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# IMPACT OF A PARASITIC PLANT ON THE STRUCTURE AND DYNAMICS OF SALT MARSH VEGETATION<sup>1</sup>

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**Abstract.** We investigated the effect of a native parasitic plant, *Cuscuta salina*, on the structure and dynamics of the plant community in a California salt marsh. *Cuscuta* was common in the middle marsh zones. The abundance of *Cuscuta* was positively correlated with the abundance of *Limonium californicum* at two sampling scales (0.25- and  $\approx 40\text{-m}^2$  quadrats). Sampling at the scale of individual plants indicated that the dominant plant in the marsh, *Salicornia virginica*, was preferred by *Cuscuta* as a host over *Arthrocnemum subterminale*, *Limonium californicum*, and *Frankenia salina*. This result was confirmed with host-choice experiments in the field.

Based on spatial correlations and host-choice experiments, we hypothesized that *Cuscuta* indirectly facilitated *Limonium* and *Frankenia*, increasing plant diversity and initiating vegetation cycles. This hypothesis was supported by sampling patches with different histories of *Cuscuta* infection. Patches with recent heavy *Cuscuta* infection had reduced *Salicornia* biomass and increased *Limonium* and *Frankenia* biomass relative to controls. This effect was most pronounced at higher elevations and in larger, older patches. The hypothesis was also supported by sampling permanent quadrats repeatedly over time. The probability that *Cuscuta* would invade a quadrat increased with increasing cover of *Salicornia*. Quadrats containing *Cuscuta* increased in *Limonium* and *Frankenia* cover between censuses relative to quadrats lacking *Cuscuta*.

Our results indicate that parasitic plants can have strong effects on the structure and dynamics of natural vegetation assemblages. However, these effects are mediated by physical and biological gradients across the landscape.

**Key words:** community dynamics, competition, *Cuscuta*, disturbance, parasitic plant, patch dynamics, *Salicornia*, salt marsh, zonation.

## INTRODUCTION

Current theories of plant community dynamics include the concept that species may replace each other in cycles over time. "Shifting-mosaic" and "mosaic-cycle" hypotheses have been proposed and modelled (Aubreville 1938, Watt 1947, Clark 1991, Remmert 1991), but the mechanisms that drive such cycles are poorly understood. Although cycles of species abundance can be initiated by regular, reoccurring disturbances (Yeaton 1978, Doyle 1982, Reice 1994) or episodes of herbivory (McNaughton 1985), cycles may also occur in the apparent absence of these phenomena (Viereck 1970, Forcier 1975, Woods 1984, Callaway and Davis 1993). In the absence of periodic disturbance or herbivory, cycles might occur in response to interspecific interactions among plants (Strong 1977, McAuliffe 1988, Callaway and Davis 1993). However, relatively little evidence exists for interaction-driven cycles within plant communities.

Interplant parasitism is a widespread phenomenon,

with over 5000 species of parasitic plants occurring worldwide, but its role in determining plant community structure is poorly understood. Despite the fact that parasitic plants are components of many natural plant communities, have strong host preferences, may strongly suppress their host plants, and may have considerable impact as crop pests (Kuijt 1969, Gibson and Watkinson 1989, 1992, Kelly 1990, Parker and Riches 1993), little is known about their impact on natural plant communities (Tinnin 1984, Price et al. 1986, Watkinson and Gibson 1988, Gibson and Watkinson 1992).

*Cuscuta salina* (marsh dodder) is a common and widespread plant parasite in saline locations on the west coast of North America. Initial observations suggested that *Cuscuta salina* preferentially infects and can strongly suppress the pickleweed *Salicornia virginica*, which dominates most elevations of California salt marshes. Using a variety of approaches, we investigated the role of *Cuscuta salina* in determining marsh plant community structure. Our research was designed to test the general hypothesis that *Cuscuta salina* initiates cycles of species abundance by suppressing *Salicornia virginica*, thereby creating patches where other species can temporarily invade.

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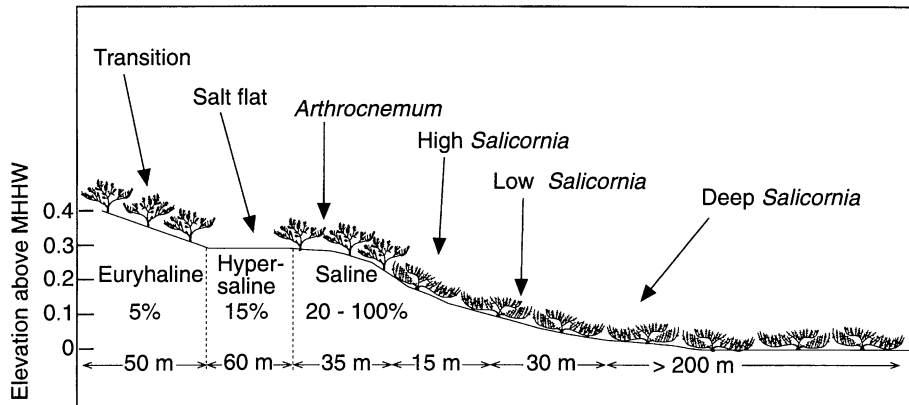


FIG. 1. Diagrammatic cross section of study site, Carpinteria, California, showing marsh zones, general patterns of soil salinity, flooding frequencies (from Callaway et al. 1990), and approximate horizontal extent of each zone. Marsh vegetation exists at higher and lower elevations than shown here. The figure is not drawn to scale. MHHW = mean high high water.

## METHODS

### *Study site and species*

Field research was conducted in Carpinteria Salt Marsh (34°24' N, 119°31'30" W), located in southern California, USA (described in Ferren 1985, Callaway et al. 1990, Pennings and Callaway 1992, Callaway 1994, Callaway and Sabraw 1994). This relatively undisturbed system experiences a mediterranean climate with most rain falling between November and April.

Plants in the marsh are distributed along a gradual elevational gradient (Fig. 1). Most of the marsh area, from several hundred metres seaward to  $\approx 70$  m inland of Mean High High Water (MHHW) is dominated by *Salicornia virginica*. We refer to distinctly different locations in the upper part of this region as the high-*Salicornia* and low-*Salicornia* zones (following Pennings and Callaway [1992]), and to the lower part of this region as the deep-*Salicornia* zone. At higher elevations, *Salicornia* is abruptly replaced by an almost monospecific stand of *Arthrocnemum subterminale*, followed by an unvegetated salt flat, a mixed-species zone dominated by *Arthrocnemum* and winter annuals (the transition zone), and finally a grassland zone (not shown in Fig. 1). *Limonium californicum* and *Frankenia salina* occur at low densities throughout the *Salicornia*, *Arthrocnemum*, and transition zones. *Jaumea carnosa* occurs at low densities in the deep-*Salicornia* zone.

*Cuscuta salina* Engelm. var. *major* Yunck. is an obligate parasitic annual (although overwintering of vegetative parts is common) widely distributed in coastal salt marshes from Mexico to British Columbia (Zedler 1982, Ferren 1985). Other varieties of *Cuscuta salina* are distributed in saline locations at low-elevation, inland sites throughout western North America. In salt marshes, *Cuscuta* forms mats of intertwined bright orange stems covering infected host plants. Stems coil tightly around host plants and produce root-like "haustoria," which penetrate into the host plant's phloem.

Dense mats of *Cuscuta* can be seen from a considerable distance and are a striking visual feature of west coast marshes. *Cuscuta* can invade new areas through vegetative growth or through dispersal of seeds.

### *Distribution of Cuscuta*

Because typical salt marsh plants are strongly influenced by gradients in edaphic and biological factors across the marsh (Bertness 1992), we expected the abundance and impact of *Cuscuta* to vary across the landscape. We used two approaches to measure the abundance of *Cuscuta* in different marsh zones. Quadrat sampling ensured that we would not miss thin isolated shoots of *Cuscuta* or small *Limonium* plants. Low altitude photo-sampling expanded the scale of the plots to describe entire patches of *Cuscuta* and *Limonium*.

To determine the relative abundance of *Cuscuta* in different marsh zones, we randomly located 100 0.25-m<sup>2</sup> quadrats in each of several marsh zones in the summers of 1993 and 1994. Within each quadrat, *Cuscuta* was qualitatively scored as absent (no infection), present in the quadrat at low density (light infection), or present in a heavy mat (heavy infection). For each year, we tested the hypothesis that the pattern of infection did not differ across marsh zones with chi-square tests. Because results of this sampling and personal observations indicated that *Cuscuta* was virtually absent in the transition and *Arthrocnemum* zones, further work focused primarily on the *Salicornia* zones.

Photo-sampling, described in the following paragraph, indicated that *Cuscuta* and *Limonium* were positively correlated across the landscape. To determine if this relationship would also hold at a much smaller scale and with a different methodology, we sampled 23 stratified-random 0.25-m<sup>2</sup> quadrats along a 150-m transect running from the *Arthrocnemum*-*Salicornia* border into the deep-*Salicornia* zone. The quadrat was divided with monofilament line into 100 cells. The presence or absence of *Cuscuta* and *Limonium* in each

cell was noted and the totals scored as percent cover. Data were arcsine-transformed before analysis. This transect also extended up into the *Arthrocnemum* and transition zones where we sampled an additional 10 quadrats to further examine the zonation pattern of *Cuscuta*.

To determine the number, size, and percent cover of patches of *Cuscuta* and *Limonium* in the three *Salicornia* zones, we mapped a 100-m photo-transect in each zone. Transects were oriented parallel to zone boundaries and were randomly located within each zone. Color slide photographs (14–16/transect, 30.9–47.7 m<sup>2</sup> in area, centered 5–8 m apart) were taken with a camera suspended from a balloon ≈6 m above the marsh surface. A 0.25-m<sup>2</sup> quadrat was included in each photograph for scale. Slides were projected onto paper and all patches of *Cuscuta* and *Limonium* were mapped. *Frankenia* patches in the projected slides could not be reliably distinguished from the background *Salicornia* and were not mapped. Mapped areas did not overlap. Sizes of all patches within an individual slide were averaged to give the slide as the unit of replication. Cover data were arcsine-transformed before analysis. We tested the hypotheses that the number, size, and cover of *Cuscuta* patches and the cover of *Limonium* patches did not differ between marsh zones with ANOVA, or, when only two zones were compared, *t* tests. We tested the hypotheses that the number and sizes of *Limonium* patches did not differ between marsh zones with Kruskal–Wallis tests because of extremely heterogeneous variances and/or non-normality.

#### Host preferences of *Cuscuta*

In the previous section we examined the distribution of *Cuscuta* across different marsh zones. To explore *Cuscuta* host preferences within marsh zones, we used a combination of observations and experiments.

To observe *Cuscuta* host preferences, we randomly located 0.01-m<sup>2</sup> quadrats in areas of high plant diversity and *Cuscuta* abundance in the high- and deep-*Salicornia* zones. We sampled at least 100 individual plants each of *Salicornia*, *Frankenia*, *Arthrocnemum*, *Limonium*, and *Jaumea*. *Arthrocnemum* and *Jaumea* occurred only in the high- and low-*Salicornia* zones, respectively. Quadrats that landed on a mixture of species were not sampled. Each sampled plant was examined for the presence of *Cuscuta* infection within the area of the quadrat. Plants were scored as uninfected (0), lightly infected with 1–10 haustoria attached (1), moderately infected with 10–30 haustoria attached (2), or heavily infected with a thick mat of *Cuscuta* and >30 haustoria attached (3), and the data from each zone analyzed with a Kruskal–Wallis nonparametric ANOVA to test the hypothesis that all species were equally infected.

To experimentally investigate *Cuscuta* host preferences, we performed host-choice experiments in the field using methods similar to those of Kelly (1990).

Stalks of *Salicornia* that were heavily infected with *Cuscuta* were cut and placed in water-filled test tubes that were staked to the marsh substrate between two different potential host species in patches free of *Cuscuta* infection. *Cuscuta* shoots from the infected *Salicornia* stalk grew into and attached to surrounding plants (1–11 shoots/replicate attached as defined by the presence of haustoria growing into host tissue). After 13 d, the availability of the two potential host plants was estimated within a 0.0625-m<sup>2</sup> quadrat centered on the test tube, and the number of *Cuscuta* shoots that had attached to each was recorded. Preference was calculated using Manly's index (Chesson 1978, 1983). This index, which corrects for variation in host availability, varies from 0 (low preference) to 1 (high preference) and, for two host species, takes on the value 0.5 if no preference for either is displayed. We set up 13–16 replicates each of four comparisons: *Salicornia* vs. *Frankenia*, *Salicornia* vs. *Arthrocnemum*, *Salicornia* vs. *Limonium*, and *Salicornia* vs. *Jaumea*. *Jaumea*, which we observed only in the deep-*Salicornia* zone, was included because we observed that some *Jaumea* plants were heavily infected by *Cuscuta*. Observed preferences were compared with 0.5 (no preference) using a *t* test or, for cases with zero variance, a non-parametric analogue. Because we used infected *Salicornia* plants as the source of *Cuscuta* in these experiments, it is possible that we were inadvertently selecting for *Cuscuta* plants that were genetically or phenotypically predisposed to prefer *Salicornia*, and therefore were biasing the results of the trials. However, because *Jaumea* was the only other plant species that regularly was heavily infected by *Cuscuta*, and because *Jaumea* was relatively rare at our site, it would have been difficult to obtain sufficient source material from any other hosts. Moreover, because most *Cuscuta* in the marsh occurs on *Salicornia*, our experiments realistically reflected the context of natural host-choice decisions in the field.

#### Effect of *Cuscuta* on community pattern

Results of the above sampling and experiments suggested that *Cuscuta* was initiating vegetation cycles by depressing *Salicornia* and thereby indirectly benefitting *Limonium* and *Frankenia*. We used two approaches to test this hypothesis. First, we examined areas with recent heavy infections of *Cuscuta*. Because *Cuscuta* infection in the recent past leaves a record, it is possible to sample patches of vegetation and unambiguously classify their recent infection history. Dense patches of *Cuscuta* may completely kill large (>1 m<sup>2</sup>) patches of host plants over the course of a summer; these patches are visible as large halos of living *Cuscuta* surrounding thick mats of dead *Cuscuta*, which have killed their food source. We called these large infected patches. We also sampled small (<1 m<sup>2</sup>) patches of heavy mats of living *Cuscuta* and called these small infected patches. We sampled both types of infected patches in

the high- and low-*Salicornia* zones ( $n = 8$  patches of each size/zone) and also sampled an equivalent number of control areas without recent *Cuscuta* infection (no living or dead *Cuscuta* within 1 m). All aboveground vegetation inside 0.0625-m<sup>2</sup> quadrats was harvested, dried at 60°C for 3 d, and weighed. Following Pennings and Callaway (1992), *Salicornia* was separated into green photosynthetic nodes and woody stems; both showed similar patterns and only data for green nodes are presented here. Five species of nonparasitic plants were found; three of these, *Frankenia*, *Limonium*, and *Salicornia* made up >99% of the biomass. The remaining two species (*Arthrocnemum*, *Distichlis spicata*) were not included in the analysis because they were so rare. Data (mass of *Frankenia*, *Limonium*, and *Salicornia*) were  $\ln(x + 0.01g)$  transformed and analyzed with MANOVA with *Cuscuta* infection, marsh zone, and patch size as the three independent variables to test the hypothesis that community structure differed between patches of different infection histories, sizes, and elevations.

Second, we repeatedly monitored a set of 29 permanent 0.125-m<sup>2</sup> quadrats in the high- and low-*Salicornia* zones in 1986, 1987, 1989, and 1990 to follow changes in community composition through time. Cover of *Cuscuta*, *Limonium*, *Frankenia*, and *Salicornia* in the quadrats was visually estimated to the nearest 5% at each census. We pooled data from all three transition periods (1986–1987, 1987–1989, 1989–1990) to examine how initial patch conditions (in particular, presence vs. absence of *Cuscuta*) affected future vegetation composition.

RESULTS

Distribution of *Cuscuta*

Random quadrat sampling suggested that patterns of *Cuscuta* infection differed dramatically between zones (Fig. 2). *Cuscuta* was entirely absent from the transition and *Arthrocnemum* zones, and was about twice as abundant in the high- and low-*Salicornia* zones, where ≈one-half the quadrats contained some *Cuscuta*, as in the deep-*Salicornia* zone, where only ≈one-fourth of the quadrats contained *Cuscuta*.

Similarly, photo-sampling indicated that the percent cover of both *Cuscuta* and *Limonium* patches increased dramatically with elevation from low densities in the deep-*Salicornia* zone to high densities in the high-*Salicornia* zone (Fig. 3A; *Cuscuta*:  $F_{2,42} = 14.48$ ,  $P < 0.0001$ , deep-*Salicornia* zone significantly different from other two [Tukey test]; *Limonium*: Kruskal–Wallis = 15.64,  $P = 0.0004$ , deep-*Salicornia* zone significantly different from other two [rank-sum tests]). The fact that these results are more dramatic than those from the quadrat sampling indicates that most *Cuscuta* plants in the deep-*Salicornia* zone are small plants that do not form patches dense enough to be visible on the photo-transect. The increase in percent cover of *Cuscuta* and

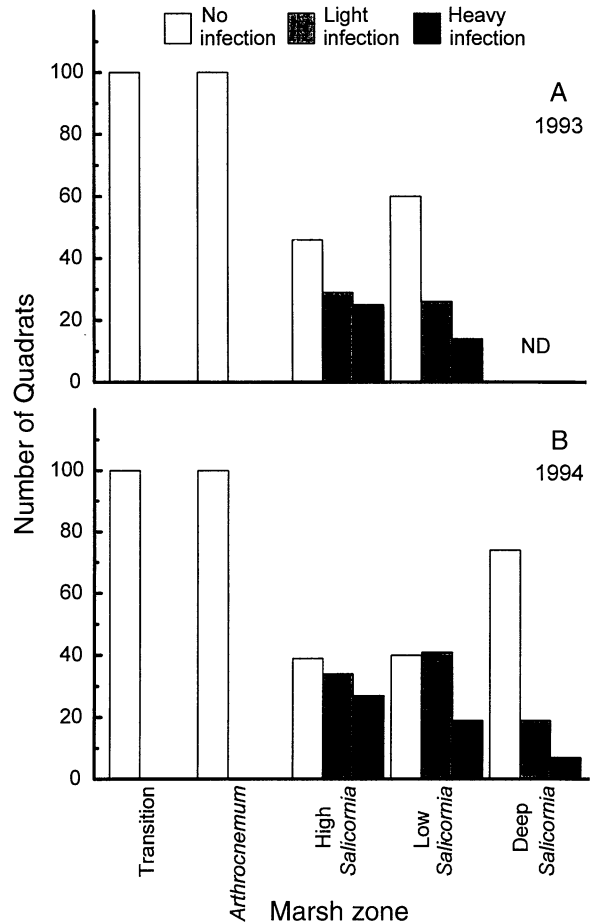


FIG. 2. Abundance of *Cuscuta* in different marsh zones in (A) 1993 and (B) 1994. Shown are the number of quadrats out of 100/zone with three levels of *Cuscuta* infection. ND indicates that the deep-*Salicornia* zone was not sampled in 1993. 1993:  $\chi^2 = 130.7$ ,  $df = 6$ ,  $P < 0.0001$ ; 1994:  $\chi^2 = 182.6$ ,  $df = 8$ ,  $P < 0.0001$ .

*Limonium* at higher elevations was caused both by an increase in patch density (Fig. 3B; *Cuscuta*:  $F_{2,42} = 10.29$ ,  $P = 0.0002$ , deep-*Salicornia* zone significantly different from other two [Tukey test]; *Limonium*: Kruskal–Wallis = 15.34,  $P = 0.0005$ , deep-*Salicornia* zone significantly different from other two [rank-sum tests]) and, in the case of *Cuscuta*, by an increase in the size of individual patches (Fig. 3C; *Cuscuta*: data log-transformed before analysis,  $F_{2,30} = 10.62$ ,  $P = 0.0003$ , deep-*Salicornia* zone significantly different from other two [Tukey test]; *Limonium*: no patches in deep-*Salicornia* zone, upper two zones not significantly different,  $t_{16} = 1.40$ ,  $P = 0.18$ ).

In addition to increasing together across marsh zones, *Limonium* and *Cuscuta* were also positively correlated within marsh zones (Fig. 4). In both the high- and low-*Salicornia* zones, percent cover of *Limonium* in photo-quadrats was strongly correlated with percent cover of *Cuscuta*. No *Limonium* patches were visible in the slides from the deep-*Salicornia* zone.

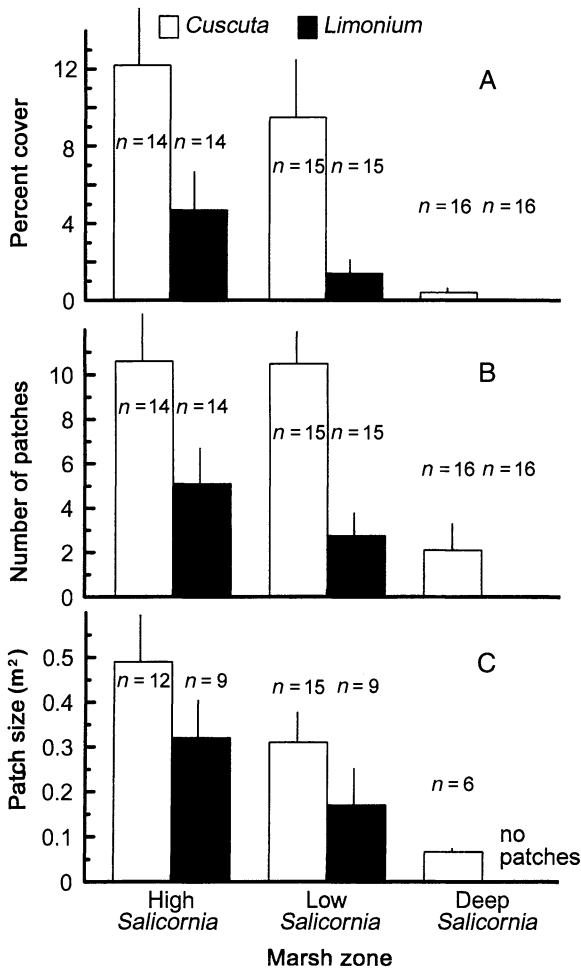


FIG. 3. Distribution of *Cuscuta* and *Limonium* in photo-quadrats ( $\approx 40 \text{ m}^2$ ) in three marsh zones. Data are means + 1 SE; sample sizes are given in or above bars. (A) Percent cover. (B) Number of patches/40  $\text{m}^2$ . (C) Average patch size in  $\text{m}^2$  (sample sizes are smaller because not all photo-quadrats contained patches).

*Limonium* and *Cuscuta* were also strongly correlated in 0.25- $\text{m}^2$  quadrats located on a transect running perpendicularly through the *Salicornia* zones (Fig. 5), indicating that this correlation is robust to major variations in sampling methodology and quadrat size. This transect also extended into the *Arthrocnemum* and transition zones, where no *Cuscuta* was found in 10 quadrats (data not shown), corroborating the result of Fig. 2 that *Cuscuta* is primarily confined to the *Salicornia* zones. This result is also corroborated by our extensive personal observations of the marsh over several years, during which time we observed only very rare *Cuscuta* infections in the *Arthrocnemum* or transition zones.

*Host preferences of Cuscuta*

In the high-*Salicornia* zone, *Salicornia* was parasitized by *Cuscuta* at much higher rates than were *Frankenia*, *Arthrocnemum*, or *Limonium* (Fig. 6A). In the

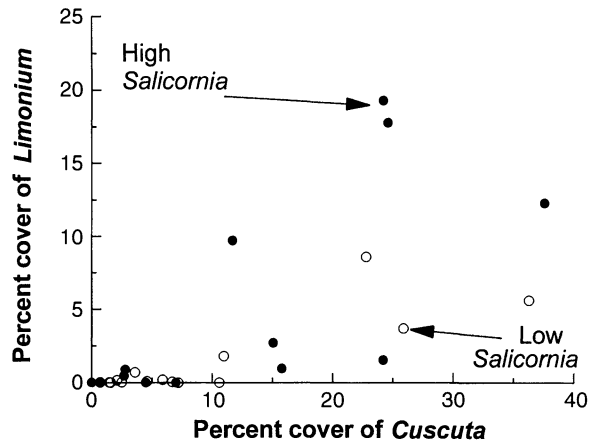


FIG. 4. Relationship between *Cuscuta* and *Limonium* in photo-quadrats ( $\approx 40 \text{ m}^2$ ) in two marsh zones. Data were arcsine-transformed before analysis. *Limonium* patches were not present in the deep-*Salicornia* zone. High-*Salicornia* zone:  $r = 0.77$ ,  $n = 14$ ,  $P = 0.0008$ ; low-*Salicornia* zone:  $r = 0.84$ ,  $n = 15$ ,  $P < 0.0001$ .

deep-*Salicornia* zone, *Salicornia* was again parasitized by *Cuscuta* at much higher rates than were *Frankenia* or *Limonium*; however, *Jaumea* was parasitized at even higher rates than was *Salicornia* (Fig. 6B).

Similar results were obtained in the host-choice experiment. When positioned between two potential host plant species in the field, *Cuscuta* overwhelmingly preferred to parasitize *Salicornia* vs. either *Frankenia*, *Arthrocnemum*, or *Limonium* (Fig. 7, preference index significantly  $> 0.5$ ). In contrast, *Jaumea* was slightly but significantly preferred by *Cuscuta* over *Salicornia* (Fig. 7, preference index significantly  $< 0.5$ ).

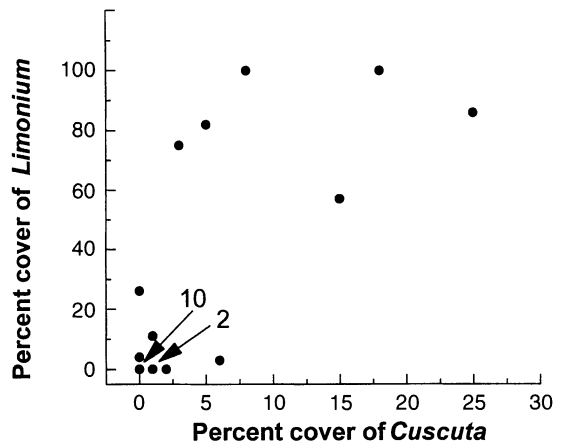


FIG. 5. Relationship between *Cuscuta* and *Limonium* in 0.25- $\text{m}^2$  quadrats on a transect running perpendicularly through the *Salicornia* zones. Data were arcsine-transformed before analysis. Multiple quadrats (10, 2) with same data values are indicated near the origin with arrows.  $r = 0.80$ ,  $n = 23$ ,  $P < 0.0001$ .

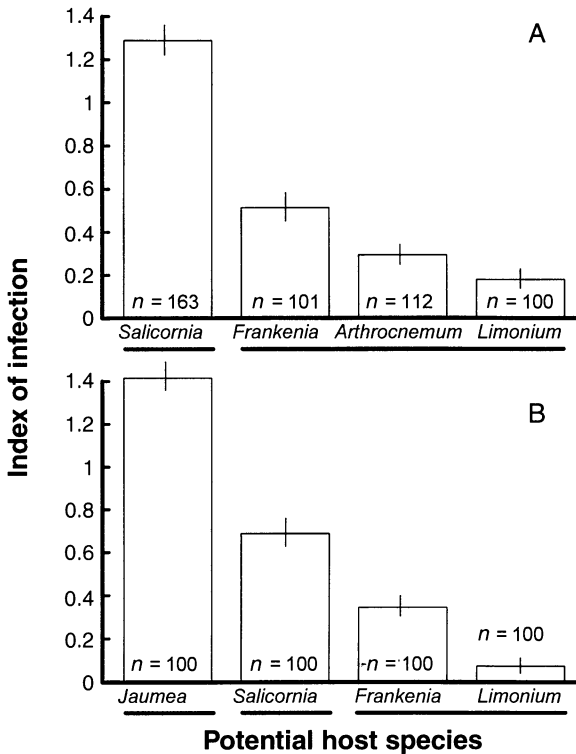


FIG. 6. Relative levels of infection by *Cuscuta* of different plant species in the (A) high- and (B) low-*Salicornia* zones. Data are means  $\pm$  1 SE; sample sizes are shown inside bars. Infection levels range from 0 (no infection) to 3 (heavy infection). (A) Kruskal-Wallis = 128.14,  $P < 0.0001$ ; (B) Kruskal-Wallis = 142.49,  $P < 0.0001$ . Species connected by a horizontal line do not differ in infection severity (rank-sum tests at  $P = 0.05/6 = 0.008$ ).

*Effect of Cuscuta on community pattern*

The plant communities found in patches with different *Cuscuta* infection histories differed strongly (Fig. 8, Table 1). Whereas uninfected control areas were dominated by *Salicornia*, recently infected areas contained relatively high abundances of *Limonium* and *Frankenia*. In fact, *Limonium* was virtually restricted to recently infected patches. The impact of recent *Cuscuta* infection was strongest in large patches in the high-*Salicornia* zone (Table 1, significant “infection  $\times$  size” and “infection  $\times$  zone” terms). In these patches, *Limonium* and *Frankenia* dominated the biomass, and *Salicornia* was present only in small amounts. On the other hand, in small or low-*Salicornia* zone infected patches, *Limonium* and *Frankenia* increased in abundance relative to control areas, but were not more abundant than *Salicornia*.

Examining the plant composition of permanent quadrats over time further supported the hypothesis that *Cuscuta* has strong effects on the community structure of marsh plants. We observed an overall increase in *Limonium* and decrease in *Frankenia* over our study period, which we attribute to the relatively dry con-

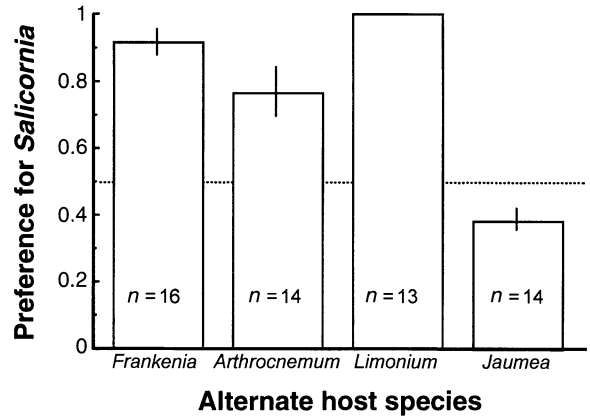


FIG. 7. Preference (Manly's index) of *Cuscuta* for *Salicornia* vs. *Frankenia* ( $t_{15} = 11.13$ ,  $P < 0.0001$ ), *Arthrocnemum* ( $t_{13} = 3.52$ ,  $P = 0.004$ ), *Limonium* (Wilcoxon signed-ranks test,  $P = 0.0002$ ), and *Jaumea* ( $t_{13} = 3.67$ ,  $P = 0.003$ ) in field choice experiments. Data are means  $\pm$  1 SE; error bars not shown if too small to be visible; sample sizes shown inside bars. Dotted line at 0.5 indicates no preference. Values above the line indicate a preference for *Salicornia*; values below the line indicate a preference for the alternate host.

ditions during these years. However, the increase in *Limonium* was restricted to quadrats infected with *Cuscuta*. Quadrats initially lacking *Limonium* but containing *Cuscuta* had significantly higher *Limonium* densities on the next census than did quadrats initially lacking *Cuscuta* (Fig. 9A, left). Similarly, quadrats initially containing *Limonium* increased in *Limonium* cover between censuses significantly faster if they also initially contained *Cuscuta* (Fig. 9A, right). *Cuscuta* also seemed to mediate the decline of *Frankenia*, but results were more variable and not statistically significant. Quadrats initially lacking *Frankenia* but containing *Cuscuta* tended to have higher *Frankenia* densities on the next census than did quadrats initially lacking both (Fig. 9B, left). Quadrats initially containing *Frankenia* tended to decrease in *Frankenia* cover less between censuses if they also initially contained *Cuscuta* (Fig. 9B, right). The abundance of *Cuscuta* was in turn strongly mediated by the abundance of its preferred host plant, *Salicornia*: the probability that *Cuscuta* would invade a quadrat fell sharply when the initial cover of *Salicornia* was  $<100\%$  (Fig. 10).

DISCUSSION

Our results suggest that *Cuscuta* is an important agent affecting the dynamics and diversity of vegetation in Carpinteria Salt Marsh. Because it prefers to parasitize the marsh-dominant *Salicornia*, *Cuscuta* indirectly facilitates the rare species *Limonium* and *Frankenia*, increasing plant diversity, and possibly initiating plant vegetation cycles. The effects of *Cuscuta* are mediated by strong physical and biological gradients across the marsh landscape.

*Cuscuta* indirectly facilitated *Limonium* and *Fran-*

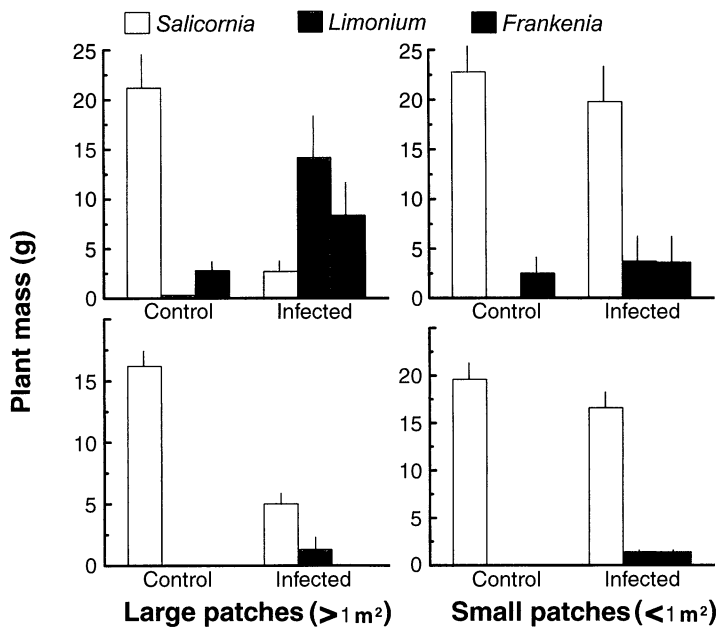


FIG. 8. Biomass of plants in control areas and in large ( $>1 \text{ m}^2$  patches of dead *Cuscuta* surrounded by a ring of living *Cuscuta*) and small ( $<1 \text{ m}^2$  patches of thick-living *Cuscuta*) areas recently infected by *Cuscuta*, in the high-*Salicornia* (top) and low-*Salicornia* (bottom) zones. Data are means  $\pm 1$  SE; error bars not shown if too small to be visible,  $n = 8$  in all cases.

kenia and increased plant diversity in the marsh because it strongly preferred to parasitize *Salicornia*, the dominant plant in the marsh, and could strongly depress the abundance of *Salicornia*. As a result, *Limonium* cover was strongly correlated with *Cuscuta* cover on a variety of spatial scales; areas of recent heavy *Cuscuta* infection correlated with patches of high *Limonium* and *Frankenia* biomass; and patches with *Cuscuta* infection in one year increased in *Limonium* and *Frankenia* cover on the following census relative to *Cuscuta*-free patches. These strong effects are particularly striking considering that even a heavy mat of *Cuscuta* comprises considerably  $<5\%$  of the biomass of the plants it smothers (S. C. Pennings and R. M. Callaway, *personal observation*). The community-level effects of *Cuscuta* are analogous to the impact of *Pisaster*, a predatory starfish, on mussel bed communities. *Pisaster* increases the diversity of primary space-holders in mussel beds by preferentially consuming the dominant mussels and freeing up the rock surface for other species (Paine 1966, 1969, 1974). Similarly, *Littorina*, a herbivorous snail, increases diversity of algal com-

munities by preferentially consuming the dominant alga, again freeing up space for other species (Lubchenco 1978). The similarities between these classic studies of strong consumers and our results with *Cuscuta* lend credence to the hope that broad generalizations are possible in ecology. It may be possible to understand the community effects of parasitic plants by drawing heavily upon predator-prey and plant-herbivore theory, rather than by developing an entirely new discipline.

The role of *Cuscuta* in plant communities probably varies depending upon the traits of the available host species in a specific area. We did not examine the interaction between *Cuscuta* and *Jaumea* in the deep-*Salicornia* zone in detail because both species occur there at low densities. However, *Cuscuta* preferred to parasitize *Jaumea* over *Salicornia*, suggesting that in the deep-*Salicornia* zone, *Cuscuta* may actually reduce diversity by preferentially parasitizing a rare species. A study of the root hemiparasite *Rhinanthus minor* led to similar conclusions (Gibson and Watkinson 1992). *Rhinanthus* decreased plant diversity at three sites but increased it at a fourth. The difference in effects was apparently mediated by the differential availability and competitive rankings of preferred hosts at each site.

Parasitism by *Cuscuta* may drive cycles of species abundance at some locations within the marsh. We hypothesize that *Cuscuta* strongly depresses *Salicornia*, which allows *Limonium* and *Frankenia* to increase in abundance. Plots lacking a high abundance of *Salicornia* then lose *Cuscuta*, which allows *Salicornia* to invade. Our evidence for this scenario varies in strength. We have presented strong circumstantial evidence that *Cuscuta* depresses *Salicornia* and facilitates *Limonium* and *Frankenia*. Moreover, the probability that *Cuscuta*

TABLE 1. MANOVA table for the effect of recent *Cuscuta* infection on plant community composition.

Source	Pillai's trace	df	F	P†
Infected or not	0.5758	3, 54	24.43	<b>&lt;0.001</b>
Marsh zone	0.3793	3, 54	11.00	<b>&lt;0.001</b>
Patch size	0.5076	3, 54	18.56	<b>&lt;0.001</b>
Infection $\times$ zone	0.1864	3, 54	4.12	<b>0.010</b>
Infection $\times$ size	0.4117	3, 54	12.60	<b>&lt;0.001</b>
Zone $\times$ size	0.1260	3, 54	2.60	0.062
Zone $\times$ size $\times$ infection	0.0928	3, 54	1.84	0.15

† Bold = significant.



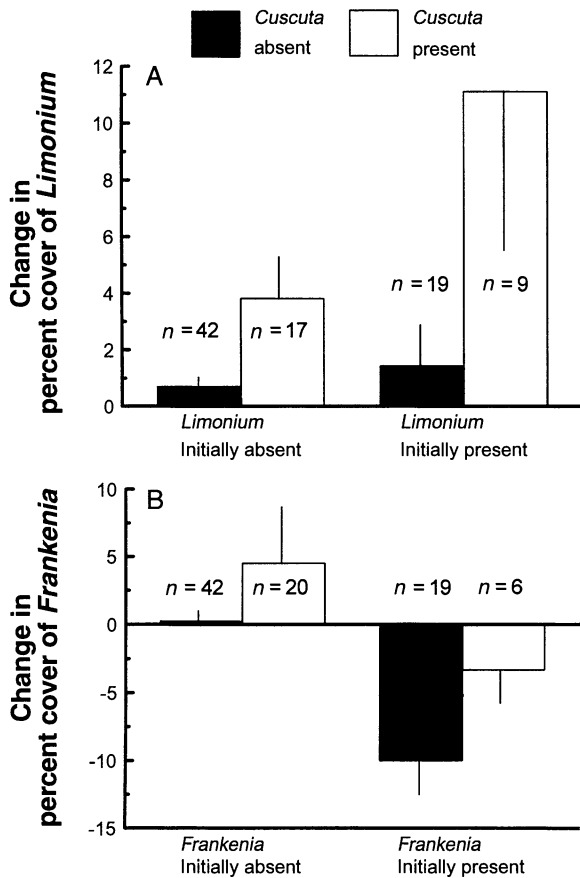


FIG. 9. Effect of *Cuscuta* on dynamics of (A) *Limonium*, and (B) *Frankenia*. Shown are changes in percent cover between sampling intervals for quadrats initially lacking or containing each plant. Data are means + 1 SE; sample sizes are given in or above bars. Data were analyzed with one-tailed rank-sum tests. *Limonium* initially absent:  $P = 0.03$ ; *Limonium* initially present:  $P = 0.023$ ; *Frankenia* initially absent:  $P = 0.26$ ; *Frankenia* initially present:  $P = 0.096$ .

would invade a plot fell sharply when the cover of *Salicornia* was <100% (Fig. 10). Because an invading *Cuscuta* tendrill must find a suitable host in order to feed and grow, one would expect a higher probability of invasion in plots with more *Salicornia*; however, it is surprising that the probability of invasion fell so quickly once *Salicornia* cover was <100%. One possible explanation for this pattern is that *Salicornia* biomass was more important to *Cuscuta* than was *Salicornia* cover. Because we measured cover as the percentage of cells in a quadrat that were occupied by even a small amount of plant material, plants with 100% cover probably had a denser growth form and contained considerably more biomass than did plants with 90% cover. Alternatively, it is possible that high *Salicornia* cover correlated with a threshold in some other factor, perhaps soil nutrients or plant age, that affected vulnerability to infection. Our evidence for the final step of the cycle is weakest: we did not have a

large enough sample size of plots completely dominated by *Limonium* or *Frankenia* to follow the reinvasion of *Salicornia*; however, the fact that *Limonium* and *Frankenia* are common only in the presence of *Cuscuta* strongly suggests that they are competitively inferior to *Salicornia*. We caution that because we did not experimentally manipulate *Cuscuta* abundance, we cannot be sure that *Cuscuta* alone is responsible for the patterns we observed. For example, it is possible that *Cuscuta* may successfully attack only plants that are weakened by competition, herbivory, salinity, flooding, lack of nutrients, or other stressors. Future experiments will directly manipulate *Cuscuta* abundance to test this hypothesis.

We have not yet documented the time scale of these putative cycles; however, we estimate that transitions from *Cuscuta*-infected *Salicornia* to *Limonium* and *Frankenia* take 1–3 yr. Plots of *Salicornia* that were cleared for competition experiments (Pennings and Callaway 1992) reverted to the surrounding control conditions 2–3 yr after the experiments ended (S. C. Pennings and R. M. Callaway, *personal observation*), suggesting that the reinvasion of *Limonium*/*Frankenia* patches by *Salicornia* operates on a similar time scale (we have experiments underway to confirm this). If these estimates are correct, this putative cycle may be faster than other plant cycles reported in the literature (McAuliffe 1988, Hall et al. 1991, Callaway and Davis 1993).

Both pattern and process in ecological communities are scale-dependent (Wiens 1989, Levin 1992). *Cuscuta* and *Limonium* are negatively correlated at a very small scale (individual plants) but positively correlated at larger scales because *Cuscuta* prefers *Salicornia* as a host, thereby indirectly facilitating *Limonium*. Similarly, although this chain of biotic interactions may be central to producing vegetation pattern within certain

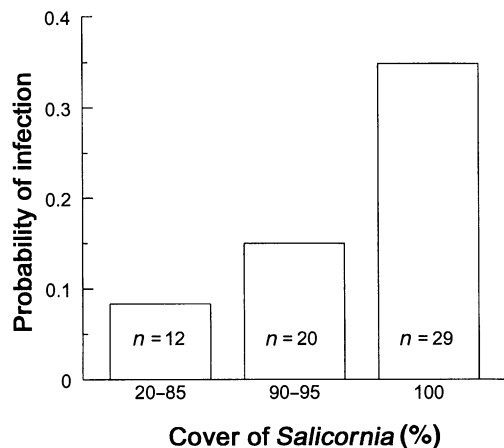


FIG. 10. Probability of *Cuscuta* invading a quadrat as a function of the initial percent cover of *Salicornia*. Sample sizes are given in bars. Data were analyzed with a  $\chi^2$  test for ordered alternatives (Rice and Gaines 1994),  $P = 0.02$ .

marsh zones, understanding larger scale differences in vegetation pattern between zones requires invoking other, abiotic, processes. Salt marsh plants live in an environment that is shaped by strong physical gradients. Flooding, soil oxygen, salinity, and other edaphic factors vary dramatically within marshes, and strongly influence plant growth, survival, and zonation patterns (Mahall and Park 1976a, b, c, Vince and Snow 1984, Bertness 1992, Bertness et al. 1992, Pennings and Callaway 1992, Shumway and Bertness 1992). Our measurements of the distribution of *Cuscuta* throughout the marsh indicate that edaphic factors ultimately mediate the impact of *Cuscuta* on vegetation patterns, either directly, or indirectly through their effects on other plant species. *Cuscuta* was absent from the *Arthrocnemum* and transition zones, probably because it lacked suitable host plants in these zones. *Salicornia*, its preferred host, is excluded from the *Arthrocnemum* zone by competition and from the transition zone by seasonally high soil salinities (Pennings and Callaway 1992). Within the *Salicornia*-dominated zones of the marsh, the abundance of *Cuscuta* increased from low to high elevations. *Cuscuta* was rare in the deep-*Salicornia* zone where it occurred in small, light patches. Although *Cuscuta* was common in both the low- and high-*Salicornia* zones, *Cuscuta* patches in the low-*Salicornia* zone tended to be lighter and smaller than in the high-*Salicornia* zone. This variation in *Cuscuta* abundance may have been caused by increased tidal flooding at lower elevations. However, an alternative hypothesis is that the quality of *Salicornia* as a host plant varied across elevation. *Salicornia* attains a greater biomass in the high- than the low-*Salicornia* zone because of reduced flooding at high elevations (Pennings and Callaway 1992).

The impact of *Cuscuta* on the plant community also varied across elevation. *Cuscuta* depressed *Salicornia* biomass in both the high- and low-*Salicornia* zones; however, recent heavy *Cuscuta* infections led to an increase in *Limonium* and *Frankenia* only in the high-*Salicornia* zone. This could have been because *Cuscuta* infections in the low-*Salicornia* zone were less virulent or more transient. Alternatively, it may have been that *Limonium* and *Frankenia* were less able to invade infected patches in the low-*Salicornia* zone, perhaps because they were negatively affected by increased flooding at lower elevations.

Although the community-level effects of parasitic plants have seldom been studied (Price et al. 1986, Watkinson and Gibson 1988), the few relevant studies suggest that parasitic plants can strongly influence plant community structure (Gibson and Watkinson 1992). We provide strong circumstantial evidence, based upon spatial and temporal pattern and mechanistic experiments, that *Cuscuta* is a major determinant of patchiness in the upper *Salicornia* zones, that *Cuscuta* indirectly increases plant diversity, and that *Cuscuta* initiates a shifting mosaic of the vegetation in the

marsh. These effects occur across, and ultimately are mediated by, strong gradients in edaphic and biological factors. A picture of California coastal marshes is emerging in which abiotic factors (Purer 1942, Mahall and Park 1976a, b, c, Zedler 1982, Callaway et al. 1990) form a template that mediates and interacts with strong biological interactions (Pennings and Callaway 1992, Callaway 1994) to determine plant community structure.

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