

## COMPLEX INTERACTIONS IN A STREAMSIDE PLANT COMMUNITY

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**Abstract.** Ecologists are increasingly finding that complex combinations of competitive and facilitative interactions influence the distribution and abundance of plants. I conducted a two-year field experiment to explore these processes in a streamside community lining the South Fork Eel River in northern California. Specifically, I tested the hypothesis that the sedge *Carex nudata* provides critical stable substrate for other plants during winter floods and protection from herbivores over the growing season. In addition to these facilitative effects, *Carex* is also hypothesized to compete with the associated species, and thus limit their size and reproduction.

To evaluate these hypotheses, I followed the performance of transplanted individuals of *Mimulus guttatus*, *M. cardinalis*, *Juncus covillei*, *Conocephalum conicum*, and *Brachythecium frigidum* and naturally occurring individuals of *Epipactis gigantea* on *Carex* tussocks with dense, thinned, pinned back, or completely clipped *Carex* stems. The five transplanted species were also planted directly onto the emergent streambed. Though streambed transplants grew as well as those on tussocks over the summer, they experienced significantly greater winter mortality, up to 100%, supporting the hypothesis that tussocks provide a critical stable substrate. In contrast, growing season competition by *Carex* reduced biomass by over 50% for five of the six species and reduced reproductive performance by over 60%. Also, over the growing season, *Carex* protected *M. guttatus* and *Epipactis* from insect larvae and deer, respectively, reducing herbivory by >75%. Additional results from a deer enclosure treatment showed that the positive effects of this “associational defense” were equal in magnitude to the negative effects of *Carex* competition on *Epipactis* biomass. The mechanisms underlying these associational defenses and the implications of my results for the relationship between disturbance and facilitation are discussed. I suggest that regarding plant interactions as combinations of facilitative and competitive components may enhance our understanding of natural communities.

**Key words:** associational defense; *Carex*; competition; facilitation; *Junonia*; *Mimulus*; riparian community.

### INTRODUCTION

Ecologists have long appreciated the diversity of mechanisms by which plants influence one another. Plants change the environment of their neighbors by adding or subtracting resources and toxins, affecting conditions such as temperature or wind velocity, and encouraging or discouraging animals (Harper 1977). Thus, a negative or positive effect of one species on another may result from any number of processes, and even more fundamentally, these processes may operate simultaneously, either opposing or reinforcing one another. Indeed, a growing number of studies indicate that plant interactions are a composite of facilitative and competitive, direct and indirect interactions that combine in complex ways to influence the distribution and abundance of species (Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998, Li and Wilson 1998, Levine 1999).

The composite nature of plant interactions poses numerous challenges to field ecologists and theoreticians interested in how these processes influence community

patterns. Since most current models of plant community structure (Grime 1979, Tilman 1988, Huston 1994) assume that plant interactions occur through a single mechanism such as resource competition, predictions from these models may not apply to systems where simultaneous interactions are the norm (Callaway 1995). Furthermore, in field ecology, the commonly used neighbor removal experiment, which only isolates the net effect of neighboring plants, may miss important details about interactions involving simultaneous facilitative and competitive processes (see *Discussion*). In a parallel discussion of the mechanisms controlling succession, Walker and Chapin (1986, 1987) argued that successional processes often involve the combination or interaction of facilitative and inhibitory mechanisms, and that this complexity is hidden by net effects. Other studies that have taken a composite perspective have yielded new insights into plant community structure. Wilson and Nisbet (1997) have found that when species interactions are composed of competition and facilitation, abrupt species boundaries can occur along smooth environmental gradients. In addition, Callaway (1997) has argued that because plant interactions reflect combinations of competition and

facilitation, species arrayed independently along gradients may be highly interdependent, challenging Whitaker's (1975) individualistic nature of communities.

Despite the growing acceptance of the composite nature of plant interactions, the factors that control the relative importance of the competitive and facilitative components are only beginning to be understood. Recent papers suggest that abiotic stress and disturbance determine the importance of these factors (Bertness and Callaway 1994, Callaway and Walker 1997, Holmgren et al. 1997, Brooker and Callaghan 1998), though the disturbance-facilitation relationship remains ambiguous (Bertness 1998). Much of the confusion arises because most documented facilitations in "physically disturbed habitats" (e.g. Wood and del Moral 1987, Chapin et al. 1994) actually involve the amelioration of stress following disturbance, as in facilitative succession (Connell and Slatyer 1977), and not the direct prevention of disturbances in the first place (Bertness 1998). Facilitations, however, can directly preclude disturbances, though nearly all evidence comes from intraspecific studies (see Harley and Bertness 1996 for review). Well documented interspecific facilitations often involve biological disturbance, such as predation or herbivory. Associational defenses, where plants protect others from herbivory (Root 1973, Atsatt and O'Dowd 1976, Pfister and Hay 1988) are common in habitats with severe consumer pressure. In contrast, herbivory tends to reduce the intensity of competition (Harper 1977, Collins et al. 1998). Consequently, like agents of physical disturbance, consumers may influence the importance of competition and facilitation (Bertness and Callaway 1994).

Resolving questions about the composite nature of plant interactions requires experiments that isolate the effects of multiple component interactions (e.g. Wood and del Moral 1987, Callaway 1994, Holzapfel and Mahall 1999). In this study, I experimentally evaluate a complex combination of species interactions influencing the distribution and abundance of plants along the South Fork Eel River in northern California.

#### *System and hypotheses*

The cespitose sedge, *Carex nudata*, densely populates riffle formations along many streams in California and Oregon. The fibrous roots and rhizomes of *Carex* form large tussocks that trap riverine sediments during flooding. The tussocks form in the active channel, a habitat maintained by winter floods, but mostly dry at low summer flow. Along the South Fork Eel River in northern California, the tussocks are discrete, average 30 cm in diameter, and are separated from one another by a mean of 40 cm of barren cobbles and water. They emerge from winter flows in the spring, produce thick vegetation, and grow until late summer. During winter months, *Carex* is largely submerged and dormant, and is typically subjected to bed-scouring floods. While these floods dislodge *Carex* seedlings and remove the

previous year's aboveground production, established tussocks are persistent, experiencing <0.5% dislodgment per year, even in a 10-yr flood (J. Levine, unpublished data).

Among the most striking features of this community is that nearly all of the >60 plant species living entirely in the active channel use sediments trapped within *Carex* tussocks as their primary substrate. This study focuses on six of these species, selected to be representative of the perennial herbaceous plants and bryophytes that characterize the system. These included *Mimulus guttatus*, the common monkeyflower, an abundant low growing rhizomatous dicot, and *Mimulus cardinalis*, the scarlet monkeyflower, a more erect related taxon. Also included were two of the most common monocots, *Epipactis gigantea*, a clonal stream orchid, and *Juncus covillei*, a rush. Representing the bryophytes were *Conocephalum conicum* and *Brachythecium frigidum*, the most common liverwort and moss, respectively.

This study explores the hypothesis that *Carex* ameliorates bed-mobilizing winter floods and provides moist substrate and protection from herbivores. This hypothesis stems from observations that the belowground structures of plants associated with tussocks are probably too small to anchor into a streambed that is mobilized by winter floods or obtain subsurface moisture during dry summer months. In addition, natural plants of *M. guttatus* and *Epipactis* in dense *Carex* rarely suffer the herbivory observed on sparsely vegetated tussocks or directly on the streambed. I observed that in these latter habitats, *M. guttatus* is frequently defoliated by larvae of the Buckeye butterfly, *Junonia coenia*, and entire clones of *Epipactis* are commonly grazed off by coast blacktail deer, *Odocoileus hemionus* ssp. *columbianus*. Though *Carex* is hypothesized to be an important facilitator or "ecosystem engineer" sensu Jones et al. (1994), its roots permeate the sediments trapped within the tussock, and its dense stems shade the tussock surface over the growing season. This leads to a second hypothesis that competition by *Carex* limits plant size and reproduction during the summer growing season.

#### METHODS

##### *Quantifying substrate use by plants in this system*

All field work was conducted along a 1.5 km stretch of the South Fork Eel River in northern California, USA. In early June 1997, I sampled the vegetation in a total of 400 0.25-m<sup>2</sup> plots spaced at 3-m intervals along 30-m transects. These transects ( $N = 40$ ) were placed at random locations 1 m away from, and parallel to, the channel margin. Within each plot, I recorded the number of ramets of each plant species and the substrate (tussock, cobbles, etc.) on which they were living (plots typically contained several substrates). For the smaller clonal plants and bryophytes, I recorded

their absolute cover, and then branch or ramet number within a 25-cm<sup>2</sup> subplot centered in the clone. For each plot, I also categorized the geomorphic habitat as riffle, sand bar, cobble bar, mud, or bedrock. To ensure that the 400 plots were representative of the actual abundances of these habitats, I recorded the linear coverage of the habitats on both sides of the 1.5 km stretch of river. This was accomplished by running a series of end to end 100-m line transects ( $N = 30$ ) parallel to, and 1 m away from, the flowing channel.

#### Field experiment

To evaluate competitive and facilitative effects of *Carex*, I followed the growth and survivorship of naturally occurring individuals of *Epipactis*, and transplants of *M. guttatus*, *M. cardinalis*, *Juncus*, *Conocephalum*, and *Brachythecium* in the following treatments: (1) tussocks where I completely clipped all *Carex* from the tussock (hereafter clipped *Carex*); (2) tussocks where *Carex* was thinned to 10 stems/100 cm<sup>2</sup> (hereafter thinned *Carex*; the *Carex* intercepted  $63.9\% \pm 2.9$  [mean  $\pm 1$  SE] of photosynthetically active radiation); (3) tussocks where *Carex* was left dense ( $25.89 \pm 0.77$  stems/100 cm<sup>2</sup>;  $95.7\% \pm 0.6$  of photosynthetically active radiation (PAR) intercepted, hereafter dense *Carex*); (4) tussocks where I pinned all *Carex* stems to the tussock to only remove aboveground competition (hereafter pinned *Carex*); (5) emergent streambed substrate adjacent to tussocks, where species were planted directly into the cobbles, pebbles, and sand (hereafter streambed); and (6) watered emergent streambed adjacent to tussocks, where transplants were placed on the streambed but continuously watered with a gravity driven drip system (hereafter watered streambed). Treatments were randomly assigned to tussocks, and spaced over four adjacent riffles (blocks) along a 1.2-km stretch of river. Riffles varied considerably in the number of tussocks they contained and this was reflected in the number of plants I assigned to each riffle (riffles contained 55, 71, 115, and 185 total plants).

All transplant species were randomly assigned to treatment in late May 1997 (see Levine 1999 for transplanting details). For each transplant species, there were 20 replicates of the four tussock treatments (*M. cardinalis* had 19 replicates), and 13 replicates of the two streambed treatments. Transplants were placed one per tussock, except for the bryophytes, which were planted two plugs per tussock (one of each species), far enough apart to prevent contact. Naturally occurring species were left intact on the experimental tussocks, though transplants were placed in uncolonized areas. Because species in this system have small root systems, belowground interactions with other tussock colonists were unlikely. Transplant mortality over the growing season was <15% for all species.

*Epipactis* was abundant enough in the sedges receiving the five transplanted target species that natural

individuals were found in all but the streambed treatments. In late May 1997 and 1998, I marked two ramets roughly 6 cm tall with fine plastic coated wire in each of the experimental tussocks with naturally occurring *Epipactis* clones. The mean of these two ramets was used for analyses. For *Epipactis*, 1998 represented a replicate experiment and not a continuation of the 1997 experiment, since different ramets were followed in the two years. To assess the effects of deer herbivory on *Epipactis* performance, I set up an additional treatment in May 1997 where I caged entire *Epipactis* tussocks with all *Carex* stems clipped. Twenty randomly located tussocks with *Epipactis* were clipped and encircled with 1 m tall cylinders of chicken wire that was crimped at the top. Direct cage effects were likely minimal because of the 5 cm diameter mesh size (1997 measurements indicated that cages reduced PAR by <8%).

Every three weeks from 28 May to 29 September 1997, I nondestructively measured the size of all target species and maintained the clipped, pinned, and thinned treatments. For *M. cardinalis*, I measured node number and maximum leaf length; for *M. guttatus*, ramet number; for *Juncus*, ramet number and height; for *Epipactis*, height, leaf number, and maximum leaf length; and for *Conocephalum* and *Brachythecium*, area. For the vascular plants, I also quantified flower number and the incidence of herbivory. In 1997, *Juncus* and *Epipactis* died back before the other species, and were thus not measured on the final sampling dates. In order to be able to relocate the transplants in the spring of 1998 (after the winter floods), at the end of the 1997 season, I marked each transplant with an engraved numbered aluminum tree tag, pinned to the tussock with a 10-cm flagged metal staple. Since pinning was not an option for marking the position of streambed transplants, these were located along transects placed between two marked sedges. In late spring 1998 I recorded whether each transplant survived the winter and I resumed 3-wk interval measuring. I did not begin until 18 June because of high water from a late spring flood.

On the last 1998 sampling date, in addition to taking the nondestructive measures of size, I harvested the plants (aboveground only), and dried and weighed them. These plants provided data for regression analyses relating the nondestructive measures to biomass for each species (*M. cardinalis*,  $R^2 = 0.97$ ; *M. guttatus*,  $R^2 = 0.90$ ; *Juncus*,  $R^2 = 0.90$ ; *Epipactis*,  $R^2 = 0.80$ ; *Conocephalum*,  $R^2 = 0.80$ ; *Brachythecium*,  $R^2 = 0.87$ ;  $P = 0.001$  for all regressions). These relationships did not significantly depend on treatment and were used to estimate the biomass of each transplant at all prior sampling dates.

#### *Carex* effects on *Mimulus guttatus* herbivory

Observations of damage to *M. guttatus* by *Junonia coenia* larvae over the first year of the study motivated an additional experiment in 1998 in which I repeated the 1997 experiment for *M. guttatus*, but this time with

a *Junonia* removal and control treatment in a full factorial design (12 replicates/treatment combination). I removed *Junonia* by hand picking early instar larvae off the *Junonia* removal plants every four days from the time *Junonia* larvae first appear in mid-July until the end of the season. Though small, larvae were easy to locate due to their distinctive frass. This removal technique effectively prevented noticeable damage in nearly all cases, and did so without introducing cage artifacts. The three times it failed were cases in which mature larvae, which are capable of causing significant damage in a single day, moved to experimental plants from others nearby. These plants were removed from the analysis.

#### Seedling experiments

For *M. cardinalis*, *M. guttatus*, and *Juncus*, I also explored how competition and facilitation influenced seedling dynamics. For each of the three species, I added 200 seeds to 100-cm<sup>2</sup> plots ( $N = 20$ ) located in all but the pinned *Carex* and watered streambed treatments. These plots were located one per tussock far enough away from the transplants to prevent interference, and each plot received one species. I added the seeds at the natural time of seed release for each species. Thus for *M. guttatus* which flowers relatively early, I added seeds in mid-July 1997, and for the other two species I added seeds in mid-September 1997. Because some of the natural seed produced in a given summer does not germinate until the following spring, I also performed a late spring seed addition in June 1998, once water levels dropped below the tussocks. Since natural seeds at this time of the year have imbibed prior to the emergence of the tussocks, I stored the seeds in river water for two weeks prior to sowing.

Following germination in 1997 and 1998, I counted seedling number every 3 wk until the end of September. These seedlings were unlikely to represent natural recruits, as no recruits were found in plots that did not receive seeds of that species (i.e., no *Juncus* emerged in *M. cardinalis* plots). In early summer 1998, I recorded the survivorship of the 1997 germinants through the winter. At the 25 September 1998 census, I harvested, dried, and weighed the largest individual in each of the plots.

#### Statistical analyses

I used ANOVA blocked by site to evaluate treatment effects on transplant biomass at the end of 1997 and 1998. The same analysis was used for seedling number and final size. When necessary, data were transformed to meet the assumptions of ANOVA. Mortality over the 1997–1998 winter unbalanced the number of transplants in each of the treatments across block in 1998. For example, some blocks contained many more streambed plants than others, confounding the blocking term with treatment. Thus, I conducted the 1998 analyses with and without the block effect. Though I pre-

sent only the latter, presence or absence of the blocking term did not influence the significance of treatment for any of the species. Similar problems emerged with flower number and seedling biomass data. Following all ANOVAs, I compared the various treatments with Tukey-Kramer post-hoc tests. Flower number data were highly non-normal with many zero values, and were thus analyzed with nonparametric Kruskal-Wallis tests, followed by nonparametric multiple comparisons (Zar 1999). Watering was not continued in 1998 because of the low survivorship of streambed transplants over the 1997–1998 winter and their failure to respond to water addition during 1997 ( $P > 0.57$  for each species). Thus for analyses subsequent to 1997 growth and reproduction, the watered streambed and streambed transplants were pooled.

To analyze *M. guttatus* biomass in the competition crossed with herbivory experiment, I used two-factor ANOVA, blocked by site. The importance of the associational defense was assessed by the interaction term, because it evaluated the degree to which the effect of *Junonia* depended on the *Carex* treatment.

I used  $\chi^2$  tests followed by multiple comparisons for proportions (Zar 1999) to evaluate treatment effects on the incidence of deer and *Junonia* herbivory, and on winter mortality. I used the same analysis for the pattern data to determine if a disproportionate number of individuals of each species was found on *Carex* tussocks. All analyses were conducted in SYSTAT 7.0 (Systat 1997) and StatXact 3 (StatXact 1997). The September 28, 1997 biomass data for the two *Mimulus* and bryophyte species in dense and thinned *Carex* treatments were used in Levine (1999) for comparison to a different set of treatments isolating indirect effects among competitors (See *Discussion*).

## RESULTS

### Substrate use

While *Carex* tussocks occupied only 33.05% of the area in the channel, the 13 most common species (Table 1) had a mean of 84% of their individuals on *Carex* tussocks. Though I present only the 13 most common species, the same general patterns were found for the other species in the system (the table stops at *M. cardinalis*, as this is the least common transplant species).

### Growing season effects of *Carex*

Competitive effects of *Carex* were evaluated by comparing the final biomass of the six target species in dense, thinned, and clipped treatments. For all species but *Brachythecium*, I found significant effects of competition on plant biomass (Figs. 1 and 2) and for all species but *M. cardinalis*, significant effects on flower number in one or both years (Fig. 3). Though nonsignificant, trends in *M. cardinalis* flower number were similar to those found for the other species (Fig. 3A and B). The species most suppressed by competition

TABLE 1. Descriptions, overall incidence, and degree of association with *Carex* tussocks for the 13 most common species along a 1.5-km stretch of the South Fork Eel River, California.

Species	Description	Incidence in 400 0.25-m <sup>2</sup> plots	Percentage of ramets found on <i>Carex</i> tussocks†
<b><i>Conocephalum conicum</i></b>	Liverwort	0.39	99
<b><i>Brachythecium frigidum</i></b>	Moss	0.37	93
<i>Equisetum arvense</i>	Horsetail	0.37	82
<i>Marchantia polymorpha</i>	Liverwort	0.36	69
<b><i>Mimulus guttatus</i></b>	Common monkeyflower	0.31	98
<b><i>Epipactis gigantea</i></b>	Stream orchid	0.28	92
<i>Calypogeja muelleriana</i>	Leafy liverwort	0.27	99
<b><i>Juncus covillei</i></b>	Rush	0.25	51
<i>Agrostis stolonifera</i>	Exotic grass	0.16	75
<i>Alnus rhombifolia</i>	White alder	0.11	78
<i>Mimulus moschatus</i>	Muskflower	0.08	95
<i>Plantago major</i>	Exotic plantain	0.08	61
<b><i>Mimulus cardinalis</i></b>	Scarlet monkeyflower	0.06	99

Note: Target species in the experiment are in bold.

† All species are significantly associated with tussocks ( $\chi^2$  test,  $P < 0.05$ ), given that tussocks occupy 33.05% of the emergent channel.

was *M. guttatus*, which in 1997 grew ten times better, and produced five times as many flowers on clipped *Carex* tussocks as compared to dense *Carex* (Figs. 1C and 3C). Though not as dramatic, evidence of competition was also found for *Epipactis*, though only after the confounding effects of herbivores were removed (see *Results: Associational defenses*). Transplants of *M. cardinalis* and *M. guttatus* in 1997 and *Juncus* in 1998 grew significantly better in the pinned versus dense *Carex* treatment (Fig. 1A, C, F), suggesting important effects of aboveground (light) competition. The absolute difference between these two treatments was greater in 1998 for all three species, though for the two *Mimulus* species, 1998 differences were not significant due in part to greater variability and reduced survival (replication) following 1997–1998 flooding (*Juncus* survival was 100% on tussocks). In general, the growth of transplants in the pinned *Carex* treatment, which only eliminated aboveground competition, and in the clipped *Carex* treatment was similar, suggesting that belowground competition may have been weak (Fig. 1). However, it is also possible that clipping did not completely eliminate belowground effects as some *Carex* roots were still active (see *Discussion*).

Dense *Carex* inhibited *Conocephalum* growth, as was evidenced by significantly greater liverwort biomass in the thinned versus dense treatment (Fig. 2A and B). However, 1997 growth in the clipped and pinned *Carex* treatments was less than in the thinned treatment (Fig. 2A), suggesting that the former two treatments may have overexposed the 1997 establishing plants to sunlight. This effect, however, was not significant in 1998 (Fig. 2B).

I found no evidence that plants grow amongst *Carex* because the streambed lacks sufficient resources. For all transplant species except *M. guttatus*, growth (Figs. 1 and 2) and flower production (Fig. 3) on tussocks

was no greater than on the streambed, even on clipped *Carex* tussocks. Moreover, watering streambed transplants did not significantly enhance their growth (Figs. 1 and 2; for all species  $P > 0.57$ ), indicating that water was not limiting to streambed transplants. A concern is that clipping might have increased the evaporation of soil water or increased soil temperature (e.g. Bertness and Hacker 1994), and thus reduced some advantages of living on tussocks. However, late summer 1999 measurements of a subsequent clipping experiment indicated that soil moisture was unaffected by clipping ( $F_{1,22} = 0.15$ ,  $P = 0.70$ ; see *Discussion*). Furthermore, though clipping increased afternoon tussock surface temperatures from 25.8 to 27.2°C, this difference was not significant ( $F_{1,22} = 1.41$ ,  $P = 0.25$ ) and clipped tussocks still did not compare to the 37.6°C on the streambed. Though the final biomass of *M. guttatus* transplants was markedly reduced on the streambed, additional manipulations showed that this resulted from differential herbivory by *Junonia* larvae on streambed plants, and not resource limitation (Fig. 4A and B).

#### Associational defenses

For both *M. guttatus* and *Epipactis*, *Carex* provided protection from herbivory. In both 1997 and 1998, the proportion of *M. guttatus* transplants completely defoliated by *Junonia* depended on treatment (Fig. 4A and B). Nearly all of the plants on the streambed were completely defoliated in both years (Fig. 4A and B) and the damage caused by the late summer increase in *Junonia* abundance was visible in the growth trajectory of streambed transplants in July and August (Fig. 1C). Overall, I found little variation in defoliation among the tussock treatments (Fig. 4A and B), though in general, there was more herbivory on tussocks in 1997 than 1998 ( $\chi^2_1 = 19.33$ ,  $P = 0.001$ ). This year to year

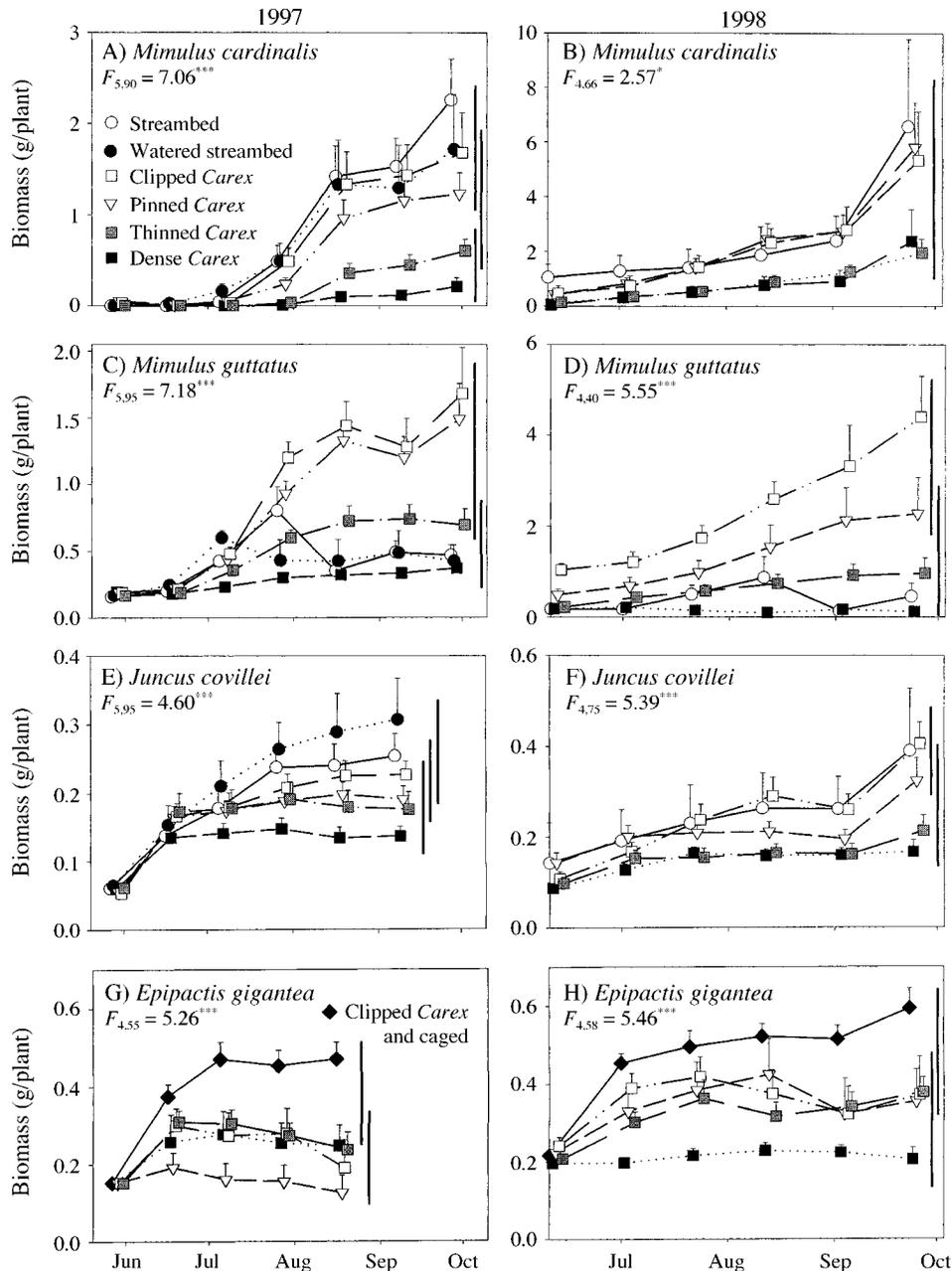


FIG. 1. Growth responses of the four vascular plant target species to various treatments in a field experiment. For all sampling dates, except 25 September 1998, symbols represent mean estimated biomass + 1 SE. For 25 September 1998, the symbols represent actual mean biomass. Note the different scales for the y-axes. Symbols for each sampling date are only offset to ease viewing of the error bars; different treatments were not sampled at different times. For the final sampling date in each year, treatments sharing a line were not statistically different from one another (Tukey tests). Block effects were not significant. The "thinned" and "clipped and caged" treatments in (H) were significantly different from one another.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

variation is consistent with personal observations that *Junonia* larvae and adults were more abundant in 1997.

Although these results suggest that *Carex* tussocks provided protection from *Junonia* herbivory, it is also conceivable that *Junonia* was responding to the size of

the *M. guttatus* transplants, which varied with treatment (Fig. 1C and D). Results, however, were inconsistent with this alternative explanation because in the 1998 *Junonia* removal treatments described below, transplants on the streambed were similar in size to those

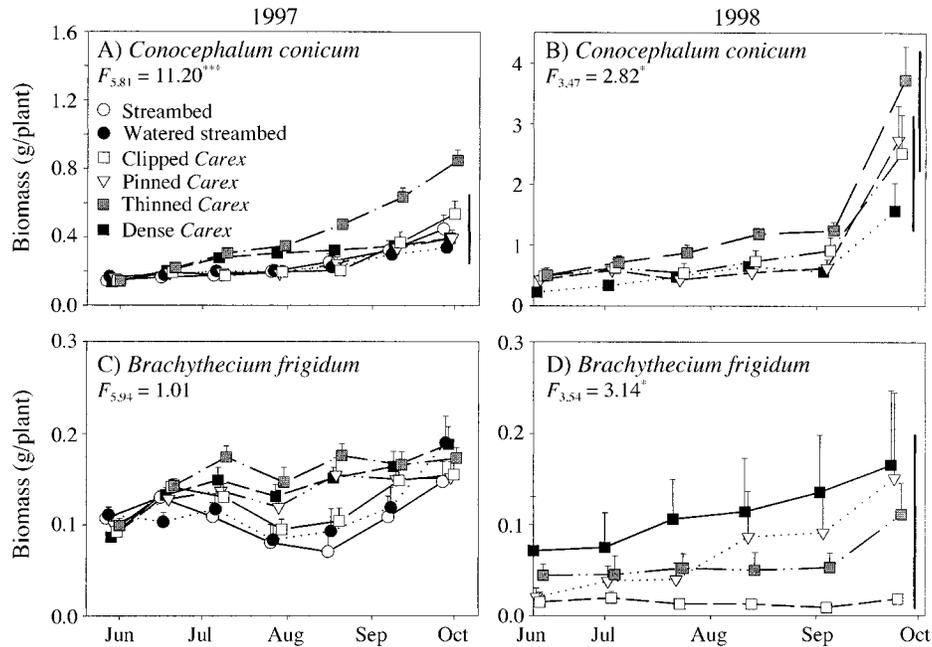


FIG. 2. Growth responses of the two bryophyte target species to various treatments in a field experiment. For all sampling dates, except 25 September 1998, symbols represent mean estimated biomass  $\pm$  1 SE. For 25 September 1998, the symbols represent actual mean biomass. Symbols for each sampling date are only offset to ease viewing of the error bars; different treatments were not sampled at different times. Note the different scales for the y-axes. For the final sampling date in each year, treatments sharing a line were not statistically different from one another (Tukey tests). The absence of a line indicates a nonsignificant effect of treatment in the ANOVA. Block effects were not significant.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

on clipped *Carex* tussocks ( $P = 0.47$ ), yet over 80% of the former were defoliated in comparison to none of the latter (Fig. 4B).

Consistent with the intertreatment variation in herbivore pressure, plants on the streambed experienced the greatest increase in growth relative to other treatments in response to *Junonia* removal, increasing over tenfold (mean  $\pm$  1 SE of *Junonia* removal plants =  $2.17 \pm 0.4$  g, mean  $\pm$  1 SE of *Junonia* control plants =  $0.19 \text{ g} \pm 0.07$ ). In contrast, on *Carex* tussocks, regardless of the treatment, *Junonia* had no effect on plant biomass. The importance of this associational defense was reflected in a significant treatment  $\times$  *Junonia* interaction in the ANOVA ( $F_{4,109} = 11.88$ ,  $P = 0.001$ ). Also significant were main effects of *Junonia* ( $F_{1,109} = 7.05$ ,  $P = 0.009$ ) and treatment ( $F_{4,109} = 23.28$ ,  $P = 0.001$ ). Block was nonsignificant ( $F_{3,109} = 0.52$ ,  $P = 0.672$ ).

Another associational defense was found for *Epipactis*, which suffered less herbivory by deer when growing in dense *Carex*. In both 1997 and 1998, none of the marked *Epipactis* in dense vegetation suffered herbivory, while over 75% of the marked ramets in 1997 and 50% in 1998 were completely grazed off in the clipped *Carex* treatment (Fig. 4C and D). In addition, eliminating deer herbivory from the clipped *Carex* treatment by caging led to a  $>100\%$  increase in plant biomass in 1997 (Fig. 1G) and over 50% increase in 1998 (Fig. 1H). The stronger effect of caging in 1997

is consistent with the more intense herbivory that year (Fig. 4C and D). Since *Epipactis* ramets in neither the dense *Carex* treatment nor the clipped and caged *Carex* treatment were subjected to herbivory, growth differences between these treatments were the result of inhibition by the *Carex* unconfounded by deer herbivory. I found that in the absence of deer, *Carex* reduced *Epipactis* growth by one half (Fig. 1G and H). This result was verified by reanalyzing the data with all eaten plants removed. Uneaten ramets on clipped *Carex* grew to over twice the size as uneaten ramets in dense *Carex* in both 1997 ( $F_{1,9} = 5.68$ ,  $P = 0.044$ ) and 1998 ( $F_{1,13} = 9.97$ ,  $P = 0.008$ ).

#### Winter mortality

For each species, winter mortality on the streambed was significantly higher than on tussocks (Fig. 5). That streambed plants were dislodged was further supported by the fact that I found no trace of the deceased plants. For the bryophytes, 95% of the *Conocephalum* and 100% of *Brachythecium* were removed from the streambed, in comparison to 60% mortality on tussocks for *Brachythecium* and 20% for *Conocephalum* (Fig. 5B and D). *Mimulus guttatus* showed similar results (Fig. 5C). Of all species, *Juncus* and *M. cardinalis* survived best on the streambed though even they experienced 70–80% mortality, a large difference in comparison to the roughly 10% mortality on tussocks (Fig.

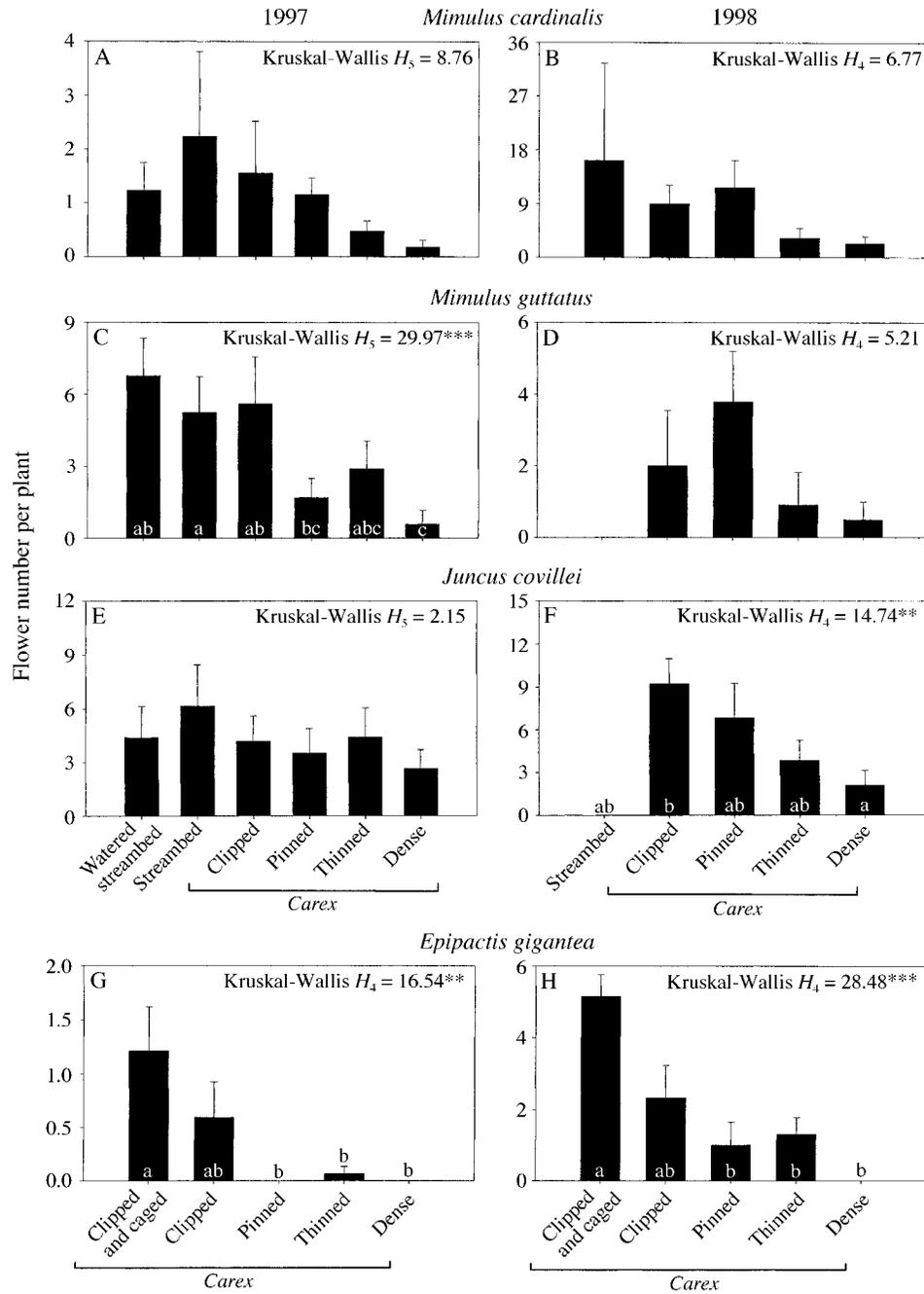


FIG. 3. Reproductive responses of the four vascular plants to various treatments in a field experiment. Bars represent mean flower production + 1 SE at the end of the 1997 and 1998 growing season. Note the different scales for the y-axes. Treatments sharing a letter were not statistically different from one another (post hoc nonparametric multiple comparisons). The absence of letters indicates a nonsignificant treatment effect in the analysis. Note that 1998 streambed mean flower production represents just a few individuals, providing little statistical power to detect differences between streambed and tussock treatments.

\*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

5A and E). Survivorship of *M. guttatus* also depended on the *Carex* treatment. Transplants subjected to dense *Carex* suffered twice the winter mortality as did plants in the clipped *Carex* treatment (Fig. 5C). *M. cardinalis*

showed a similar, but nonsignificant trend (Fig. 5A). One concern is that winter survivorship recorded over the 1997–1998 El Niño might not be representative of other years with less total discharge. However, data

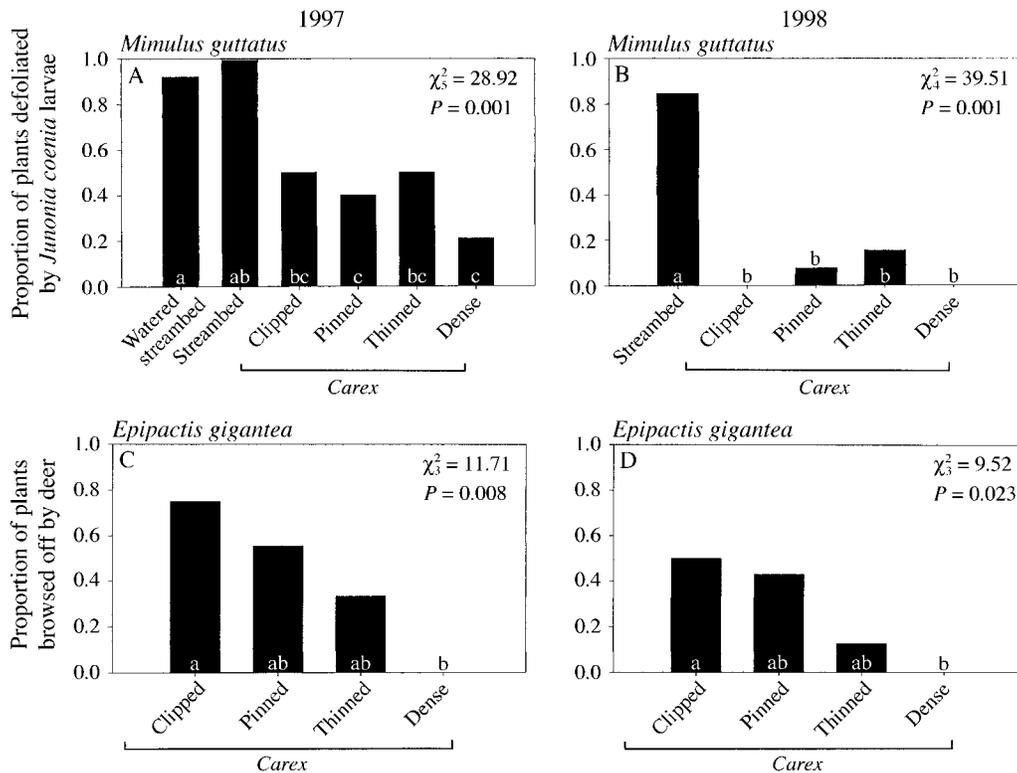


FIG. 4. Herbivory patterns in the various treatments. For *M. guttatus*, bars represent the proportion of all transplants that were completely defoliated in 1997 and 1998. Note that the 1998 defoliation results come from *M. guttatus* transplants established in 1998 following the same protocols as the 1997 experiment. For *Epipactis*, bars represent the proportion of all ramets in 1997 and 1998 grazed by deer, which typically left just a few leaves and several centimeters of stem. Treatments sharing a letter were not statistically different from one another (post hoc multiple comparisons for proportions).

from an on-site gaging station indicated that peak bed-mobilizing flows over the 1994–1995, 1995–1996, 1996–1997, and 1998–1999 winters were comparable or more severe than over the 1997–1998 winter (M. Power, unpublished data).

#### Seedling results

As was found for the more mature plants, seedlings were inhibited by *Carex*. The number of seedlings at the end of the growing season was significantly greater in the clipped versus dense *Carex* treatment for all species (Fig. 6A–D). In addition, there was a trend for greater seedling size when *Carex* was clipped (Fig. 6E–G). The facilitative effects of *Carex* on seedlings were more ambiguous. As was found for more mature plants, seedling growth in the streambed and clipped *Carex* treatment was similar (Fig. 6E–G). *Juncus* and *M. guttatus* growth on the streambed was actually somewhat greater than on clipped *Carex* tussocks, though growing season survivorship was lower on the streambed (Fig. 6). *Mimulus guttatus* was the only species that germinated in 1997 prior to winter flooding, and was thus the only species for which I obtained winter survivorship. Overall, survivorship was very low in all treatments, with the only survivors found in the clipped and

thinned *Carex* treatments. Even in these treatments, mean survivorship was <0.5%.

#### DISCUSSION

Nearly all plant species lining the channel of the South Fork Eel River use the sediments trapped within *Carex* tussocks as substrate. The most common vascular plant and bryophyte species had a mean of 84% of their individuals growing within tussocks, significantly more than would be expected by chance given that tussocks occupy 33% of the emergent channel substrate (Table 1). Tussock formation, and the subsequent colonization by other species is common in many other herbaceous communities throughout the world, including grasslands (Watt 1947), freshwater marshes, peatlands (Dawkins 1939, Tomaszewska 1993), salt marshes (Castellanos et al. 1994), and alpine systems (Billings and Mooney 1959, Tsuyuzaki and Tsujii 1992). The more general phenomenon of plants creating substrate for others is particularly common in riverine systems. Vegetation is well known to stabilize streambanks (Hupp and Simon 1991) and several studies have suggested that plants stabilizing substrate can be critical to the establishment and survival of others (Harris 1987, Dudley and Grimm 1994). For example, Johnson

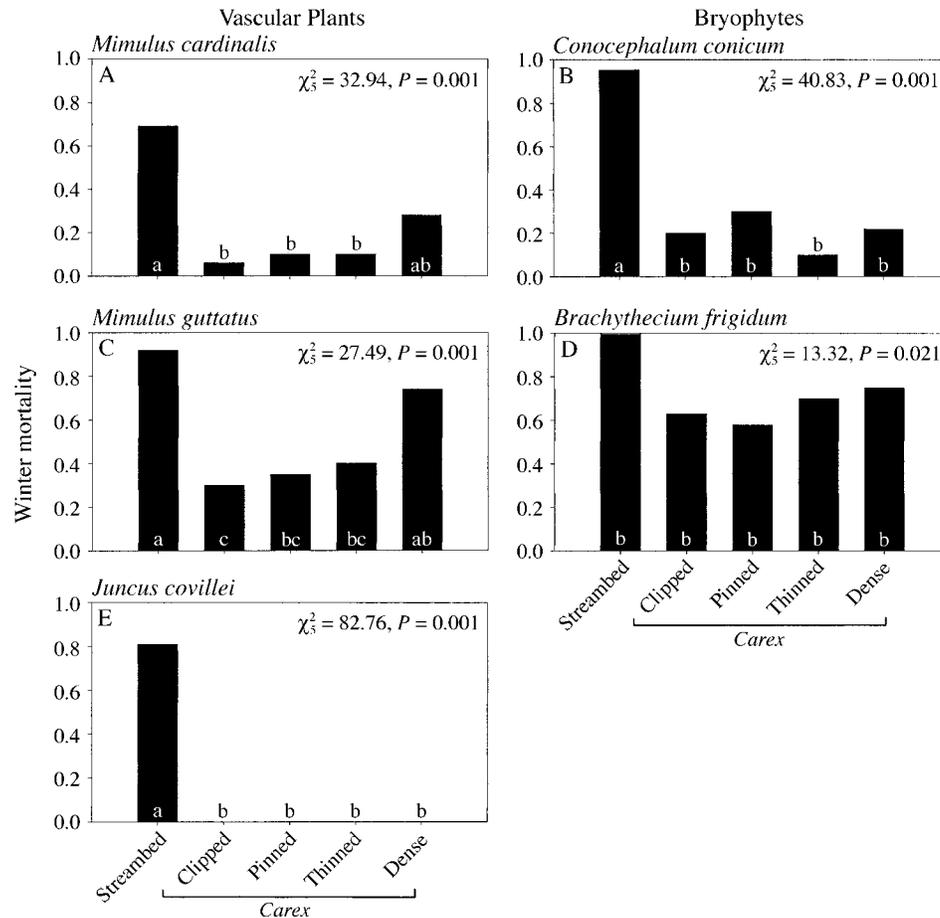


FIG. 5. Winter mortality of the five transplanted target species in the various treatments. Bars represent the proportion of all transplants that died over the 1997–1998 winter. Treatments sharing a letter were not statistically different from one another (post hoc multiple comparisons for proportions).

(1994) observed that in a small Kansas stream, the roundleaf monkeyflower better survived flooding when growing in a sedge meadow as compared to the streambed. Such facilitative interactions seem general and are assumed in many stream restoration efforts (Dahm et al. 1995), though rigorous experimental studies of these interactions are rare. In part, such investigations have been precluded by the size and longevity of many riparian plants. The assemblage of herbaceous species along the Eel River provided a rare opportunity to explore the complex interactions among streamside plants.

The results of this study indicated that the effects of *Carex* on other plant species in this system resulted from multiple processes, some separated seasonally, while others operated simultaneously. For all species in the experiment, *Carex* tussocks provided an important stable substrate during winter flows (Fig. 5). Depending on the species, plants growing directly on the streambed experienced 70–100% winter mortality, as compared to 0–60% on tussocks, suggesting that flooding maintains the spatial association of *Carex* with the

small herbaceous plants and bryophytes that characterize the system. During the growing season, *Carex* competition reduced plant size and reproduction for all species but *Brachythecium* (Figs. 1–3). That *Brachythecium* was not suppressed is not surprising considering the shade tolerance of most mosses (Glime and Vitt 1984).

In this experiment, I used clipping to remove competition by *Carex*. Like all approaches to neighbor removal, this approach has its limitations, particularly for assessing belowground competition (Aarssen and Epp 1990). In this experiment, clipping seemed to affect more than just aboveground stems, because in 1999, a full one year after clipping was terminated, the previously clipped tussocks were less than one-fifth as productive as unclipped tussocks. This concurs with the findings of many studies that repeated and complete removal of aboveground biomass depresses root production in graminoids (e.g. Ruby and Young 1953, Carman and Briske 1982, Ruess et al. 1983, Stanton 1983, Simoes and Baruch 1991; and see Jameson 1963 for review). Nevertheless, how much nutrient or water

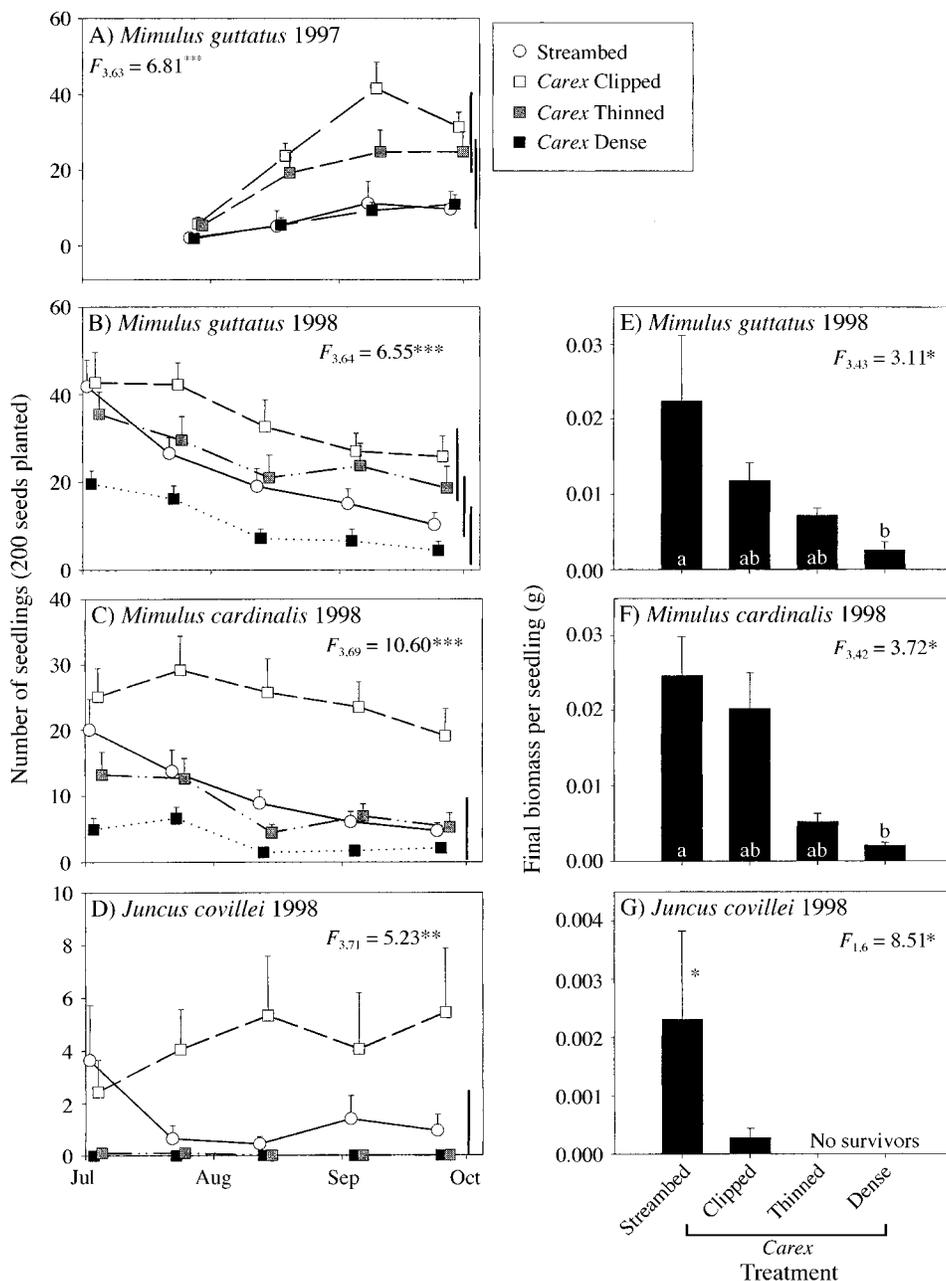


FIG. 6. (A–D) Effects of treatment on seedling numbers over time. Symbols for each sampling date represent mean seedling number + 1 SE and are only offset to ease viewing of the error bars; different treatments were not sampled at different times. For the final sampling date for each species, treatments sharing a line were not statistically different from one another (Tukey tests). Block effects were not significant, except for *Juncus* ( $F_{3,71} = 6.26$ ,  $P = 0.001$ ). (E–G) Effects of treatment on final seedling biomass in 1998. Bars represent mean biomass + 1 SE. Treatments sharing a letter were not statistically different from one another (Tukey tests). Note the different scales for the y-axes.  
 \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

competition that remains in clipped treatments is unclear (Aarssen and Epp 1990), and in this study, even though some *Carex* seems to have been killed, some regrew. Thus my results may have underestimated belowground competition for nutrients or water. These factors, however, may be minor. A separate NPK fer-

tilization experiment with *M. guttatus*, *Juncus*, and *Conocephalum* planted into clipped and dense tussocks suggested that the growth of these species was not nutrient limited. (*M. guttatus*:  $F_{1,38} = 0.37$ ,  $P = 0.546$ ; *Juncus*  $F_{1,38} = 1.15$ ,  $P = 0.291$ ; *Conocephalum*:  $F_{1,18} = 0.20$ ,  $P = 0.657$ ). The other major belowground

resource, water, is highly available in this system due to the partial submergence of tussocks in stream water. Even in late summer 1999, tussock sediments were >30% water by mass, and this high soil moisture was unaffected by clipping (see *Results*).

In addition to the direct competitive effects of *Carex* during the growing season, *Carex* also provided protection from herbivores for both *Epipactis* and *M. guttatus* (Fig. 4). For *Epipactis* biomass, the positive effects of this "associational defense" were equal in magnitude to the negative effects of *Carex* competition in 1997 (Fig. 1G), and to a lesser degree in 1998 (Fig. 1H). Other plant interactions mediated by a third species have been shown to be prevalent in this system. Levine (1999) examined the interactions between the species living on tussocks, and showed that *Carex* suppression of *M. guttatus* released *Conocephalum* and *M. cardinalis* from competition by *M. guttatus*. For *Conocephalum*, this effect was stronger than direct *Carex* competition, resulting in a net positive interaction.

Three important points emerge from these results. First, the interaction between *Carex* and each associated species reflects multiple component interactions. For example, *M. guttatus* experiences facilitation by *Carex* during scouring floods, as well as competition and protection from herbivores over the growing season. *Conocephalum* experiences the same flood-related facilitation and competition, but also benefits from an indirect facilitation mediated by *M. guttatus* (Levine 1999). The second major point is that the interactions between *Carex* and the associated species, though complex, were somewhat consistent across species: similar facilitative effects of *Carex* were found for bryophytes, graminoid and nongraminoid monocots, and dicots. And while the degree of competitive suppression varied among species (Figs. 1 and 2), much of this variation depended on whether the species was a bryophyte or vascular plant. Furthermore, while the associational defense was important for only two of the species, these were the only two suffering severe herbivory. Because of this consistency across species, I believe that the interactions uncovered in this study may apply to the full range of species living on *Carex* tussocks. The third point is that these interactions were intimately tied to winter floods, providing rare experimental evidence for facilitations that directly preclude agents of physical disturbance from operating. This result supports the prediction that facilitations are important forces in disturbed habitats (Brooker and Callaghan 1998).

#### *Mechanisms underlying the associational defenses*

Associational defenses occur when plants that are susceptible to herbivory gain protection from herbivores when associated with other plants (Pfister and Hay 1988). Plants provide these defenses by physically or chemically deterring herbivores, reducing the visual apparency of vulnerable plants, harboring herbivore

predators, or functioning as decoys (Root 1973, Atsatt and O'Dowd 1976).

*Junonia*, the specialist herbivore of *M. guttatus* attacked and defoliated almost all of the plants on the streambed in both 1997 and 1998, while plants on tussocks suffered much less herbivory (Fig. 4A and B). Given that adult *Junonia* use visual cues to search for oviposition sites (Hafernik 1982), the most likely hypothesis for the differential herbivory of *M. guttatus* planted directly on the streambed is that these plants were more visible to adult *Junonia* when on the light background of the streambed versus the less contrasting background of the tussock. Nevertheless, *Junonia* may also be using chemical cues to search for oviposition sites (Hafernik 1982, Scott 1975). Further experiments are required to tease apart these specific mechanisms, though the other potential processes behind associational defenses seem less likely. The tussocks were not a decoy for herbivores, as *Junonia* does not eat *Carex*. In addition, given that the clipped tussocks with no vegetation structure still provided protection from herbivory, it is unlikely that *Carex* physical deterred *Junonia* oviposition or harbored predators.

Slightly different mechanisms may underlie the protection from deer herbivory that *Epipactis* obtained in dense *Carex* (Fig. 4C and D). For *Epipactis*, it was the stems of the *Carex* that provided the protection, though whether herbivore pressure would have been even more severe on the streambed was not examined. Because *Carex* stems are silica rich, scabrous, and difficult to distinguish from *Epipactis* at a distance, the most likely mechanism underlying this effect is that *Carex* physically deterred deer, or visually concealed *Epipactis* ramets. Associational defenses involving ungulate grazing have been found in many other systems including African savanna (McNaughton 1978), California oak woodland (Callaway 1992) and Northern U.S. forests (Buckley et al. 1998).

#### *Effects of competition on winter mortality*

Competition by *Carex* reduced the size and reproduction of nearly all species in this study, but for *M. guttatus* in particular, competition over the growing season may have reduced the ability of *M. guttatus* to survive winter submergence and flood scour. Plants in the dense *Carex* treatment had twice the mortality of plants in the clipped *Carex* treatment (Fig. 5C), even though all were alive at the time of first submergence. Similar, but nonsignificant trends were found for *M. cardinalis* (Fig. 5A). Plants in dense *Carex* may have been unable to produce enough roots to sufficiently anchor into tussocks or may have been unable to acquire enough carbon during the growing season for maintenance respiration over the period of winter submergence. Regardless of the specific mechanism, examples of interspecific competition influencing the ability of a species to withstand agents of disturbance are rare. The best intraspecific examples come from the

marine intertidal. Sandflat bivalves growing in high density are particularly susceptible to pulses of sedimentation (Peterson and Black 1988), while crowded barnacles and mussels are more likely to be dislodged by waves (Paine and Levin 1981, Bertness et al. 1998).

#### *The composite nature of plant interactions*

An important consequence of the composite nature of plant interactions is that the effects of one component interaction may depend on another. Results from this study suggest that if tussocks did not stabilize substrates, a much smaller proportion of the population of each species would be found on tussocks. Reducing this proportion would also reduce the importance of competition, since strong effects of competition at the population level depend on the fact that most individuals of each species grow amongst the *Carex*. This study also indicates that different interactions can influence different features of plant populations. The facilitative effects of *Carex* were responsible for the spatial aggregation of species on tussocks, while its competitive effects reduced plant size and reproduction. Callaway and Walker (1997) provide similar examples.

In systems where plant interactions occur through multiple processes, total or net interactions may hide important details. Recognizing the net positive effect of *Carex* on the associated species is important for explaining the spatial aggregation of species on tussocks. However, the important role of competition in limiting plant size and fecundity is hidden in this net effect. In addition, understanding the multiple ways *Carex* influences the associated species greatly enhances our ability to predict how the system would respond to perturbations that influence just a subset of the component interactions, such as a growing deer population or an altered hydrologic regime.

Many advances in our understanding of how plants influence one another point to the appropriateness of taking a composite perspective on plant interactions. Recent studies have suggested that plants influence one another via hydraulic lift (Dawson 1993), fungal associates (Cullings et al. 1996, Marler et al. 1999), and effects on physical stresses (Callaway 1995) and biogeochemical processes (Hobbie 1992). These previously under-appreciated interactions may be quite common and operate in conjunction with more widely documented competitive interactions. As our appreciation for the number of ways plants influence one another continues to grow, taking a composite perspective may become increasingly necessary for understanding how plant interactions influence the distribution and abundance of species.

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