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# Facilitation May Buffer Competitive Effects: Indirect and Diffuse Interactions among Salt Marsh Plants

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**ABSTRACT:** Direct interactions among plant species may be highly modified by indirect or diffuse effects within a multispecies community. We investigated the direct and diffuse effects of two salt marsh perennials, *Monanthechloe littoralis* and *Arthrocnemum subterminale*, on winter annuals and the perennial herb *Limonium californicum* in a salt marsh in central California. In permanent plots, *Monanthechloe* had expanded substantially in the upper marsh over the past 13 yr, while *Arthrocnemum* and all annual species had decreased. These dynamics suggest that *Monanthechloe* may directly outcompete most other species in the upper marsh. In contrast, *Arthrocnemum* is known to facilitate some annual species. In our field experiments, *Monanthechloe* strongly suppressed *Arthrocnemum*, all four common annual species, and *Limonium* in direct interactions. In contrast, *Arthrocnemum* directly facilitated the winter annuals *Parapholis incurva* and *Lasthenia glabrata*, competed with *Spergularia marina*, and did not have a significant effect on *Limonium*. However, when the combined effects of *Monanthechloe* and *Arthrocnemum* were tested, *Arthrocnemum* ameliorated the negative effect of *Monanthechloe* on all four species. Although isolated *Arthrocnemum* competed with *Spergularia* and had no direct effects on *Limonium*, *Arthrocnemum* in the presence of *Monanthechloe* facilitated both species. We hypothesize that *Arthrocnemum* buffered the strong competitive effects of *Monanthechloe* on *Lasthenia* and *Parapholis* via direct positive effects and benefited *Spergularia* and *Limonium* through its competitive effect on *Monanthechloe*. These findings add to the growing body of literature emphasizing the importance of diversity and interdependence in the functioning of plant communities.

**Keywords:** competition, diffuse interactions, facilitation, indirect interactions, positive interactions, salt marsh.

Pairwise, direct interactions often fail to predict the way

species interact within communities. Within a trophic level, additional species can alter pairwise interactions via direct and indirect pathways (Lawlor 1979; Stone and Roberts 1991; Miller 1994; Wootton 1994) and through the cumulative, “diffuse” effects of many direct effects acting on a single species (Davidson 1980; Wilson and Keddy 1986a, 1986b; Vandermeer 1990). For example, Levine (1976) demonstrated that the addition of a third competitor to a model of two competing species could change the cumulative effect of a species from competitive to facilitative because of the suppression of a shared competitor. Similarly, models of interactions among invading exotic and native species have suggested that natives may be completely displaced in pairwise interactions but can coexist with exotics in diverse communities, apparently because of the greater number of indirect interactions (Case 1991). Despite the potential importance of indirect interactions in plant communities, only a few experiments have attempted to demonstrate the existence of interactions in which “a competitor’s enemy is a friend” (Wilson and Keddy 1986a; Miller 1994; Levine 1999).

Direct interactions among plants can also be facilitative (Callaway 1995), and although positive interactions have been demonstrated in many experiments, little is known about indirect interactions involving species with facilitative effects. In the upper zones of coastal salt marshes in southern California, the two dominant perennial species appear to have strikingly opposite effects on most co-occurring winter annual species. *Arthrocnemum subterminale*, a succulent subshrub, has been shown to facilitate two annual species, *Parapholis incurva* and *Lasthenia glabrata* (Callaway 1994); whereas *Monanthechloe littoralis*, a clonal grass, appears to eliminate virtually all annuals by establishing a thick vegetative mat (R. M. Callaway and S. C. Pennings, personal observation). Furthermore, long-term monitoring (see “Results”) at our study site indicates that *Monanthechloe* is increasing in abundance and displacing *Arthrocnemum* and winter annual species. Together, these patterns suggest the potential for unusual indirect interactions. We hypothesized that *Monanthechloe* might directly outcompete annual

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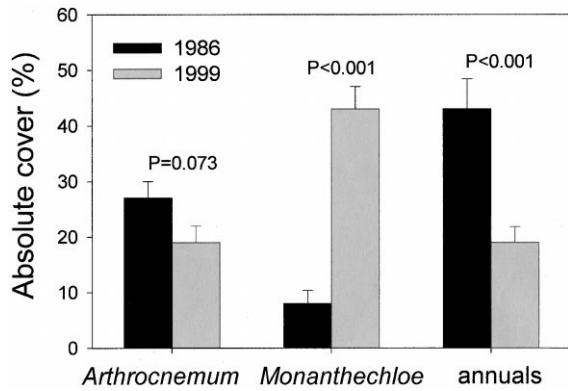


Figure 1: Percentage cover of *Monanthechloe littoralis*, *Arthrocnemum subterminale*, and winter annual species in permanent plots in Carpinteria Salt Marsh, California, in 1986 and 1999. Bars represent 1 SE.

species but that the positive effect of *Arthrocnemum* might buffer annual species from the full negative effect of *Monanthechloe*. We tested these hypotheses in four ways: first, by correlating changes in the relative abundance of *Monanthechloe* with the abundance of other species over the past 13 yr, second, by measuring patterns of abundance of annual species associated with *Arthrocnemum* in the presence and in the absence of *Monanthechloe*, third, by conducting field experiments in which we measured the direct effects of the perennials on each other and on annual species and a perennial herb, and finally, by conducting field experiments in which we measured the effects of *Monanthechloe* on other species in the presence and in the absence of *Arthrocnemum*.

#### Study Site

We conducted our study in the upper “transition zone” at the Carpinteria Salt Marsh Reserve (34°24'N, 119°31'W), approximately 15 km south of Santa Barbara, California. This site was described extensively in Ferren (1985), Callaway et al. (1990), and Pennings and Callaway (1992, 1996), and direct interactions among species in the transition zone have been examined in Callaway (1994). The dominant perennial species in the transition zone, approximately 0.4–0.6-m elevation above mean high high water, are the small shrub *Arthrocnemum subterminale* (Parish) Standl. and the highly rhizomatous, mat-forming *Monanthechloe littoralis*. Winter annual species are distributed along an elevation-and-salinity gradient and include *Spergularia marina*, *Parapholis incurva*, *Hutchinsia procumbens*, *Lasthenia glabrata*, and *Juncus bufonius* (nomenclature follows Ferren 1985). The relative abundance of these species and their

position on the elevation gradient varies substantially among years, at least partly due to variation in precipitation (Callaway and Sabraw 1994).

#### Methods

To document the natural dynamics of species in the upper marsh, we quantified the absolute cover of *Arthrocnemum*, *Monanthechloe*, and winter annuals in 59 permanent plots in 1986 and 1999. We also correlated the change of *Monanthechloe* absolute cover with the change of *Arthrocnemum* cover and the percentage change of cover of all annual species combined in each plot. For simplicity, and because of the year-to-year variation in the relative abundances of different annual species among years and with

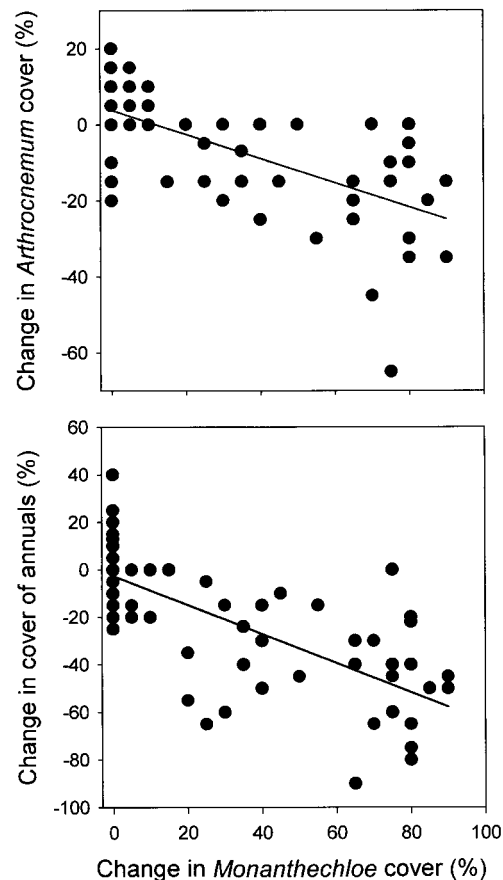
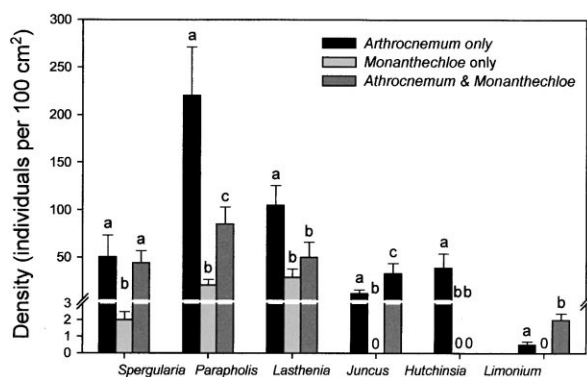


Figure 2: Regression relationship between the change in percentage cover of *Monanthechloe littoralis* and the change in percentage cover of *Arthrocnemum littoralis* and annual species in Carpinteria Salt Marsh, California. For *Arthrocnemum*,  $y = 3.80 + x(-0.32)$ ,  $r^2 = 0.39$ ,  $P < .01$ ; for annuals,  $y = -2.53 + x(-0.61)$ ,  $r^2 = 0.49$ ,  $P < .01$ .



**Figure 3:** Densities of annual species in plots containing the perennials *Monanthechloe littoralis*, *Arthrocnemum subterminale*, or both in Carpinteria Salt Marsh, California. Bars represent 1 SE, and shared letters for a species indicate no significant difference between means (ANOVA, post-ANOVA Tukey,  $P < .05$ ).

elevation, all annual species were combined for these analyses.

To document current spatial associations among species, we sampled the density of all annual species and new recruits of the perennial herb *Limonium* in May 1998 in 100-cm<sup>2</sup> quadrats in patches with the perennial community represented by only *Arthrocnemum* ( $n = 20$ ), only *Monanthechloe* ( $n = 20$ ), and both *Arthrocnemum* and *Monanthechloe* ( $n = 20$ ). In patches dominated by *Monanthechloe*, *Monanthechloe* was present at 100% cover and with a mat 2–3 cm deep. Plots were chosen by randomly locating a point on transects and then moving in a random direction until one sample of each of the three different patch types were encountered. For each individual species, and all annual species combined, one-way ANOVAs and post-ANOVA Tukey tests were used to compare densities among patch types. All data for individual species were log transformed to improve normality.

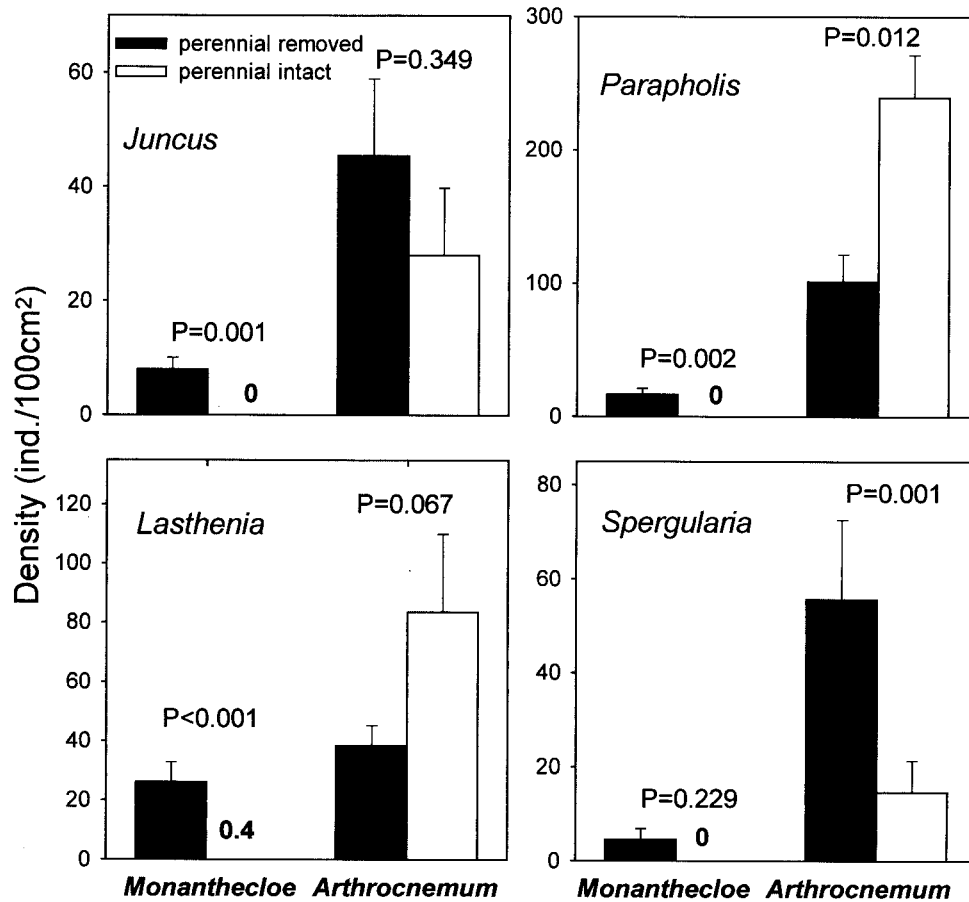
In May 1997, we removed either *Monanthechloe* or *Arthrocnemum* from patches in which either one or the other occurred, avoiding patches containing both perennial species together, in order to examine the direct effects of the two large perennials on the annual species and on *Limonium*. Because site effects might confound the effects of the perennials, we chose patches that were as intermixed as possible. At the beginning of the experiment, annuals and *Limonium* were present in plots with only *Arthrocnemum* but not in plots with *Monanthechloe*. For each perennial species, we established 10 400-cm<sup>2</sup> removal plots and 10 control plots. In May 1998, we counted all individuals of all annual species in the center 100 cm<sup>2</sup> of each plot. *Limonium* densities were sampled in June 1999 in

the entire 400-cm<sup>2</sup> plot because densities were much lower. Effects were tested using a one-way ANOVA (SPSS 1997) for each of the four most abundant annual species, *Juncus*, *Parapholis*, *Lasthenia*, and *Spergularia*, and the perennial herb *Limonium* in each removal treatment. Data for other annual species were not analyzed because they were present in only a small fraction of the plots.

To examine the interactive effects of *Monanthechloe* and *Arthrocnemum* on annual species and *Limonium*, we established a second experiment in May 1997. Before manipulation, each 100-cm<sup>2</sup> plot contained a single *Arthrocnemum* individual and 100% cover of *Monanthechloe* forming a 2–4-cm deep mat. We established the four following treatments: removal of *Monanthechloe*, removal of *Arthrocnemum*, removal of both perennials, and both perennials left intact ( $n = 10$  for each). No annuals or *Limonium* were present in plots at the beginning of the experiment. We counted all individuals of all annual species in May 1998 and *Limonium* recruits in June 1999. We measured recruits of the perennial *Limonium* after 2 yr because it recruited much more slowly than the annuals. We analyzed the results of this experiment using a two-way ANOVA for each of the four annual species and *Limonium* in which the presence or absence of each perennial was considered as a main effect. We also used these treatments to assess the effect of *Monanthechloe* on *Arthrocnemum*. At the time that the experiment was established, a 50 × 50-cm grid subdivided into 100 5 × 5-cm cells was placed over the central *Arthrocnemum* individual and the number of cells occupied by *Arthrocnemum* was counted. In May 1998, cells were counted again and the change in number of cells occupied was compared among *Monanthechloe* removal treatments separately using a one-way ANOVA. In 10 other plots, we measured the effect of *Arthrocnemum* on *Monanthechloe*. We chose plots in which *Arthrocnemum* occurred at 90%–100% cover and *Monanthechloe* occurred at <50% cover. In 10 plots, we removed *Arthrocnemum* and compared changes in the cover of *Monanthechloe* to that in the 10 control plots. Measurements of cover and analyses were the same as used for examining the effects of *Monanthechloe* on *Arthrocnemum*.

## Results

*Monanthechloe* appeared to be expanding in the marsh at the expense of all of the other species we studied. In 59 plots on permanent transects, *Monanthechloe* increased from 8% cover in 1986 to 43% in 1999 (fig. 1). During the same time period, *Arthrocnemum* decreased from 27% to 19%, and total annual cover decreased from 43% to 19%. Within individual 0.125-m<sup>2</sup> plots, increases in *Mon-*



**Figure 4:** Densities of the four most common annual species in response to the removal of *Monanthechloe littoralis* or *Arthrocnemum subterminale* at Carpinteria Salt Marsh, California. Bars represent 1 SE. For the *Monanthechloe* only and the *Monanthechloe* plus *Arthrocnemum* plots, the cover of *Monanthechloe* was 100%, and the depth of the vegetative mat was the same ( $2.7 \pm 0.4$  cm and  $2.8 \pm 0.6$  cm, respectively).

*anthechloe* abundance were significantly correlated with decreases in *Arthrocnemum* and annual cover (fig. 2).

Winter annual species coexisted with *Arthrocnemum* but not with *Monanthechloe*, and the presence of *Arthrocnemum* in patches of *Monanthechloe* was correlated with high abundances of annual species. In 1998, most annual species were significantly ( $P = .061$  for *Spergularia*) more common when only *Arthrocnemum* was present than when only *Monanthechloe* was present (fig. 3). Even though the cover and thickness of *Monanthechloe* were similar in plots with *Monanthechloe* alone and plots with *Monanthechloe* and *Arthrocnemum* together, the densities of *Spergularia*, *Parapholis*, and *Juncus* were significantly higher in patches of *Monanthechloe* when *Arthrocnemum* was also present than when only *Monanthechloe* was present. *Limonium* was absent in plots with only *Monanthechloe*, uncommon in plots with only *Arthrocnemum* ( $0.5 \pm 0.2$  individuals/100 cm<sup>2</sup>), and most abundant where both *Monanthechloe* and

*Arthrocnemum* were present (fig. 3;  $2.0 \pm 0.4$  individuals/100 cm<sup>2</sup>; ANOVA,  $df = 2, 56$ ,  $P < .001$ ). The difference between the latter two sites was significant (Tukey,  $P < .001$ ).

In single-species removal experiments, the direct effects of *Monanthechloe* on annuals and *Limonium* were consistently negative (fig. 4; table 1). One season after treatments were established, annuals were virtually absent in *Monanthechloe* patches but present in *Monanthechloe* removal plots at densities ranging from 3 to 28 individuals/100 cm<sup>2</sup>. Two seasons after treatments were established, no *Limonium* occurred in the presence of *Monanthechloe*, whereas *Limonium* density was  $3.6 \pm 1.7/400$  cm<sup>2</sup> when *Monanthechloe* was removed. The direct effects of *Arthrocnemum* ranged from strongly negative on *Spergularia* to strongly facilitative on *Parapholis* and *Lasthenia*. However, all four annual species were much more abundant in both *Arthrocnemum*-only treatments than in the treatment

**Table 1:** ANOVA table for the direct effects of *Monanthechloe littoralis* and *Arthrocnemum subterminale* on the density of winter annuals

Species	F	P
<i>Monanthechloe</i> removal:		
<i>Juncus balticus</i>	14.40	.001 <sup>a</sup>
<i>Parapholis incurva</i>	12.72	.002 <sup>a</sup>
<i>Lasthenia glabrata</i>	14.42	.001 <sup>a</sup>
<i>Spergularia marina</i>	1.55	.229
<i>Arthrocnemum</i> removal:		
<i>Juncus balticus</i>	.93	.349
<i>Parapholis incurva</i>	34.71	<.001 <sup>b</sup>
<i>Lasthenia glabrata</i>	3.79	.067 <sup>b</sup>
<i>Spergularia marina</i>	5.11	.001 <sup>a</sup>

Note: For all species, df = 1, 19.

<sup>a</sup> Direction of effect is negative.

<sup>b</sup> Direction of effect is positive.

where *Monanthechloe* was removed. *Arthrocnemum* had no significant direct effect on *Limonium*: *Limonium* density was  $1.9 \pm 1.4/400$  cm<sup>2</sup> when *Arthrocnemum* was removed and  $1.6 \pm 1.5/400$  cm<sup>2</sup> when it was present (*t*-test,  $P > .5$ ). The magnitude of the effects of *Monanthechloe* and *Arthrocnemum* may not be directly comparable within this experiment because of the different populations of annuals present when removal was established. At the time experiments were established, no annuals were present in the plots with *Monanthechloe*, but annuals were abundant in the plots with *Arthrocnemum*. Therefore, *Monanthechloe* plots probably did not have large seed banks or seed inputs, compared to *Arthrocnemum* plots, at the beginning of the experiment.

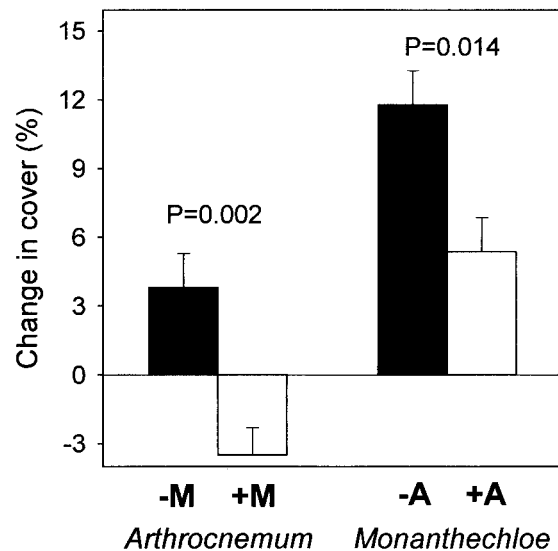
The direct effect of *Monanthechloe* on *Arthrocnemum* was also negative (fig. 5). *Arthrocnemum* cover increased  $4\% \pm 2\%$  when *Monanthechloe* was removed but decreased by  $3\% \pm 1\%$  when *Monanthechloe* was not present ( $F = 13.78$ ,  $df = 1, 19$ ,  $P = .002$ ). *Arthrocnemum* also had significant competitive effects on *Monanthechloe* (fig. 5;  $F = 6.90$ ,  $df = 1, 19$ ,  $P = .014$ ), but the cover of *Monanthechloe* increased significantly whether *Arthrocnemum* was present.

Field experiments indicated that *Arthrocnemum* reduced the competitive effects of *Monanthechloe*, corroborating the spatial patterns described in figure 3. In the factorial experiment designed to examine the combined and indirect effects of the large perennials, competition from *Monanthechloe* was by far the strongest overall effect and was significant for each of the annual species and for *Limonium* (figs. 6, 7; table 2). When *Arthrocnemum* was left intact but *Monanthechloe* was removed, the density of *Parapholis* was over five times higher than when both perennials were removed. In intact patches of *Monanthechloe*,

*Parapholis* survived only when *Arthrocnemum* was present. Similar patterns were observed for *Lasthenia* and *Juncus*, but the direct effects of *Arthrocnemum* were not as strong. The most striking indirect effects in the factorial field experiment occurred for *Spergularia* and *Limonium*. In the absence of *Monanthechloe*, *Spergularia* was much more common when *Arthrocnemum* was removed, indicating a competitive effect of *Arthrocnemum*. But when the dominant competitor *Monanthechloe* was present, *Arthrocnemum* strongly facilitated *Spergularia*. *Limonium* was indifferent to the presence of *Arthrocnemum* when *Monanthechloe* was absent, but in the presence of *Monanthechloe*, *Limonium* recruits were only found in plots in which *Arthrocnemum* was also present.

## Discussion

Strong direct competition, facilitation, and indirect facilitation occurred among plant species in the upper marsh at Carpinteria. *Monanthechloe* increased in abundance in the upper margins of Carpinteria Salt Marsh and displaced annuals and *Limonium*; however, *Arthrocnemum* buffered the competitive effects of *Monanthechloe* on several of these species. In patches of *Monanthechloe*, more annuals occurred with *Arthrocnemum* than in its absence (fig. 3). In the presence of *Monanthechloe* in field experiments, *Parapholis*, *Lasthenia*, *Spergularia*, and *Limonium* were more abundant with *Arthrocnemum* pre-



**Figure 5:** Change in cover of *Monanthechloe littoralis* and *Arthrocnemum subterminale* over one growing season in response to the removal of the other species. Bars represent 1 SE.

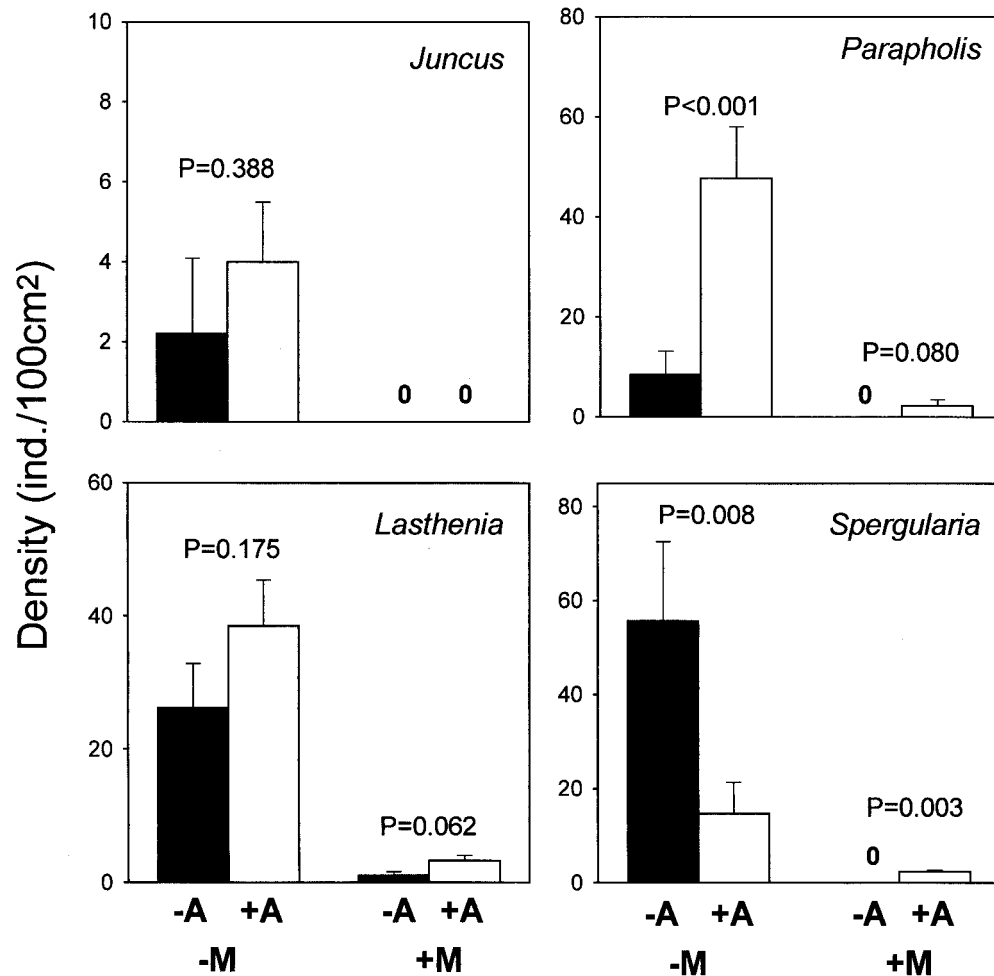


Figure 6: Densities of the four most common annual species after the factorial removal of *Monanthechloe littoralis* and *Arthrocnemum subterminale* at Carpinteria Salt Marsh, California. Bars represent 1 SE. See table 2 for results of the ANOVA.

sent than when it was removed (fig. 6). We suggest that there were two different types of indirect interactions that may explain our results. First, webs of indirect effects (sensu Lawlor 1979; Miller 1994; Wootton 1994) probably explain the results with *Spergularia* and *Limonium*. In the absence of *Monanthechloe*, *Arthrocnemum* competed with *Spergularia* and had no effect on *Limonium*, but in the presence of *Monanthechloe*, *Arthrocnemum* facilitated *Spergularia* and *Limonium*, probably because *Arthrocnemum* had a competitive effect on *Monanthechloe*. Second, “diffuse” interactions (sensu Wilson and Keddy 1986a) may best explain the effects of *Arthrocnemum* on *Parapholis* and *Lasthenia* (i.e., a direct positive effect of *Arthrocnemum* on these annual species canceling out a direct negative effect of *Monanthechloe*) because *Arthrocnemum* had positive effects on these species with or without *Monanthechloe*.

To our knowledge, there have been few experimental demonstrations of indirect effects among plants. Miller (1994) quantified direct and indirect effects among five old-field plant species and consistently found important indirect positive effects. Takahashi (1997) showed that indirect interactions were important for the regeneration of two subalpine conifer species. Levine (1999) demonstrated that *Carex nudata*, a riparian sedge, had a strong indirect effect on the liverwort *Conocephalum conicum* by reducing the abundance of *Mimulus guttatus*, a strong competitor of *Conocephalum*. Wilson and Keddy (1986a) manipulated direct effects among wetland plants and found indications of indirect effects. In nonexperimental studies, the results of Petranka and McPherson (1979) suggested that prairie shrubs facilitate tree species by allelopathically suppressing grasses. However, these studies all differed from ours in

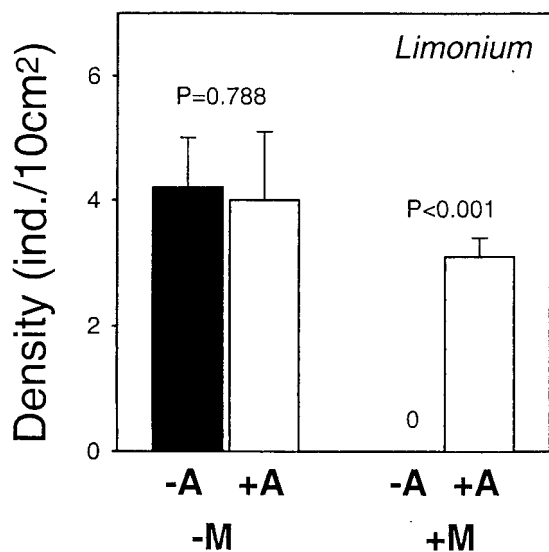


Figure 7: Density of *Limonium californicum* after the factorial removal of *Monanthechloe littoralis* and *Arthrocnemum subterminale* at Carpinteria Salt Marsh, California. Bars represent 1 SE.

that they only examined species with direct competitive effects.

The competitive effect of *Monanthechloe* on *Arthrocnemum*, *Limonium*, and all of the annual species was stronger and more consistent than the positive effects of *Arthrocnemum* on other species. However, weak or “feeble” indirect effects among consumers have been shown to have important overall effects in communities (Berlow 1999). The mechanisms by which *Monanthechloe* outcompetes annuals and *Limonium* are not known; however, heavy mats of *Monanthechloe* create very dense shade, around 0.5%–1% of ambient sunlight (data not presented). Correlative evidence suggests that *Arthrocnemum* may facilitate other species by decreasing soil salinity, moderate shading (ambient light is reduced by about 60%), and increasing soil moisture (Callaway 1994). The direct effects of *Arthrocnemum* described here—facilitation of *Parapholis* and *Lasthenia* but competition with *Spergularia*—correspond to the findings of previous studies (Callaway 1994).

Bertness and Callaway (1994) hypothesized that positive interactions increased in importance with abiotic stress and low productivity. Wilson and Keddy (1986a, 1986b) estimated the strength of diffuse competition in a lake shoreline plant community by incorporating the number of neighbor species removed into the effect of neighbor removal. With this approach they showed that diffuse interactions were particularly strong when total plant biomass was high. In fact, when biomass was the lowest, target species were smaller in the absence of all neighbors than

in their presence, indicating a cumulative facilitative diffuse effect. We found that the total removal of neighbors was never optimal for annual species or for *Limonium*. For every individual species, and for the analysis of all annual species together (table 2), the presence of *Arthrocnemum* after the removal of *Monanthechloe* resulted in higher abundances. In support of Wilson and Keddy (1986b), the transition zone of the marsh in which we worked is the zone of lowest biomass and productivity in the Carpinteria Salt Marsh (Pennings and Callaway 1992).

Our experiments were limited in that we did not quantify the effects of the annuals on the shrubs, which was primarily because the relative biomass of the shrubs was much higher. However, Pugnaire et al. (1996) and Moro et al. (1997) presented evidence that the effect of the understory herb *Marrubium vulgare* on the shrub *Retama sphaerocarpa* was positive and that the dense cover of understory herbs provided a ground cover to retain water. Holzapfel and Mahall (1999) demonstrated experimentally that winter annuals in the Mojave Desert had weak competitive effects on overstory *Larrea tridentata* shrubs.

We only removed the effects of the perennial canopies and did not manipulate root effects. However, root interactions among the species with which we worked appear to be relatively weak. Callaway (1994) conducted experiments in which canopies and roots were manipulated factorially. Canopy effects of *Arthrocnemum* were strong (negative for *Spergularia* and positive for *Parapholis* and *Hutchinsia procumbens*), but root effects were weak and significant only for *Parapholis*. In the experiments reported here, *Arthrocnemum* did not resprout after cutting, suggesting that roots had died, and invasion of *Monanthechloe* into plots from belowground was minimal. Therefore, we believe that we manipulated the most important mechanism of interaction between the perennials and annuals.

Indirect interactions involving consumers are well documented (Paine 1966; Lubchenco 1978; Kerfoot and Sih 1987; Connell 1990; Wootton 1994; Pennings and Callaway 1996), but progress toward understanding indirect interactions among competitors has been primarily theoretical until recently (MacArthur 1972; Pianka 1974; Buss and Jackson 1979; Case 1991; Stone and Roberts 1991; Miller and Travis 1996). Our results for *Spergularia* and *Limonium* corroborate the general conclusions of recent studies of indirect effects—that an enemy’s enemy is a friend—but to our knowledge, no other studies have explicitly manipulated the combined effects of a species with strong competitive effects and another with strong facilitative effects. We found an array of direct and indirect responses, with significant direct competition and facilitation and significant indirect facilitation. Direct and indirect positive effects appeared to buffer the competitive effects of the



**Table 2:** ANOVA table for the factorial effects of *Monanthechloe* and *Arthrocnemum* on winter annuals and the perennial *Limonium californicum*

	df	MS	F	P
<i>Juncus bufonius:</i>				
<i>Arthrocnemum</i> effect	1	15.6	1.02	.320
<i>Monanthechloe</i> effect	1	75.6	4.92	.033 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	3.0	.20	.660
Error	36	15.4	...	...
<i>Parapholis:</i>				
<i>Arthrocnemum</i> effect	1	4,951	14.44	.001 <sup>b</sup>
<i>Monanthechloe</i> effect	1	6,477	18.89	<.001 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	2,907	8.45	.006
Error	36	343	...	...
<i>Lasthenia:</i>				
<i>Arthrocnemum</i> effect	1	600	6.25	.017 <sup>b</sup>
<i>Monanthechloe</i> effect	1	1,134	11.81	.002 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	156	1.62	.211
Error	36	96	...	...
<i>Spergularia:</i>				
<i>Arthrocnemum</i> effect	1	75.6	10.21	.003 <sup>a</sup>
<i>Monanthechloe</i> effect	1	65.0	8.77	.005 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	65.0	8.77	.005
Error	36	12.1	...	...
<i>Limonium:</i>				
<i>Arthrocnemum</i> effect	1	10.0	14.63	<.001 <sup>b</sup>
<i>Monanthechloe</i> effect	1	4.9	7.17	.011 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	8.1	11.85	.001
Error	36	.7	...	...
Total annuals:				
<i>Arthrocnemum</i> effect	1	11,560	21.53	<.001 <sup>b</sup>
<i>Monanthechloe</i> effect	1	13,176	24.54	<.001 <sup>a</sup>
<i>Arthrocnemum</i> × <i>Monanthechloe</i>	1	3,610	6.72	.014
Error	36	537	...	...

Note: "Total annuals" include *Hutchinsia procumbens*.

<sup>a</sup> Direction of effect is negative.

<sup>b</sup> Direction of effect is positive.

rapidly expanding competitive dominant and maintain higher plant diversity in the upper marsh.

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### Literature Cited

- Berlow, E. L. 1999. Strong effects of weak interactions in ecological communities. *Nature (London)* 398:330–334.
- Bertness, M. D., and R. M. Callaway. 1994. Positive interactions in communities. *Trends in Ecology & Evolution* 9:191–193.
- Buss, L. W., and J. B. C. Jackson. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *American Naturalist* 113: 223–234.
- Callaway, R. M. 1994. Facilitative and interfering effects of *Arthrocnemum subterminale* on winter annuals. *Ecology* 75:681–686.
- . 1995. Positive interactions among plants. *Botanical Review* 61:306–349.
- Callaway, R. M., and C. Sabraw. 1994. Effects of variable precipitation on the structure and diversity of a California salt marsh community. *Journal of Vegetation Science* 5:433–438.
- Callaway, R. M., S. Jones, W. R. Ferren, and A. Parikh. 1990. Ecology of a Mediterranean-climate estuarine wet-

- land at Carpinteria, California: plant distributions and soil salinity. *Canadian Journal of Botany* 69:1139–1146.
- Case, T. J. 1991. Invasion resistance, species build-up and community collapse in metapopulation models with interspecies competition. *Biological Journal of the Linnean Society* 42:239–266.
- Connell, J. R. 1990. Apparent versus “real” competition in plants. Pages 9–26 in J. B. Grace and D. Tilman, eds. *Perspectives on plant competition*. Academic Press, New York.
- Davidson, D. W. 1980. Some consequences of diffuse competition in a desert ant community. *American Naturalist* 116:92–105.
- Ferren, W. R., Jr. 1985. Carpinteria Salt Marsh: environment, history, and botanical resources of a southern California salt marsh. The Herbarium, University of California, Santa Barbara, Calif. Publication 4.
- Holzappel, C., and B. E. Mahall. 1999. Bidirectional facilitation and interference between shrubs and annuals in the Mojave Desert. *Ecology* 80:1747–1761.
- Kerfoot, W. C., and A. Sih. 1987. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, N.H.
- Lawlor, L. R. 1979. Direct and indirect effects of *n*-species competition. *Oecologia (Berlin)* 43:355–364.
- Levine, J. M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762–1769.
- Levine, S. H. 1976. Competitive interactions in ecosystems. *American Naturalist* 110:903–910.
- Lubchenco, J. 1978. Plant species diversity in a marine intertidal community: the importance of herbivore food preference and algal competitive abilities. *American Naturalist* 112:23–39.
- MacArthur, R. H. 1972. *Geographical ecology*. Harper & Row, New York.
- Miller, T. E. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* 143:1007–1025.
- Miller, T. E., and J. Travis. 1996. The evolutionary role of indirect effects in communities. *Ecology* 77:1329–1335.
- Moro, M. J., F. I. Pugnaire, P. Haase, and J. Puigdefabregas. 1997. Effect of the canopy of *Retama sphaerocarpa* on its understory in a semiarid environment. *Functional Ecology* 11:425–431.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- Pennings, S. C., and R. M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. *Ecology* 73:681–690.
- . 1996. Impact of a parasitic plant on the structure and dynamics of salt marsh vegetation. *Ecology* 77:1410–1419.
- Petranka, J. W., and J. K. McPherson. 1979. The role of *Rhus copallina* in the dynamics of the forest-prairie ecotone in north-central Oklahoma. *Ecology* 60:956–965.
- Pianka, E. R. 1974. Niche overlap and diffuse competition. *Proceedings of the National Academy of Sciences of the USA* 71:2141–2145.
- Pugnaire, F. I., P. Haase, and J. Puigdefabregas. 1996. Facilitation between higher plant species in a semiarid environment. *Ecology* 77:1420–1426.
- SPSS. 1997. SPSS. Version 7.5. SPSS Inc., Chicago.
- Stone, L., and A. Roberts. 1991. Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72:1964–1972.
- Takahashi, K. 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understory. *Journal of Vegetation Science* 8:529–536.
- Vandermeer, J. 1990. Indirect and diffuse interactions: complicated cycles in population embedded in a large community. *Journal of Theoretical Biology* 142:429–442.
- Wilson, S. D., and P. A. Keddy. 1986a. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *American Naturalist* 127:862–869.
- . 1986b. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology* 67:1236–1242.
- Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. *Annual Review of Ecology and Systematics* 25:443–466.