

RESPONSES OF INDIVIDUAL WETLAND PLANT SPECIES TO SHADING BY THE DOMINANT, EARLY-SUCCESSIONAL RUSH, *JUNCUS EFFUSUS* L.

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ABSTRACT

Juncus effusus (soft rush, Juncaceae) is a perennial species of freshwater wetland plant capable of year-round photosynthesis and growth at temperate latitudes. This species has been shown to produce dense canopies that significantly depress species diversity of the surrounding plant assemblage during early secondary succession in newly exposed wetland areas. Experimental reduction of shading by *J. effusus* in a recently-drained beaver impoundment revealed a strong regulatory influence of this dominant freshwater emergent plant on species richness and composition of the surrounding plant community. Analyses of biomass, species composition, and light reduction by *J. effusus* indicated that growth of certain species varied with shading intensity. Examination of responses on a species-by-species basis indicated the potential for shifts in community composition toward a plant assemblage of primarily perennial species and those well-adapted to wetland conditions (obligate to facultative wetland indicator status). Perennial grasses and sedges appeared best able to tolerate or avoid shading, while the non-rhizomatous annual sedge, *Eleocharis obtusa*, and non-rhizomatous dicot species such as *Rhexia virginica* and *Xyris* spp. exhibited depressed biomass accumulation when exposed to *J. effusus* shading.

INTRODUCTION

The importance of light as a regulator of plant community structure has been indicated by a number of investigators (Tilman 1985; Gibson 1988; Foster and Gross 1998; Grace 1999, 2001), and light reduction by dominant plant species has been shown to have varying effects among subordinate species, with potential to alter the direction of plant community succession (Facelli and Pickett, 1991; Twolan-Strutt and Keddy 1996; Grace and Pugsek 1997; Olf et al. 1999). Differential responses among species also may influence selection of plant phenotypes

within an environment by favoring species with taller stature or an ability to detect and avoid shading (Tilman 1985; Robson, Whitlam, and Smith 1993; Schmitt and Wulff 1993; Aphalo, Ballaré, and Scopel 1999; Peer, Briggs, and Langenheim 1999; Walck, Baskin, and Baskin 1999).

In addition to competition for light, plants face a multitude of other potential stressors, the importance of which may vary depending upon numerous spatial and temporal factors of the environment in which the plants are located. For example, the resource-ratio theory of succession states that the relative importance of above-versus below-ground competitive interactions will increase as a result of changes in soil nutrients and plant assemblage over time (Tilman 1985). In wetland systems, however, successional time frames may be compressed because soil productivity is generally very high (Wetzel 1990), and above-ground competition may be intense at early successional stages (Twolan-Strutt and Keddy 1996). Other stressors, then, such as chemically reducing conditions within wetland sediments or frequent inundation, may result in successional patterns favoring early-successional plant species adapted to intense above-ground competition and the suite of physiological stresses associated with saturated wetland sediments.

Effects of the dominant freshwater rush *Juncus effusus* on vascular plant species composition were studied in a developing wetland plant community during years two and three after natural drainage of a 50-year-old beaver pond and exposure of wetland sediments. Those studies demonstrated that reductions in cover, richness, and diversity of the plant community surrounding isolated *J. effusus* individuals were correlated with intensity of shading, with each of these measures being lowest in areas where measured light reduction was highest (Ervin and Wetzel 2002). Analyses of biomass, species composition, and light reduction suggested differential responses among species to shading

effects of *J. effusus*. Such differences among species' shading tolerance could indicate the potential for shifts in community composition as populations of *J. effusus* expand to fill a wetland area. The present analyses were conducted to determine the magnitude of responses by individual species and whether patterns exist among the species most strongly affected by or most tolerant of shading by *J. effusus*.

MATERIALS AND METHODS

Field studies were conducted in a freshwater marsh on the Oakmulgee Division of the Talladega National Forest in Hale County, Alabama (32°54' N, 87°26' W). The wetland was a relict of a beaver impoundment of Payne Creek, a first-order coastal plain stream that was impounded for approx. 50 years, until 1996. At the initiation of the study, a substantial portion of the newly-exposed sediments had been colonized by aquatic and wetland vegetation, including portions of an expanding population of *Juncus effusus*.

Eight permanent study plots were set up in March 1998 in which *J. effusus* tussocks were to serve as focal study plants and permanent transects were established along the diagonals of a 1-m × 1-m square plot surrounding each tussock. The development of the surrounding vascular plant community was monitored at 10, 20, 30, and 40 cm from the edge of the tussock in 20-cm × 20-cm subplots. Within each subplot, percent area cover was estimated for each plant species, or other taxonomic group for plants that could not be identified to species because of developmental stage. During March through August 1998, plant community development was monitored in 1-m² plots surrounding *J. effusus* tussocks and in immediately adjacent 1-m² plots with no *J. effusus* (1998 reference plots) to determine the effects of *J. effusus* presence on species composition. Beginning in March of 1999, in four of the plots with *J. effusus* present ("manipulated" plots), all culms were maintained in a vertical position with the aid of wire supports to allow maximal penetration of sunlight to the sediments; the remaining four plots were left with naturally arched culms to serve as 1999 reference plots.

Data collected during the 1998 observational study were grouped into five time intervals (weeks 1 and 2, 6 through 8, 9 through 11, 14

and 15, and 19 through 21), in an effort to include each of the eight plots only once within each time interval and reduce data redundancy within sampling periods (see Ervin and Wetzel, 2002 for additional details). Total percent cover of selected species (those that were present in five or more subplots at the termination of the 1999 experiment) was analyzed using repeated measures multivariate analysis of variance (RM MANOVA), with either the five temporal groupings (1998) or weekly measurements (1999) as the repeat, or time, factor. Analyses were conducted with DataDesk 6.0 (Data Description, Inc.); statistical significance was evaluated with $\alpha = 0.05$.

RESULTS

Eight taxa were present in sufficient numbers of subplots to conduct these analyses: *Andropogon virginicus* L., "broomsedge," *Dulichium arundinaceum* (L.) Britt., "three-way sedge," *Eleocharis obtusa* (Willd.) Schultes in R. & S., "blunt spikerush," *Erianthus giganteus* (Walt.) Muhl., "sugarcane plumegrass" or "giant plumegrass," *Polygonum hydropiperoides* Michx., "swamp smartweed," *Rhexia virginica* L., "Virginia meadow beauty," and unidentified immature grasses and *Xyris* species "yellow-eyed grass." Of these eight, only four groups demonstrated growth enhancement correlated with experimental reduction of *Juncus effusus* light interception (Table 1, Figure 1). Only *A. virginicus* demonstrated growth suppression by *J. effusus* in both years of the study (Figures 1A and 2A). *Eleocharis obtusa*, *Rhexia virginica*, and *Xyris*, while not exhibiting *Juncus effusus*-correlated growth suppression in 1998 (Table 1, Figures 2B, 2C, and 3B), were significantly affected in 1999, during which percent area cover of none of these species exceeded that produced in 1998.

Conversely, *Polygonum hydropiperoides*, while not demonstrating any statistically-detectable difference between *J. effusus* and reference plots in 1998, demonstrated increased biomass production in reference plots in 1999, compared with plots in which shading was removed (Figure 4). Percent cover of *P. hydropiperoides* in reference plots in 1999 was roughly equal to that in either set of plots during 1998, whereas cover for this species was actually lower in the manipulated plots during 1999. The remaining three taxa showed no significant effect of *J.*

effusus presence or shading in either year (Figures 3A and 5).

DISCUSSION

Patterns among affected species

Responses among the 8 taxa for which the above analyses were presented suggested that in order to persist in these rapidly changing wetland environments, species must be adapted to both shading (either by avoidance or tolerance) and to stresses imposed by wetland environments. Species that are of relatively diminutive stature (*E. obtusa*, *R. virginica*, *Xyris* spp., Figure 1B, C, D) are at a disadvantage in competition with *J. effusus* for light resources, and species not adapted to wetland conditions (the facultative upland *A. virginicus*, Figure 1A) face the dual challenge of intense competition for light and stresses associated with saturated organic wetland sediments. Two of these four species (*E. obtusa* and *R. virginica*, Figure 2) exhibited positive correlation of growth with *J. effusus* presence in the 1998 study, but production of these was reduced by 50% - 70% in 1999 (as indicated by percent cover estimates), relative to 1998 data in the *J. effusus* plots. *Andropogon virginicus* and *Xyris*, whose growth also was stimulated significantly by experimental shade reduction, displayed decreased percent area cover in 1999 vs. 1998. It is possible that the greater surface coverage in *Juncus* plots by *E. obtusa* and *R. virginica* during 1998 was due to competitive interactions with other perennial graminoid species in the reference plots, but that possibility was not directly evaluated.

The data also suggested that perenniation and a rhizomatous growth habit are additional adaptations providing some measure of success in these highly productive systems. For example, perennial wetland grasses and sedges (facultative- to obligate-wetland indicator status; those already mentioned, plus the sedge *Scirpus cyperinus* (L.) Kunth, "woolgrass"), most of which perenniate and grow via subterranean rhizomes, showed little effect of *J. effusus* shading in these analyses (Figures 3A and 5) or other examinations of community interactions (Ervin and Wetzel 2002). The availability of numerous below-ground rhizomes and the energy stores they provide is likely a great advantage in establishment and maintenance of

subdominant herbaceous species in these wetland communities because of year-round photosynthesis by the dominant *J. effusus* (Mann and Wetzel 1999, Wetzel and Howe 1999) and the strong effects of *J. effusus* shading during the active growing season. In fact, *E. giganteus*, which forms dense perennial tussocks and reaches heights of 2.5m, exhibited hints of enhanced growth in areas influenced by *J. effusus* shading (Figure 3B). These results are in accordance with the high correlation of rhizomatous growth and adaptation to life in aquatic or wetland habitats exhibited among monocot families (Grace 1993).

The one non-graminoid species whose growth appeared to be enhanced in areas that remained shaded by *J. effusus* in the 1999 experiment was *P. hydropiperoides* (Figure 4). This species extends vegetatively via layer-type above-ground stems during the growing season and was capable of actively avoiding direct impacts of competition with *Juncus effusus* for light (in a manner consistent with phytochrome-mediated responses as discussed by Schmitt and Wulff 1993). Thus, apparent tolerance of *J. effusus* shading in this community seemed to be correlated with adaptation to wetland growth conditions as well as various mechanisms for reducing or avoiding above-ground competition.

The findings of this study, then, correspond with previous conclusions of the major importance of light in structuring plant communities in productive habitats (Tilman 1985, Twolan-Strutt and Keddy 1996, Grace and Pugsek 1997, Foster and Gross 1998) and on the potential interactions among environmental factors in determining competitive outcomes (Van den Berg et al. 1998, Mitchell et al. 1999). Furthermore, the apparent importance of adaptation to wetland growth conditions, as indicated by persistence of species having wetland-adapted indicator status, supports the hypothesis proposed by Grace (2001) that nonresource factors (perhaps chemically reducing organic sediments in this case) can regulate plant species richness independently of community biomass. In the present examination, *Andropogon virginicus*, although a relatively tall, early-successional perennial grass, was significantly suppressed by *J. effusus* shading. Others have shown that *A. virginicus* is capable of outcompeting *Pinus taeda* in early-successional terrestrial communities by creating sufficient water stress to inhibit growth of *P.*

taeda (Mitchell et al. 1999). Thus, the adaptation of *A. virginicus* to competition in dry environments likely precluded that species from effective competition with *J. effusus* in saturated wetland soils.

Implications

Differential sensitivity of individual species to competition with *Juncus effusus* in wetland plant communities strongly suggests the potential for directional change in community composition as *Juncus effusus* populations, or populations of similarly competitive species, establish themselves in early-successional wetlands. Because of the high productivity of freshwater wetland systems (Wetzel 1990), above-ground resources (i.e., light) may become limiting over much shorter time scales than in less productive habitats, leading to a strong influence of large-canopy-forming species during early stages of secondary succession. Indeed, numerous studies of wetland restoration or creation have indicated stabilization of the vascular plant community within relatively short time periods (3 to 5 years). For example, wetland plant communities in freshwater marshes created in Illinois were composed almost entirely of wetland-adapted plant species within the first year after flooding, and all four experimental wetlands were similar in species composition 3 years after flooding (Fennessy, Cronk, and Mitsch 1994). Similarly, in two artificial wetlands in Ohio, where plant community composition was monitored over a three-year period, virtually the same sets of species colonized each of the wetlands, with most of the differences attributable to species planted in one of the two impoundments (Mitsch et al. 1998). This "self-design" phenomenon of wetland systems (Mitsch et al. 1998) may be the result of a combination of a stressful environment selecting against mal-adapted species and intense above-ground competition selecting in favor of an even narrower suite of traits within wetland species, such as tall stature, perenniation, and rhizomatous growth.

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Table 1. Comparisons among plant life history elements of effects of shading by *J. effusus*.

Species	Ind. Status*	Life History	Affected by treatment in	
			1998	1999
<i>A. virginicus</i>	FACU	perennial	yes	yes
<i>D. arundinaceum</i>	OBL	perennial	no	no
<i>E. obtusa</i>	OBL	annual	yes ⁺	yes
<i>E. giganteus</i>	FACW	perennial	--	no
unid. Poaceae	FACW-OBL	annual/perennial	--	no**
<i>P. hydropiperoides</i>	OBL	perennial	no	yes ⁺
<i>R. virginica</i>	FACW +	perennial	yes ⁺	yes
<i>Xyris</i> spp.	FACW-OBL	perennial	no	yes

* Wetland indicator status for the Southeast Region (Reed et al. 1996): OBL (obligate wetland) occur almost always under natural conditions in wetlands (estimated probability >99%); FACW (facultative wetland) usually occur in wetlands (estimated probability 67%-99%); FACU (facultative upland) occasionally found in wetlands (estimated probability 1%-33%), but usually occur in non-wetlands (estimated probability 67%-99%).

** Indicator status and life history given for species known to occur in the wetland (*Leersia oryzoides* (L.) Sw., *Panicum dichotomiflorum* Michx., and *Sacciolepis striata* (L.) Nash, only one of which (*P. dichotomiflorum*, FACW annual) is not an OBL perennial.

⁺ Indicates species whose growth was positively correlated with the presence of *J. effusus* shading.

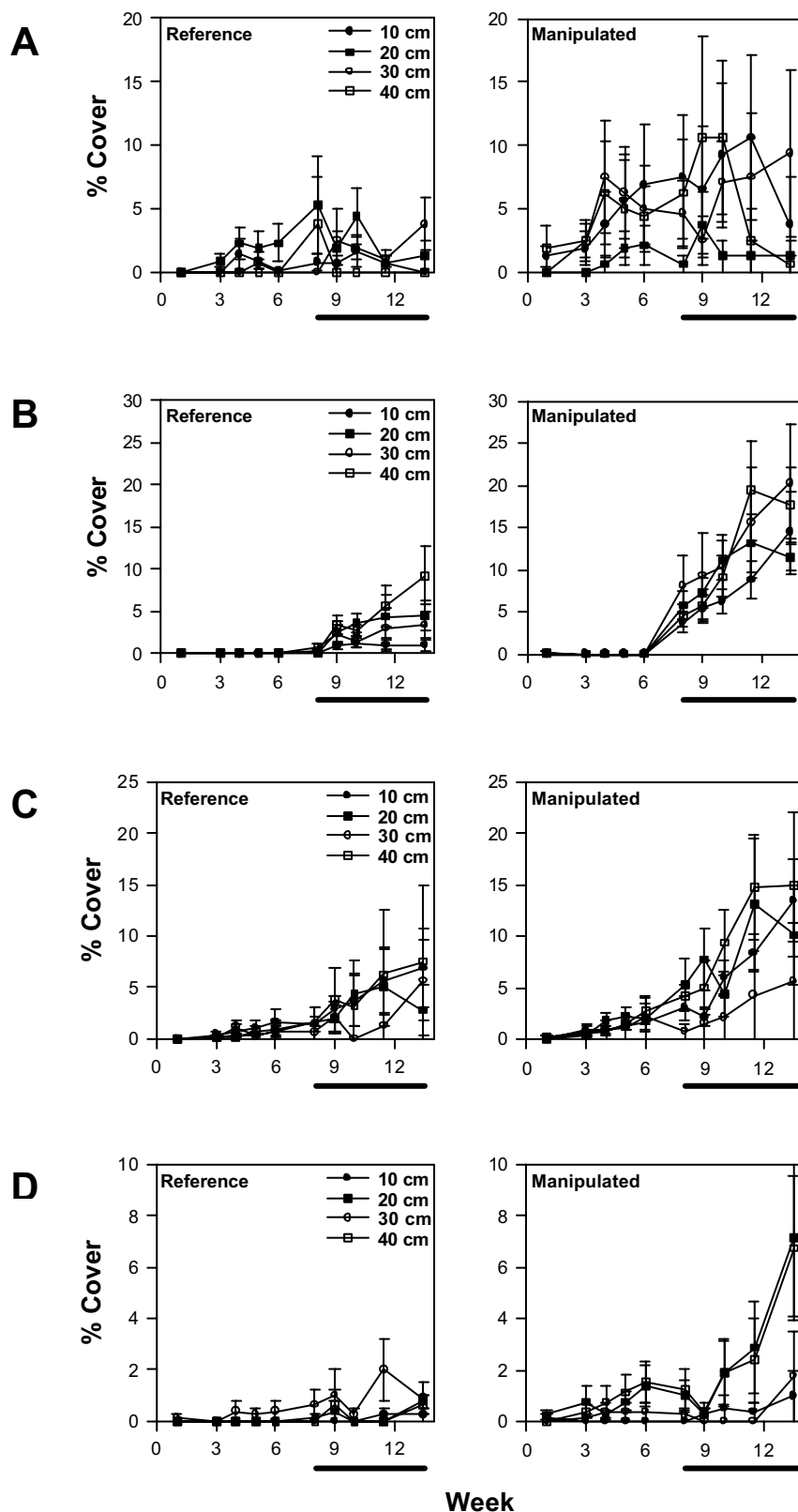


Figure 1. Responses of taxa significantly suppressed by *J. effusus* shading in the 1999 experimental study. Symbols represent mean $\pm$ 1 SE. A) *A. virginicus*: treatment $P < 0.01$; B) *E. obtusa*: treatment $P < 0.001$; C) *R. virginica*: treatment $P = 0.01$; D) *Xyris* spp.: treatment $P = 0.01$. Bars beneath time axis represent the period during which *J. effusus* culms were arched over in Reference plots, exerting shading influence on surrounding species.

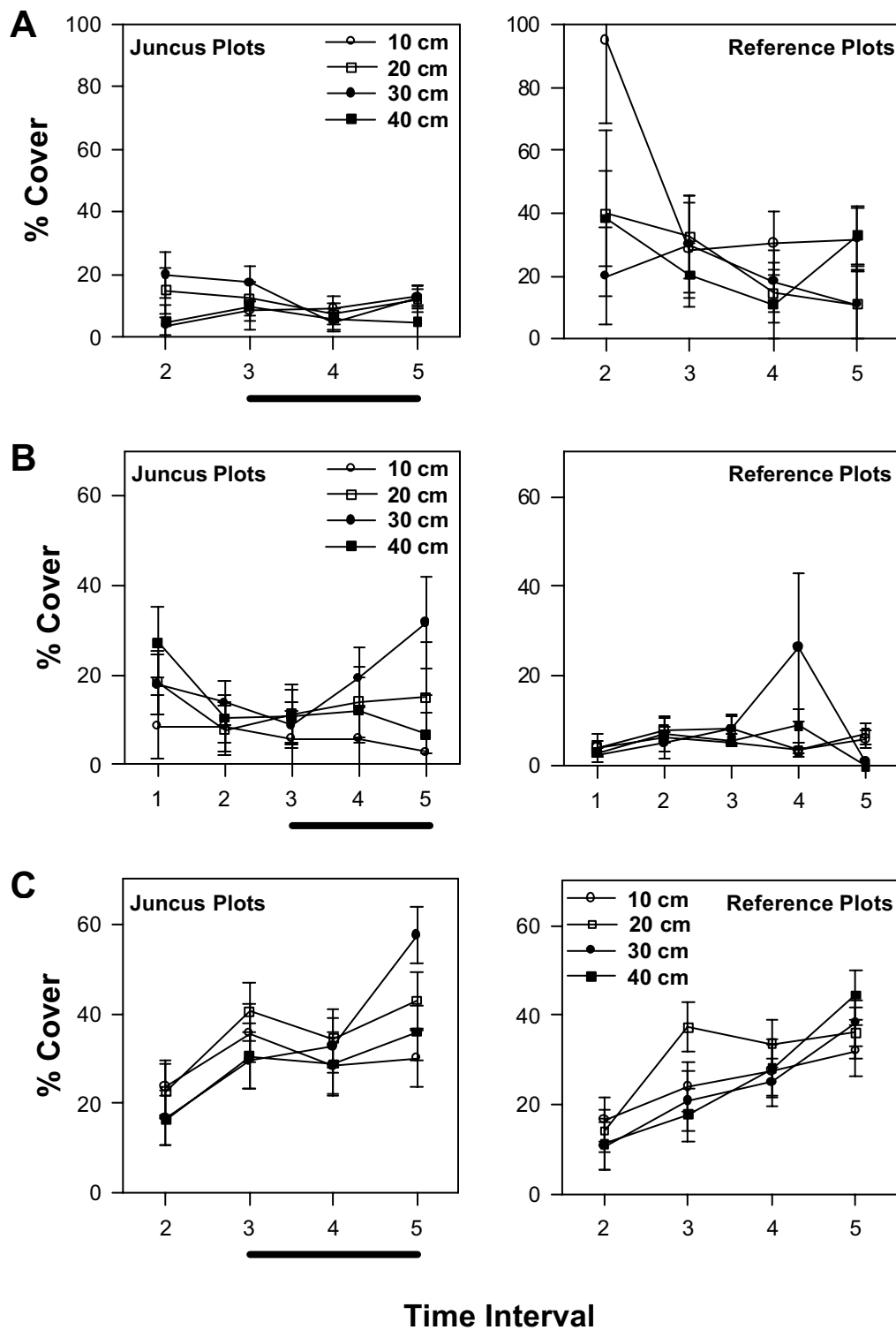


Figure 2. Responses of taxa significantly correlated with presence of *J. effusus* in the 1998 observational study. Symbols represent mean $\pm$ 1 SE. A) *A. virginicus*: treatment $P < 0.001$; B) *E. obtusa*: trtmt $P < 0.008$; C) *R. virginica*: trtmt $P = 0.02$. Bars beneath time axis represent the period during which *J. effusus* culms were arched over, exerting shading influence on surrounding species in the *Juncus* plots.

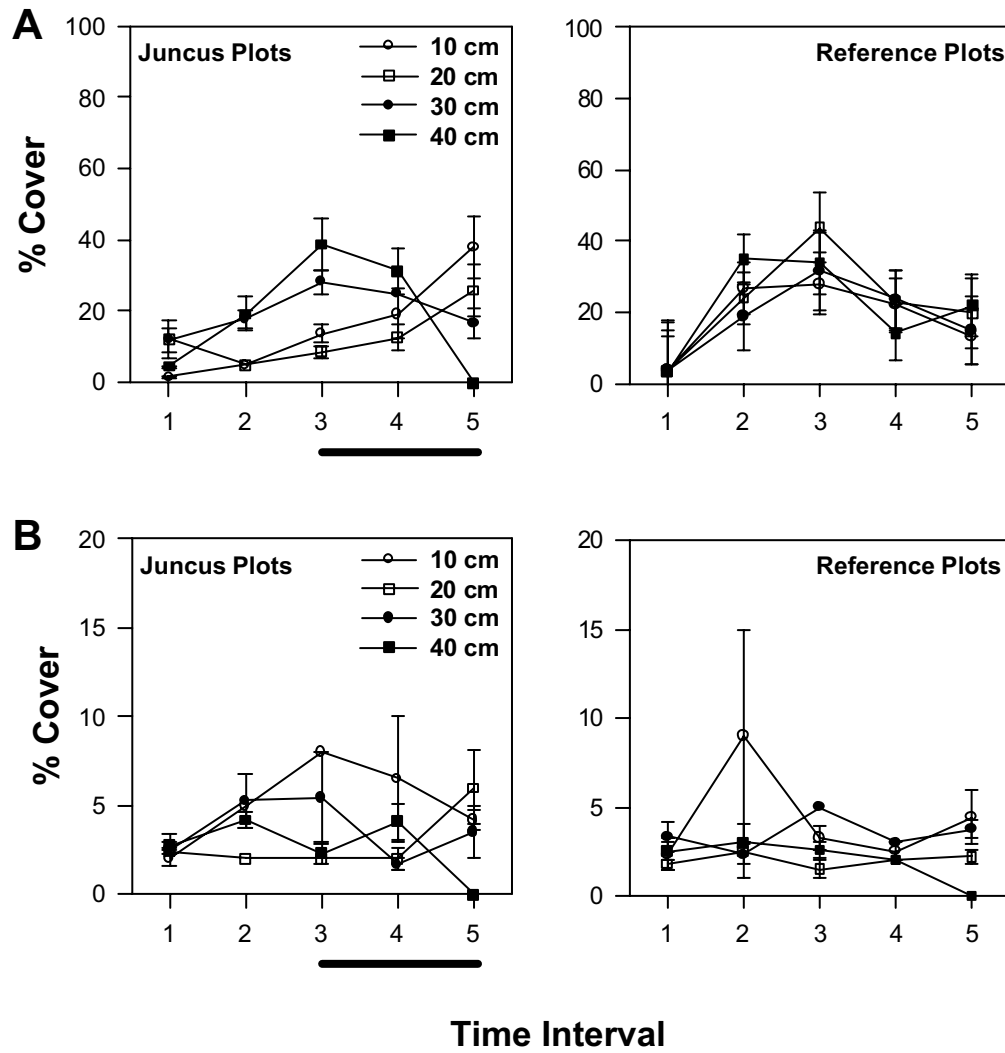


Figure 3. Responses of remaining taxa not significantly affected by *J. effusus* presence in the 1998 study. Symbols represent mean $\pm$ 1 SE. A) *D. arundinaceum*: treatment $P = 0.11$; B) *Xyris* spp.: trtmt $P = 0.71$.

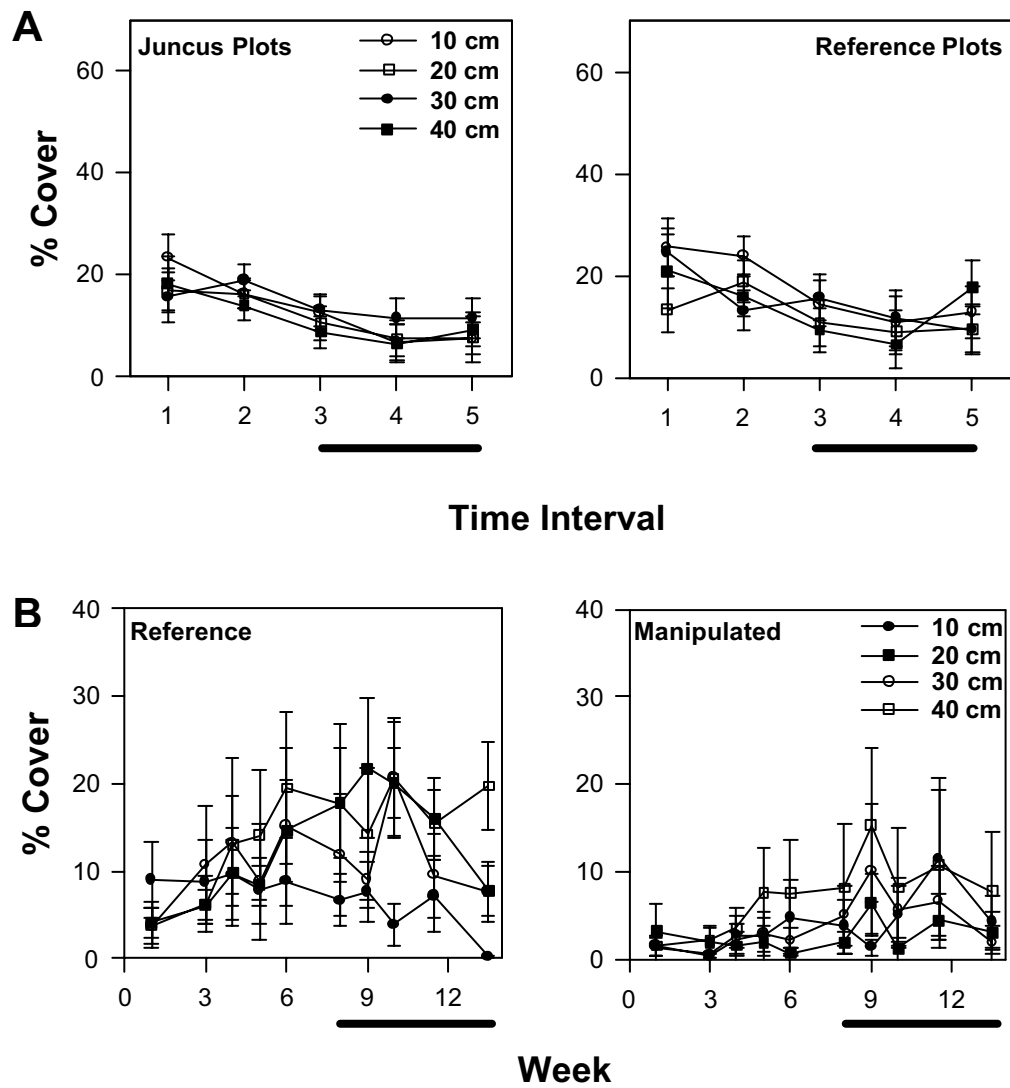


Figure 4. Growth response of *Polygonum hydropiperoides*, which exhibited no significant correlation with *Juncus* presence in 1998 (A: $P = 0.14$) but positive correlation with *J. effusus* shading in the 1999 study (B: $P < 0.001$). Symbols represent mean ± 1 SE; treatment.

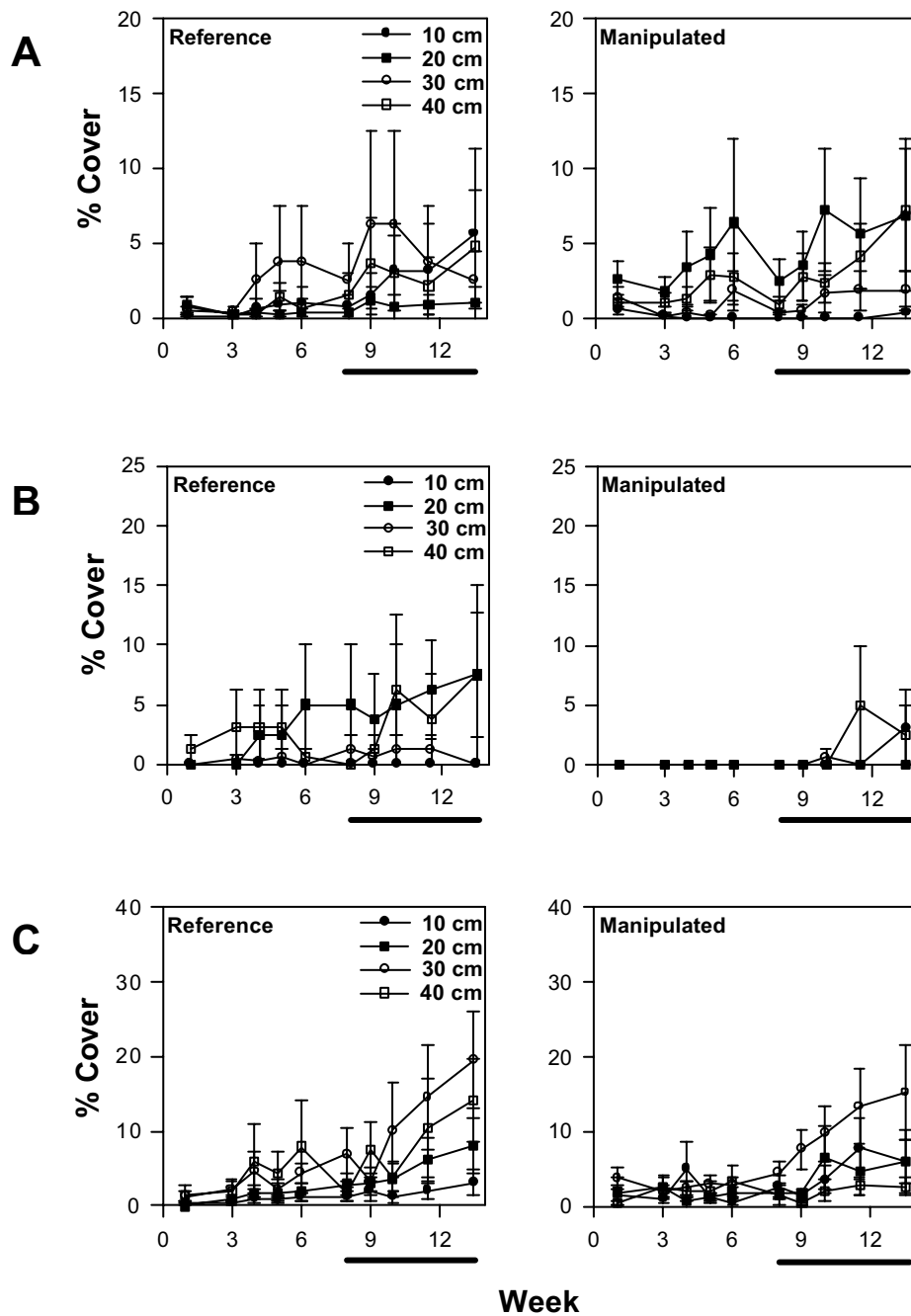


Figure 5. Responses of taxa not significantly affected by *J. effusus* shading in the 1999 experimental study. Symbols represent mean $\pm$ 1 SE. A) *D. arundinaceum*: treatment $P = 0.84$; B) *E. giganteus*: trtmt $P = 0.07$; C) unidentifiable grasses: trtmt $P = 0.47$.