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IMPACT OF A PARASITIC PLANT ON THE STRUCTURE AND DYNAMICS OF SALT MARSH VEGETATION

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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 ~40-m² 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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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 ~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 Engel. 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-m² quadrats in each of several marsh zones in the summers of 1993 and 1994. Within each quadrant, Cuscuta was qualitatively scored as absent (no infection), present in the quadrant 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-m² 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

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.
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 m² 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-m² 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-transfomred 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-m² 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-m² 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 of 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 m²) 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 m²) 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-m² quadrats was harvested, dried at 60°C for 3 d, and weighed. Following Penning 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-m² 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: F₁,42 = 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 Limonium at higher elevations was caused both by an increase in patch density (Fig. 3B: Cuscuta: F₁,42 = 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, F₁,30 = 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, t₁₀ = 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.

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**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, $P < 0.0001$.
Limonia and Cuscuta were also strongly correlated in 0.25-m² 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 quadrant 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 Limonia (Fig. 6A). In the deep-Salicornia zone, Salicornia was again parasitized by Cuscuta at much higher rates than were Frankenia or Limonia; 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 Limonia (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).

![Figure 4](image-url)  
**Fig. 4.** Relationship between Cuscuta and Limonia in photo-quadrats (~40 m²) in two marsh zones. Data were arcsine-transformed before analysis. Limonia patches were not present in the deep-Salicornia zone. High-Salicornia zone: $r = 0.77$, $n = 14$, $P = 0.0008$; low-Salicornia zone: $r = 0.84$, $n = 15$, $P < 0.0001$.

![Figure 5](image-url)  
**Fig. 5.** Relationship between Cuscuta and Limonia in 0.25-m² 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. $r = 0.80$, $n = 23$, $P < 0.0001$. 

In the high-Salicornia zone, Salicornia was parasitized by Cuscuta at much higher rates than were Frankenia, Arthrocnemum, or Limonia (Fig. 6A). In the deep-Salicornia zone, Salicornia was again parasitized by Cuscuta at much higher rates than were Frankenia or Limonia; however, Jaumea was parasitized at even higher rates than was Salicornia (Fig. 6B).
Fig. 6. Relative levels of infection by <i>Cuscuta</i> of different plant species in the (A) high- and (B) low-<i>Salicornia</i> zones. Data are means ± 1 se; sample sizes are shown inside bars. Infection levels range from 0 (no infection) to 3 (heavy infection). (A) Kruskal–Wallis = 128.14, <i>P</i> < 0.0001; (B) Kruskal–Wallis = 142.49, <i>P</i> < 0.0001. Species connected by a horizontal line do not differ in infection severity (rank-sum tests at <i>P</i> = 0.05/6 = 0.008).

**Effect of Cuscuta on community pattern**

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

Examining the plant composition of permanent quadrats over time further supported the hypothesis that <i>Cuscuta</i> has strong effects on the community structure of marsh plants. We observed an overall increase in <i>Limonium</i> and decrease in <i>Frankenia</i> over our study period, which we attribute to the relatively dry conditions during these years. However, the increase in <i>Limonium</i> was restricted to quadrats infected with <i>Cuscuta</i>. Quadrats initially lacking <i>Limonium</i> but containing <i>Cuscuta</i> had significantly higher <i>Limonium</i> densities on the next census than did quadrats initially lacking <i>Cuscuta</i> (Fig. 9A, left). Similarly, quadrats initially containing <i>Limonium</i> increased in <i>Limonium</i> cover between censuses significantly faster if they also initially contained <i>Cuscuta</i> (Fig. 9A, right). <i>Cuscuta</i> also seemed to mediate the decline of <i>Frankenia</i>, but results were more variable and not statistically significant. Quadrats initially lacking <i>Frankenia</i> but containing <i>Cuscuta</i> tended to have higher <i>Frankenia</i> densities on the next census than did quadrats initially lacking both (Fig. 9B, left). Quadrats initially containing <i>Frankenia</i> tended to decrease in <i>Frankenia</i> cover less between censuses if they also initially contained <i>Cuscuta</i> (Fig. 9B, right). The abundance of <i>Cuscuta</i> was in turn strongly mediated by the abundance of its preferred host plant, <i>Salicornia</i>; the probability that <i>Cuscuta</i> would invade a quadrat fell sharply when the initial cover of <i>Salicornia</i> was <100% (Fig. 10).

**DISCUSSION**

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

<table>
<thead>
<tr>
<th>Source</th>
<th>Pillai’s trace</th>
<th>df</th>
<th>F</th>
<th>P†</th>
</tr>
</thead>
<tbody>
<tr>
<td>Infected or not</td>
<td>0.5758</td>
<td>3, 54</td>
<td>24.43</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Marsh zone</td>
<td>0.3793</td>
<td>3, 54</td>
<td>11.00</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Patch size</td>
<td>0.5076</td>
<td>3, 54</td>
<td>18.56</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Infection × zone</td>
<td>0.1864</td>
<td>3, 54</td>
<td>4.12</td>
<td>0.010</td>
</tr>
<tr>
<td>Infection × size</td>
<td>0.4117</td>
<td>3, 54</td>
<td>12.60</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Zone × size</td>
<td>0.1260</td>
<td>3, 54</td>
<td>2.60</td>
<td>0.062</td>
</tr>
<tr>
<td>Zone × size × infection</td>
<td>0.0928</td>
<td>3, 54</td>
<td>1.84</td>
<td>0.15</td>
</tr>
</tbody>
</table>

† Bold = significant.
would invade a plot fell sharply when the cover of Salicornia was <100% (Fig. 10). Because an invading Cuscuta tendril 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
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 declassed 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 (Purser 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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LITERATURE CITED


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