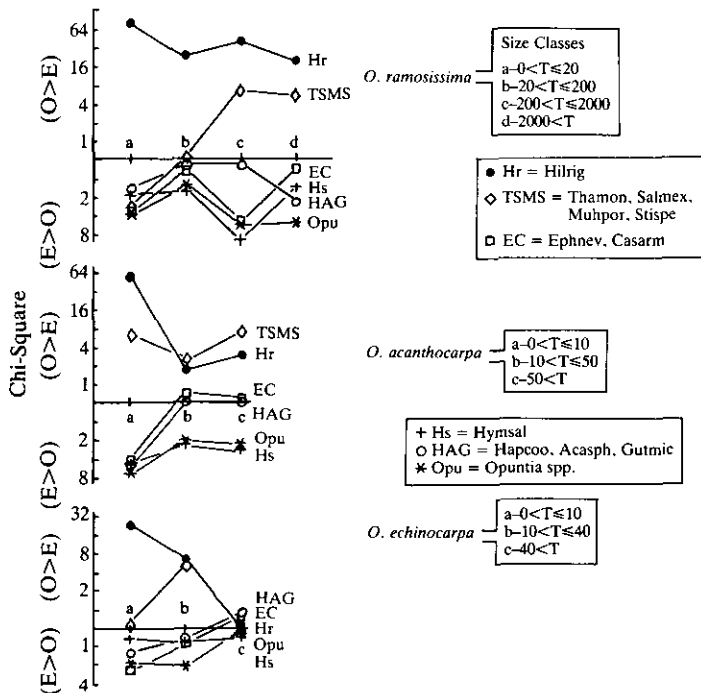
The most common cholla at the Mid Hills site is *O. ramosissima*, with 138 individuals found in 0.25 ha. Of the 24 smallest (in size class 'a',  $T = 1-20$ ), all were rooted in plant cover; at a site where overall plant cover is 54.3% this association might happen by chance with  $p = 4.3 \times 10^{-7}$ . Similarly, all forty of the smallest *O. acanthocarpa* ( $T \leq 10$ ) are rooted within plant cover, again with a vanishingly small probability of this happening by chance. Given that the cholla seedlings are strongly associated with plant cover, are they distributed among different plant species at random? Fig. 3 shows how the different size classes of chollas are associated with different plants or plant groups. There is a strong tendency for all three species to be found in *Hilaria* clumps (even though this grass is just half as common at this site as it is at YV). But while *Hilaria* declines slowly under the growing *O. ramosissima*, it does so more precipitously under the denser canopies of



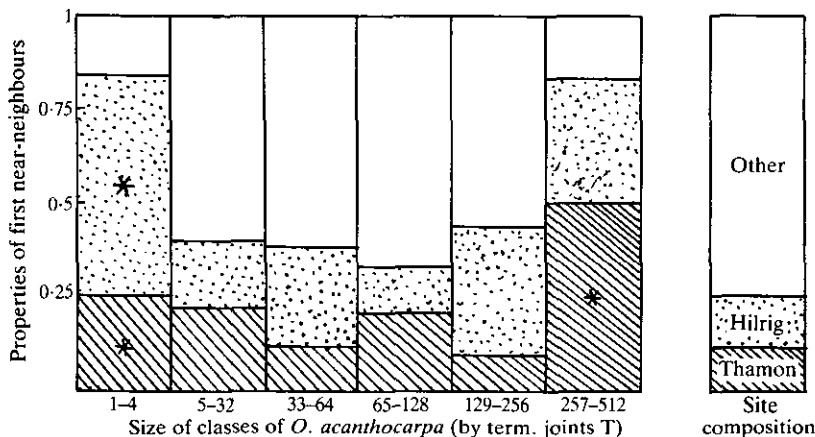
**Figure 2.** The segregation of *Opuntia echinocarpa* by different size classes  $T$  at Yucca Valley with cover of different plant species is shown by chi-square values. Association with *Hilaria rigida* declines with increasing cholla size, but that with *Krameria* is maintained through larger cholla sizes. Species ranked to the right are avoided by the juveniles, but are noninteractive with the adults. Species in the midrange, *Eriogonum fasciculatum* and *Salazaria mexicana*, appear to invade the largest chollas, which may act their nurse plants.  $O$  = observed,  $E$  = expected; starred dots indicate statistical significance at  $P < 0.05$ .

*O. echinocarpa*, and at an intermediate rate under *O. acanthocarpa*, implying shading effects on the nurse by the growing chollas. Chollas of all species and sizes tend to avoid other *Opuntia*, and also some other shrubs such as *Hymenoclea*. Two species groups, HAG (*Haplopappus cooperi*/*Acamptopappus sphaerocephalus*/*Gutierrezia microcephala*) and 'EC' (*Ephedra nevadensis*/*Senna armata*), in which species are grouped by similarity in stature and growth form, tend to be negatively associated with cholla seedlings, especially those of *O. acanthocarpa*, but they and adult chollas seem non-interactive (in that they occur as neighbours according to chance). A third group of species, 'TSMS' (dominated by *Thamnosma montana* and including the mint *Salazaria* and two perennial grasses *Muhlenbergia porteri* and *Stipa speciosa*) is negatively associated with seedling *O. ramosissima*, but these species can apparently establish adjacent to the adults. Species in this group are favoured nurse plants of young *O. acanthocarpa*, which as adults apparently foster their erstwhile nurse species in reciprocal fashion.

The reciprocal nursing phenomenon is illustrated a little more clearly in Fig. 4. Whereas *Hilaria* shows a limited ability to persist under the growing *O. acanthocarpa*, *Thamnosma* seems particularly good at recolonizing the space around the adult chollas, after first dying out following their nurse phase. A further indication that this happens is given by the fact that protégé *O. acanthocarpa* are rooted on average  $5.7 \pm 5.3$  cm from nurse *Thamnosma*, whereas protégé *Thamnosma* are rooted significantly further away ( $40.0 \pm 17.8$  cm) from adult (nurse) *O. acanthocarpa* ( $t = 3.78$ ;  $p < 0.01$ ).



**Figure 3.** Associations of three different cholla species at the Mid Hills, Mojave Desert, with the cover of different plant species and species groups. All cholla species show a nurse effect with *Hilaria rigida*, but the nurse declines at different rates under different growing chollas. One species group, TSMS, invades the largest *Opuntia ramosissima* and midsize *O. echinocarpa*, and seems to participate in reciprocal nursing with *O. acanthocarpa*. (Species abbreviations in the key use the first three letters of genus and species; refer to Table 2 for full species names).



**Figure 4.** Reciprocal nursing is indicated for *Thamnosma montana* and *Opuntia acanthocarpa* at the MH site, with statistically significant associations in both smallest and largest size classes of chollas, but not in intermediate sizes. *Hilaria rigida* acts as a nurse plant, but does not in turn invade adult chollas to a significant extent.



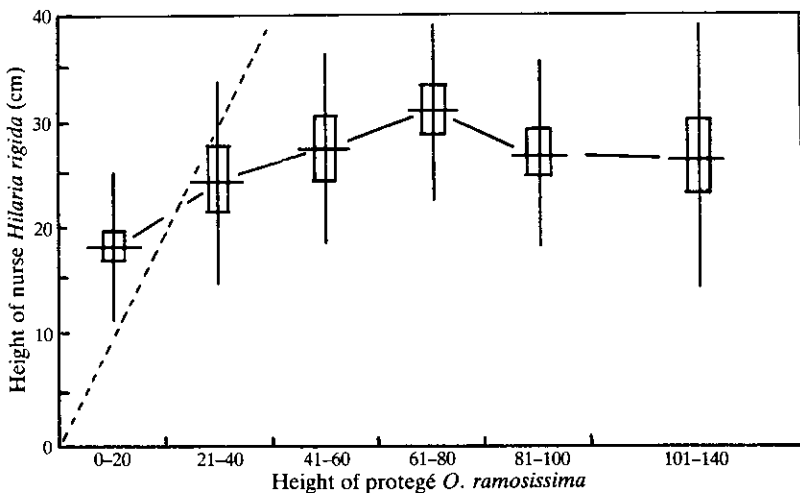
Although it appears that *Hilaria* is eventually replaced by its protegés, Fig. 5 shows that the grass grows taller (and presumably sets more seed) around the growing juvenile chollas, and begins to decline only after the growing chollas exceed  $\pm 70$  cm in height. It should be stressed that these variations in *Hilaria* are measured over topographically uniform conditions, and the height of the associated cactus is the only apparent microsite variable. Thus there may be a symbiotic relationship in the early nursing stages, with baby *O. ramosissima* escaping detection in *Hilaria*, but its spiny presence affording some protection to the grass from large mammalian herbivores as they both grow taller.

### Granite Mountains

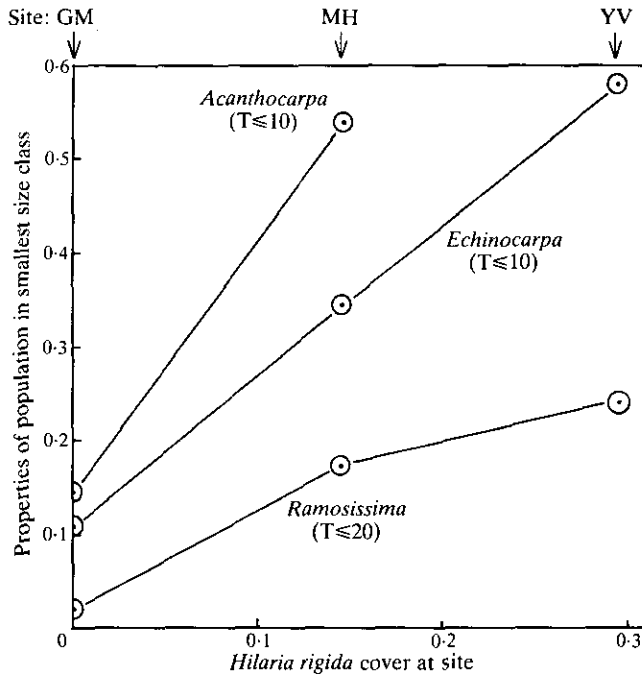
The Granite Mountains site is quite different from the first two in one obvious respect: *Hilaria rigida* is absent. Despite the absence of this prime nurse plant, chollas are as common at this site as at the previous two (see Table 1). In the first two sites, around three-quarters of the juvenile chollas are associated with *Hilaria*; here, with no *Hilaria* present, seedlings are correspondingly scarcer. The influence of this reduction in nurse plant availability is reflected in the difference in size- or age-distributions among sites, with only 15% (*O. acanthocarpa*) or less (other chollas) of the Granite Mountains populations contained in the smallest size classes (see Fig. 6).

Despite the relative paucity of smaller individuals at this site, the youngest *O. acanthocarpa* again tend to be preferentially located within the cover of other plants, with 17 of 18 individuals in size class 'a' ( $1 \leq T \leq 20$ ) within cover ( $p < 0.001$  that this happens by chance). But size class 'b',  $21 \leq T \leq 100$ , is distributed at random with respect to cover (6/16 in cover,  $p > 0.10$ ). In the other common chollas at this site, *O. ramosissima*, juveniles are too rare to permit an evaluation of potential nurse plants.

Different size classes of *O. acanthocarpa* are associated with different plants or plant groups at the GM site. Size class 'a' ( $T \leq 20$ ) is strongly associated with *Thamnosma montana* and *Menodora spinescens* (see Fig. 7), both of which (but especially the former) tend again to become preferentially associated with the largest ( $T \geq 200$ ) *O. acanthocarpa*



**Figure 5.** The nurse plant *Hilaria rigida* increases significantly in stature (ordinate) as its protégé *Opuntia ramosissima* grow in size ( $t$ -test;  $P < 0.05$ ); the larger *O. ramosissima* may reduce browsing on the nurse plant. The declining nurse stature under the tallest *O. ramosissima* correlates with their declining frequency under growing *O. ramosissima*, perhaps through shading effects.



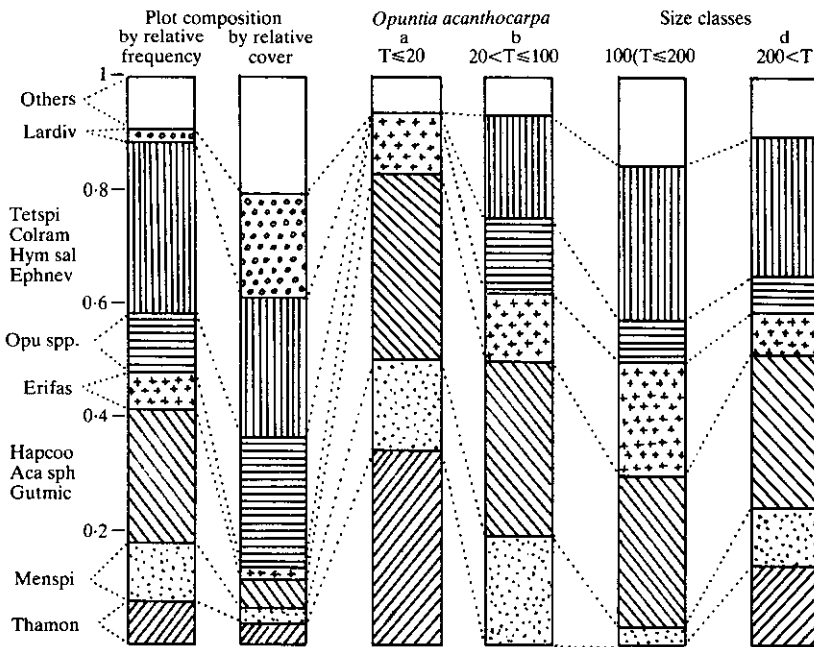
**Figure 6.** *Hilaria rigida* cover varies widely among the three Mojave Desert sites GM, MH and YV. This variation correlates with changes in the age/size distribution of the chollas present, although it does not affect the representation of chollas in the total cover of the vegetation.

individuals, indicating reciprocal nursing. As Fig. 7 show, all size classes tend to be negatively associated with *Opuntia* and with *Larrea divaricata* (which together account for 42% of the cover at this site). One group of plants, *Tetradymia/Coleogyne/Hymenoclea/Ephedra* of combined cover 24%, is negatively associated with juvenile cacti, but relatively neutral with respect to larger *O. acanthocarpa*, while *Eriogonum fasciculatum* tends to associate more often than expected by chance with the middle-sized individuals of this cholla.

#### Nurse plant characteristics

The *Opuntia* spp. in question belong to a suite of dry-fruited species (others are fleshy-fruited), with fruits maturing in late summer and falling to the ground during the ensuing months. In the winter and spring few fruits remain on the shrubs, but many entire fruits can be found on the ground. These fruits are light and dry, spiny and nearly spherical; many remain beneath the parent plant months after falling, but others are found dispersed from the parent, possibly blown around by wind; the surface flow of water following heavy rains may also transport the fruits, and being carried to nests by woodrats (*Neotoma*) may further contribute to their dispersal.

In late winter the majority of fallen fruits are found under the parents or in shallow erosion gullies (where in either situation the survival of germinated seeds is apparently minimal, since virtually no seedlings occur in these situations). But elsewhere in the vegetation, different plant species serve as traps for the spiny, wind-blown fruits with



**Figure 7.** Associations of different size classes of *Opuntia acanthocarpa* with different plant species at the Granite Mountains site. The two important nurse plants are *Thamnosma montana* and *Menodora spinescens*, which are represented by modest relative density and cover in the plot (see two left-hand columns), but are both overrepresented as nurses for juvenile *O. acanthocarpa* ( $T \leq 20$ ). The latter declines less rapidly than the latter with the growing cactus, and shows a weaker tendency to invade the largest chollas; the former shows a clear reciprocal nursing relationship, being significantly commoner than expected with both smallest and largest chollas, but absent from the two intermediate size classes.

variable effectiveness. A survey of cholla fruits at the YV site discovered thirty-six entire fruits either in the open or in (or under) other plant species. Dividing numbers of fruits found by plant cover (or by open ground 'cover'), 'fruit trapping effectiveness' was calculated for various plant species as shown in Table 3. Notably the species ranked 1–3 in fruit trapping effectiveness correspond to the species ranked as most effective in nursing seedling cacti (Fig. 1): *Hilaria rigida*, *Krameria* spp., and *Tetradymia spinosa*.

The important feature of fruit-trapping plants seems to be the extent and density of their vegetation at ground level, as this serves to intercept the wind-blown fruits. I measured shading characteristics and ground-level vegetation density of the more common species at the YV and GM sites, with results shown in Table 3. At the GM site (where fruits lying on the ground were not included) species ranking 1–3 in ground-level vegetation density (N.B. *Hilaria* is absent and *Krameria* very rare) are *Thamnosma montana*, *Menodora spinescens*, and *Eriogonum fasciculatum*. These are just those species ranking 1–3 with positive associations with young chollas and classified above as nurse plants.

Thus the species that apparently act as nurse plants for young chollas are those that are densely spreading at ground level and can trap dispersing fruits. They are also species that cast a lot of shade, with figures as high as 96% in *Hilaria* and 84% in *Krameria* (the YV nurses), and 76% and 67% for *Thamnosma* and *Menodora* respectively (the MH nurses). Other species that cast a dense shade, such as *Coleoyne*, *Salazaria*, *Senna*, and *Opuntia* itself, have low densities at ground level and also have low fruit-trapping potentials.

**Table 3.** Fruit-trapping, shading and density characteristics of some Mojave Desert plants. Nurse plants strongly (\*\*) or less strongly (\*) associated with seedling chollas are so indicated. Plants absent from a site marked '—'

Plant species	Fruit trap* effectiveness	% shading†	Ground-level density†
<i>Krameria</i> spp. **	53	84	24
<i>Hilaria rigida</i> * (Thurb.) Benth.	44	96	27
<i>Tetradymia spinosa</i> Hook. & Arn.	40	51	1
<i>Opuntia ramosissima</i> Engelm.	40	43	1
<i>Ephedra nevadensis</i> S. Wats	34	30	12
<i>Yucca schidigera</i> Roezl ex Ortgies	34	51	2
<i>Eriogonum fasciculatum</i> Benth.	32	55	14
<i>Coleogyne ramosissima</i> Torrey	26	69	3
Open ground	17	0	0
<i>Salazaria mexicana</i> Torrey	0	81	3
<i>Gutierrezia microcephala</i> (DC.) A. Gray	0	43	9
<i>Hymenoclea salsola</i> Torrey & A. Gray	0	23	2
<i>Senna armata</i> (S. Wats.) Irwin & Barneby	0	73	3
<i>Opuntia echinocarpa</i> Engelm. & Bigelow	++	82	0
<i>Acamptopappus sphaerocephalus</i> (Harv. & A. Gray) A. Gray	0	31	7
<i>Haplopappus cooperi</i> (A. Gray) Hall	0	40	0
<i>Larrea divaricata</i> Cav.	0	5	2
<i>Yucca brevifolia</i> Engelm.	0	12	0
<i>Thamnosma montana</i> ** Torrey & Frém.	—	76	22
<i>Menodora spinescens</i> ** A. Gray	—	67	18
<i>Opuntia acanthocarpa</i> Engelm. & Bigelow	—	39	4

\* Measured at the YV site; † measured at YV and GM sites.

## Discussion

The predominant pattern is that juvenile chollas occur significantly more often than expected in the cover of other plants; nurse plants then can be defined as those species with which juvenile chollas show preferential association. *Hilaria rigida* and *Krameria* serve this function for all chollas, and *Thamnosma montana* and perhaps *Menodora spinescens* do also for *O. acanthocarpa* at GM where other nurse species are absent. The patterns of association change with cholla size (= age); nurse plants are supplanted by the growing chollas, which in turn are 'colonized' by plants finding suitable germination and growing conditions in their immediate vicinity. Nurse plants might in fact compete both above ground (for light) and below ground (for water) with seedling chollas, yet nurse plants evidently provide the necessary conditions for germination and survival; the vast majority of the juvenile chollas are found in such associations and not elsewhere. Although *Hilaria* especially is an important nurse plant (Figs 1–4), adult cholla density is just as high in its absence (Table 1); it seems then that the size of the adult populations is neither seed nor seedling limited, nor limited by the survival rate of the juveniles (assuming this to be variable with nurse plant quality). As adult chollas tend to be uniformly spaced in the vegetation (Cody 1986a), growing space for the adults, and their wide-spreading root systems, is the most likely limiting factor, at least in these study sites.

Both *Hilaria* and *Krameria* decline in frequency under growing chollas; this appears to be due to the effects of shading by the chollas, as the decline is more pronounced under the denser cholla species. It seems unlikely that the nurse plants are adversely affected by competition for water, since *Hilaria* is very shallowly rooted (unlike the chollas) and *Krameria* is a root parasite on various shrubby species. On the other hand, the Granite

Mountains *O. acanthocarpa* nurse plants, *Thamnosma* and *Menodora*, are both more deeply rooted, and the decline of the former under growing chollas might be attributable to root competition (and predicting more shallow roots in *Menodora*, with its better survival following the nurse stage).

A symbiotic interaction between *O. ramosissima* and *Hilaria* seems possible, in that the young chollas may reduce browsing on the grass, and enable it to grow taller where the two grow together (Fig. 5). Such effects might also apply to other nurse species. Although both *Krameria* and *Thamnosma* show virtually no browsing damage at the field sites (and may be chemically protected), *Menodora* and *Eriogonum* are heavily browsed, and may derive a measure of protection from harbouring growing chollas. Recall that both species, especially the former, survive cholla growth well after nursing young *O. acanthocarpa* (Fig. 7).

Reciprocal nursing seems likely with *O. acanthocarpa* and its nurse *Thamnosma* (at both the MH and GM sites), and perhaps to a lesser extent with *Menodora* at GM. Supplanting of the nurse plants by their protégés in this case might be attributable to root competition for water, with both tiny chollas (with shallow root systems and low water demand) and large chollas (with deeper root systems and high demand) compatible with *Thamnosma* but intermediate-sized chollas not so compatible.

Reciprocal nursing may produce a cyclical succession, such that a patch of ground might be occupied sequentially over time first by one species *X* and then another *Y*; patches occupied by *X* are invisable only by the juveniles *y* of the other species, and vice versa. The notion of reciprocal nursing is close to the concept of intransitive competition, often cited in the marine ecological literature (e.g. Buss, 1986). Where marine invertebrates compete for space within the intertidal (e.g. bryozoa) or subtidal (e.g. coral) zones, species *A* may overcome species *B* which in turn overcomes species *C*; yet species *C* can take over species from species *A*. In desert vegetation a similar intransitivity may be mediated apparently by different ages or sizes in the plant species involved. A loop analysis approach (see Appendix A) shows that reciprocal nursing can be broadly stable, but with cycles in population sizes of nurse and protégé likely. A further and rather surprising conclusion is that there may be indirect benefits to nurse species, in that their populations are enhanced (in density) through evolution in the protégés, but not by evolution in other system components (see Appendix A).

Some plant species are successful invaders of the space around adult chollas, especially *Eriogonum fasciculatum* and *Salazaria mexicana*, with the former but not the latter serving to some extent as a nurse plant for *O. acanthocarpa*. The two perennial grasses in this vegetation other than *Hilaria*, namely *Stipa speciosa* and *Muhlenbergia porteri*, also show a significant association with adult chollas (Fig. 3), perhaps thereby gaining a measure of protection from large mammalian herbivores to which they are both susceptible. *Stipa* in particular is a prime forage plant, and is browsed virtually to the ground where unprotected from cattle. Invasion of the space beneath adult chollas is more discernible in those chollas with more open canopies (i.e. not *O. echinocarpa*), and might well be facilitated by jackrabbit browsing on the lower branches of adult chollas (pers. obs.; L. Sosa-Burgos MS) which opens up their perimeters to light and therefore provides potential growth sites in close proximity to the larger cacti.

Early seedling survival, if not germination also, is evidently most strongly associated with the plants that are effective fruit traps. Plant species that have dense vegetation low to the ground serve as effective traps for wind-blown cholla fruits, and these are just the species that serve as cholla nurse plants. The same species also cast a dense shade, but other plants with dense shade but little or no ground-level vegetation are ineffective fruit traps and unimportant as nurse plants. Parents and congenics are evidently poor cholla nurses in all cases, despite the abundance of fruit on the ground nearby (Table 3); this might presumably be the case either because of poor protection from browsing jackrabbits afforded juveniles under adult chollas, severe root competition with the growing juveniles, or both.

Nurse plants are not all equally good hosts for growing chollas, and cholla seedlings seem to survive less well in the grass *Hilaria* than in woody shrubs such as *Krameria*; whether this is because the woody shrubs provide better protection than grass for the cholla juveniles, the grass is a stronger competitor for water than is the root-parasitic *Krameria*, or whether the cholla juveniles later eliminate the grass more readily than the shrubs through shading and/or root competition and therefore the association does not persist, is not clear.

Chollas can and do germinate in the open, but such seedlings are relatively scarce, apparently because they suffer very high browsing rates from jackrabbits, cottontails *Sylvilagus*, and perhaps woodrats *Neotoma*. As evidence for this, their remains are routinely found — much chewed and skeletal stems surrounded by piles of faeces, particularly of *Lepus*. Overall, the evidence suggests that the primary influences of nurse plants on cholla germination and survival are biotic (via dispersal mechanisms, protection from herbivory, and possibly amelioration of root competition for moisture), rather than abiotic (shading and/or frost protection).

A series of experimental exclosures has been established to cast more light on the alternative factors promoting cholla establishment under different sorts of nurse plants, and the results from these experiments are pending. This work will not illuminate the interesting long-term dynamics suggested by the loop model, but should help evaluate the roles of predation and herbivore protection in its component links.

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### Appendix: a Theoretical addendum

Using the qualitative techniques of loop analysis (Levins, 1975; Puccia & Levins, 1985), the simplest representation of reciprocal nursing is given in Fig. 8. Here two vertices represent the populations of adult individuals of species *X* and *Y*, which are self-damped and in competition due to space limitations; two other vertices *x*, *y* represent the juvenile individuals of the species, each succoured by and eventually displacing adults of the other species, and each contributing eventually to the adult populations of its own species. For (asymptotic) stability, feedback at all levels  $F_i$  must be negative; here the feedback is given by

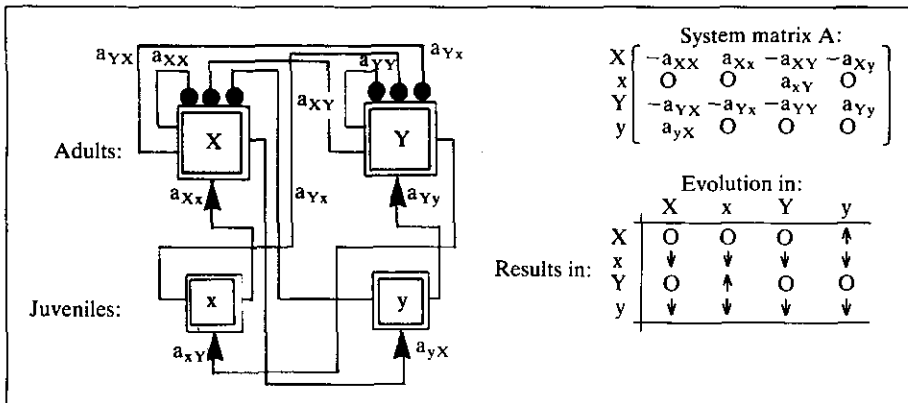
$$\begin{aligned} F_1 &= -a_{XX} - a_{YY}; F_2 = -a_{XX} a_{YY} + a_{XY} a_{YX} - a_{Xy} a_{yX} - a_{Yx} a_{xY}; \\ F_3 &= -a_{XX} a_{Yx} a_{xY} - a_{YY} a_{Xy} a_{yX} - a_{XY} a_{yX} a_{Yy} - a_{YX} a_{xY} a_{Xx}; \\ F_4 &= -a_{Yx} a_{xY} a_{Xy} a_{yX} + a_{yX} a_{Yy} a_{xY} a_{Xx} = -a_{xY} a_{yX} (a_{Yx} a_{Xy} - a_{Yy} a_{Xx}). \end{aligned}$$

Note that competition among adults ( $a_{XY} a_{YX}$ , contributing to positivity in  $F_2$ ) is offset by three negative components in the  $F_2$ , and that the  $F_4$  will be net negative as long as nurse-protégé competition ( $a_{Yx} a_{Xy}$ ) is strong while growth and/or survival ( $a_{Yy} a_{Xx}$ ) remains weak or tenuous. The system depicted assumes no limit in seed supply (no direct links from adults to seedlings); if in fact seed production were limiting, two positive terms would be added to the  $F_2$ , four positive terms to the  $F_3$ , and one positive term to the  $F_4$ , making asymptotic stability much less likely.

If all  $F_i$  are negative the system in Fig. 8 would be asymptotically stable, but might be cyclically unstable if the condition  $F_1 F_2 + F_3 > 0$  is not satisfied. This term is evaluated as

$$a_{XX}^2 a_{YY} + a_{YY}^2 a_{XX} - a_{XY} a_{yX} a_{Yy} - a_{YX} a_{xY} a_{Xx} - (a_{XX} + a_{YY}) (a_{XY} a_{YX} - a_{Xy} a_{yX}).$$

The last bracketed term is most probably positive (showing stronger competition between adults *X*, *Y* than between adults and their respective protégés), and thus the expression has



**Figure 8.** Loop diagram of two plant species, X and Y, with a reciprocal nursing association: adults X, Y act as nurse plants for juveniles y, x, of the other species. Negative interactions are shown with circular termini, positive ones with arrows. Adults compete, and are self-damped; juveniles compete with nurses, but are favoured by their nurses and then contribute to the adult populations. The system matrix is shown at upper right; the effects of evolution within each of the four components are shown at the lower right. Note that evolution within the protégé does not favour the protégé directly, but only indirectly via boosting the density of the respective nurse plants. No other evolution in this system favours the component in which it actually occurs, but instead produces either no change or a reduction in the population density of the various system components.

four negative and but two positive terms, making it likely net negative and likely that cycling occurs in the system.

The effects of evolution within different components of the system of Fig. 8 can be examined in terms of its results on population levels as follows. Suppose evolution favored a factor  $C_X$  that occurs only in X's growth equation (e.g. its photosynthetic efficiency). Then evaluation of the determinant of the system matrix A (see figure) with the first column replaced by the column vector  $\{-\partial f_X/\partial C_X \ 0 \ 0 \ 0\}$  produces zero, showing that such evolution does not result in enhanced population size in X. Substituting the new column vector at the second, third, and fourth positions in A, and evaluating the determinant, shows respectively that such evolution in X produces declines in both x and y, and no effect in Y.

To examine the effects of evolution in some factor  $C_x$ , e.g. survivorship in the juvenile x, the column vector  $\{0 \ -\partial f_x/\partial C_x \ 0 \ 0\}$  is substituted into the appropriate positions (columns one through four in A), with the results summarized in Fig. 8. The connectivity of the system is such that the only positive effects of population enhancement are on X and Y through evolution, paradoxically, in y and x respectively, even though y and x are in direct competition with X and Y! There may be, then, subtle advantages to the nurse plant in cyclical succession.

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