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THE INTERACTIVE EFFECTS OF FIRE AND HERBIVORY ON A COASTAL MARSH IN LOUISIANA

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Abstract: Both vertebrate herbivores and fire have long been known to have dramatic and important effects on wetland vegetation. However, the interactive effects of burning and herbivory have received less attention. In this study, conducted in the coastal marshes of the Pearl River Basin in Louisiana, USA, both the effects of herbivory and fire as well as the interaction between these effects were examined in three marsh community types: *Sagittaria lancifolia*, *Panicum virgatum*, and *Spartina patens*. At five sites for each of the three community types, the effects of burning and fencing to exclude herbivores were determined over two years.

Results showed that total biomass was reduced by burning but increased by fencing, with no interactive effects on total biomass. Species density (the number of species per unit area) was enhanced in plots that were both burned and fenced. *Spartina patens* was an important component in all three communities. Cover estimates indicated that *S. patens* responded to burning and fencing differently from the other dominant species. In the *Panicum virgatum* community, *P. virgatum* cover was enhanced by burning and fencing while *S. patens* cover was reduced. In the *Sagittaria lancifolia* community, *S. lancifolia* and *Vigna luteola* were enhanced by burning and fencing while *S. patens* was reduced. In the *S. patens* community, *Scirpus americanus* was enhanced by fencing, but burning had no significant effect on cover of either dominant species. These and other data are generally consistent with the hypothesis that herbivory favors *S. patens* while burning favors other dominant species. Thus, the relative effects of fire and herbivory have an influence (along with other factors such as salinity) on the dominance of *S. patens* in coastal marshes.

Key Words: fire, herbivory, coastal marsh, species density, plant cover, plant biomass, nutria

INTRODUCTION

Vertebrate herbivores have been shown to have a significant impact on plant community structure in Gulf of Mexico coastal wetlands (Chabreck 1959, Linscombe et al. 1981, Wright and Bailey 1982). Among the most intense examples of herbivory reported are those dealing with muskrat (*Ondotra zibethica rivalicius* Bangs; O'Neil 1949), snow geese (*Chen caerulescens* L.; Adams 1956, Bazely and Jefferies 1986), and nutria (*Myocastor coypus* Molina; Chabreck 1959, Fuller et al. 1985, Shaffer et al. 1992, Visser (pers. comm), Nyman et al. 1993, Taylor and Grace 1995, Taylor et al. 1995). Throughout the region, however, a range of different effects has been observed (Nyman et al. 1993, Taylor and Grace 1995, Grace and Ford 1996). The effects of herbivores on coastal wetlands have also been shown to depend on a number of factors such as food preference (Shaffer et al. 1992), animal density (Linscombe et al. 1981), and habitat conditions (Shaffer et al. 1992).

Fire has long been a natural force affecting wetlands (Lynch 1941, Wright and Bailey 1982, Mitsch and Gosselink 1986, Chabreck 1988, Kirby et al. 1988) and has been shown to alter the effects of herbivory in some situations (Smith and Kadlec 1985), although not in all (Taylor et al. 1994). Records for Louisiana indicate that hunters and trappers have regularly set fires in the marshes for at least the past 100 years (Lowery 1981), and at present, fires are common (Nyman and Chabreck 1995). A primary motivation behind the current burning practices is the belief that fire promotes high population densities of wildlife by favoring palatable plant growth (O'Neil 1949, Linscombe et al. 1981, Chabreck 1982, Mendelssohn et al. 1988).

Relatively few studies have examined the interactive effects of fire and herbivory on wetlands. Some of the reported effects of fire and herbivory on vegetation suggest several ways in which the interaction between these two forces might affect marsh vegetation. One possible effect comes from the fact that burning has been reported to enhance the nutritive value of vegetation, which may lead to greater subsequent use of burned vegetation by grazers (e.g., Whelan 1995, Bond and van Wilgen 1996). In the Great Salt Lake Marsh, fire was observed to enhance herbivore use of the habitat, presumably due to increases in protein content of the vegetation following fire (Smith and Kadlec 1985). Such an effect, however, has not always been reported. Taylor et al. (1994) found no short-term change in herbivory impacts due to burning in an oligohaline marsh in coastal Louisiana. Another possible interactive effect follows from the observation that fire may act to alter the relative abundances of plant species, which may affect patterns of herbivory and their impacts. For some plants of the coastal marshes of the Gulf of Mexico region, fire has been shown to tip the competitive balance away from late-successional species such as *Spartina patens* (Aiton) Muhl and towards species with more rapid regrowth capabilities (e.g., *Scirpus americanus* Pers., Mendelssohn et al. 1988). For some cases, the species favored by burning are also favored by herbivores, which could lead to a substantial interaction between the effects of herbivory and fire on the vegetation.

At present, our understanding of the interactive effects of fire and herbivory is currently limited by the small number of such studies and their limited scope. In the Gulf of Mexico coastal region, studies of fire and herbivory effects have been almost exclusively confined to a single marsh type, brackish marsh. This paper reports results of a two-year study of the effects of herbivory and fire on three contrasting marsh communities: *Panicum virgatum* L.-dominated, *Sagittaria lancifolia* L.-dominated, and *Spartina patens*-dominated. The study site for this work was the Pearl River basin in Louisiana (Taylor and Grace 1995). The Pearl River drains about 2.3 million ha from south central Mississippi into the extreme southeastern part of Louisiana. Study sites for this research were chosen to represent the three community types based on the dominant vegetation.

METHODS

In fall 1992, a survey of the locations of marshes of different types was conducted within the Pearl River landscape, and five sample sites were arbitrarily selected for each of the three plant community types studied here. At each site, two 10 m × 10 m main plots were selected, and one was randomly chosen for burning. Within each main plot, 2 m × 2 m subplots were established with one subplot being randomly selected for fencing by using plastic-coated weldwire of 5-cm mesh and 0.6-cm rebar as corner posts. The other subplot was simply marked with rebar. Bailing wire was fashioned into U-shaped pieces and inserted through the fencing into the ground to discourage animals from burrowing under the fences. Within each 2 m × 2 m subplot, the inner 1 m^2 was designated for study, with the remaining perimeter area reserved as a buffer. Fire breaks 2 m wide were cut around the main plots for fire control and maintained throughout the study.

Subplots were censused in fall 1992 for areal cover of all species. One randomly selected main plot at each site was burned and the other was left unburned. All subplots were censused in fall 1993, and then the main plots originally burned were reburned. In fall 1994, cover was estimated and plants were harvested in 0.25 m^2 subsamples within each subplot. Harvested biomass included all living and dead material above the ground surface and was dried at 105° C and weighed.

The assumptions of parametric analysis were tested using SAS (SAS Institute 1988). Normality of residuals was evaluated using the Wilks-Shapiro test (Sokal and Rohlf 1981). Homogeneity of variances was evaluated using discriminant function analysis on the model residuals with a chi- square test criterion (SAS Institute 1988). Final biomass was transformed to ln(biomass + 1) in order to achieve normality and homogeneity of variances for the analysis. Values were detransformed for presentation (Sokal and Rohlf 1981). Species cover and density were found to be normal and homoscedastic.

The basic experimental design was a split-split plot design with 10 × 10 m main plots within each of the five sample sites representing the first split and 2 × 2 m subplots representing the second split. Data analyses were conducted using the GLM procedure in SAS (SAS Institute 1988). For final biomass and species density, the main effect MARSH was tested using the SITE BY MARSH interaction term, the effect of burning and the interaction between marsh and burning

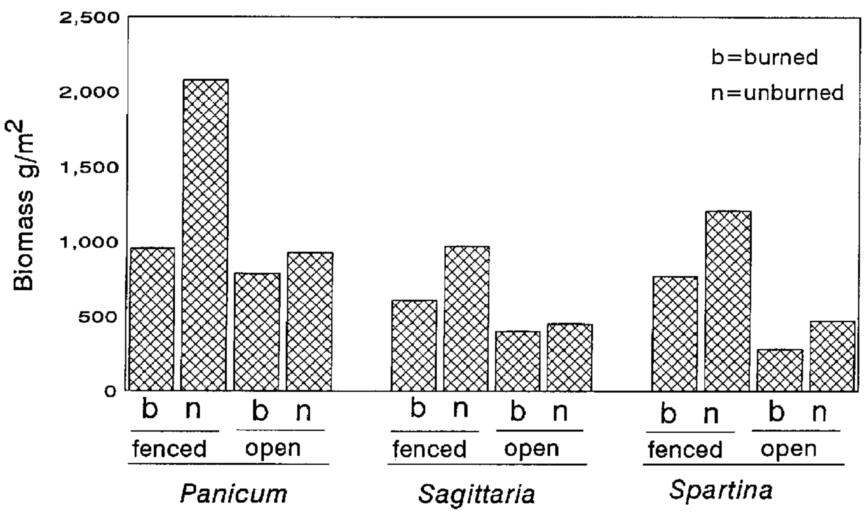

Figure 1. Effects of burning and fencing on biomass for the *Sagittaria, Panicum,* and *Spartina* communities. (b=burned, n=unburned). Error bars represent ± 1 standard error.

were tested by using the SITE BY BURN (MARSH) interaction term, and effects of fencing and interactions between fencing and higher terms were tested using the total error term. Cover data were analyzed separately for each marsh type and, therefore, BURN was tested using the BURN BY SITE interaction, and FENCE and BURN BY FENCE were tested using the total error. *A posteriori* tests for differences between marshes were accomplished by using the Tukey's HSD test (SAS Institute 1988). Data on species coverage for the most abundant species in each community were tested for treatment effects separately for each marsh because of limited overlap in dominant species. Following the recommendation of Yoccoz (1991), an alpha level of 0.10 was used to evaluate hypotheses, with primary emphasis placed on magnitude of effect as indicative of biological significance.

RESULTS

Total biomass differed significantly among marshes ($F=5.89$, $p=0.02$) with the *Panicum* marsh having greater values than either of the other marshes (Figure 1). Burning also had a significant effect, reducing above-ground biomass for all community types ($F=13.24$, $p=0.003$); on average, biomass was reduced by a third (Figure 1). This effect held true for both fenced and unfenced plots. Fencing, however, significantly increased biomass ($F=53.86$, $p<0.001$). There were no significant interactions between the treatments.

Species density at the beginning of the study (1992) was greatest in the *Sagittaria* community ($p<0.001$), with an average value of 8.15 ± 0.32 (± 1 standard error) compared to means of 6.55 ± 0.04 for the *Panicum* community and 6.20 ± 0.28 for the *Spartina* community. By the end of the study (1994), species density in untreated plots (unfenced and unburned) had increased since the beginning of the experiment by an average of approximately 1.8 ± 0.8 species in the *Panicum* community ($p=0.0088$, Figure 2); however, in the other communities, there was no significant change over time in untreated plots.

ANOVA results indicated that there was a significant interactive effect of burning and fencing on species density ($F=6.31$, $p=0.02$). In all three communities, the biggest increase in species density occurred in plots that were burned and fenced (Figure 2). The response to this treatment combination was most dramatic in the *Sagittaria* community where species increased by an average of nearly 4 per plot. In both the *Spartina* and *Panicum* communities, plots that were burned and fenced increased in species density by approximately 2.4 species. In the *Sagittaria* and *Spartina* communities, all other treatments had no effect on species density. In the *Panicum* community, both burned and unburned plots that were unfenced showed an increase in species density during the experiment, perhaps because of between-year effects.

In the *Panicum* community, cover of *S. patens* was significantly reduced in plots that were fenced and burned ($F=6.87$, $p=0.03$, Figure 3). Burning had no significant effect on *P. virgatum* cover ($p=0.65$). Fencing had a modest effect on *P. virgatum* ($p=0.06$), with fenced plots having greater coverage by this species.

For all three dominant species in the *Sagittaria* community, burning had an effect on cover: *Sagittaria lancifolia* ($F=5.01$, $p=0.056$), *Spartina patens* ($F=4.35$, $p=0.071$), and *Vigna luteola* (Jacquin) Bentham ($F=7.34$, $p=0.03$) (Figure 4). Cover for *S. patens* was

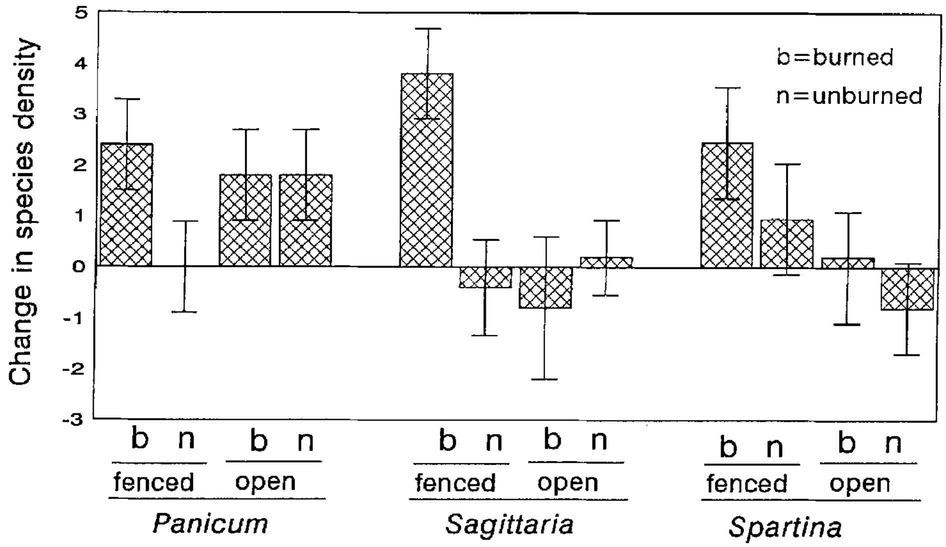

Figure 2. Effects of burning and fencing on change in plant species density for the *Sagittaria, Panicum,* and *Spartina* communities. (b=burned, n=unburned). Means and standard errors are based on least squares adjusted values. Error bars represent ± 1 standard error.

reduced by burning, while cover for both *Sagittaria lancifolia* and *V. luteola* was dramatically increased (Figure 4). There was no significant effect of fencing on *S. lancifolia* or *S. patens,* but *V. luteola* increased the most when fenced and burned (F=4.21, p=0.07).

In the *Spartina* community, burning had no significant effect on percent cover of either *Scirpus americanus* or *S. patens* (Figure 5). Only *S. americanus* was affected by fencing (F=18.76, p=0.005), which dramatically increased cover from approximately 20% to over 50% (Figure 5).

DISCUSSION

In this study, fencing increased biomass by approximately two-fold in the three marsh community types (Figure 1). Herbivory has been well-documented to have strong effects on wetland vegetation. Herbivory on 200 one-year-old seedlings of baldcypress, *Taxodium distichum* (L.) Rich. resulted in 100% mortality in only 2 years in Manchac Marsh of Lake Pontchartrain (Myers et al. 1995). In the recently emergent delta islands of Louisiana, Visser (1991) showed that high

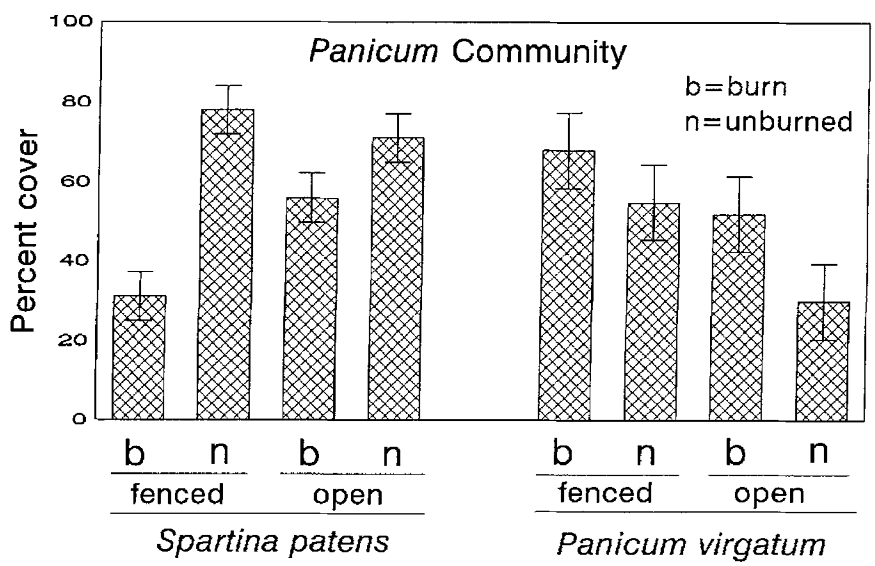

Figure 3. Effects of burning and fencing on plant cover of *Spartina patens* and *Panicum virgatum* in the *Panicum* community. (b=burned, n=unburned). Error bars represent ± 1 standard error.

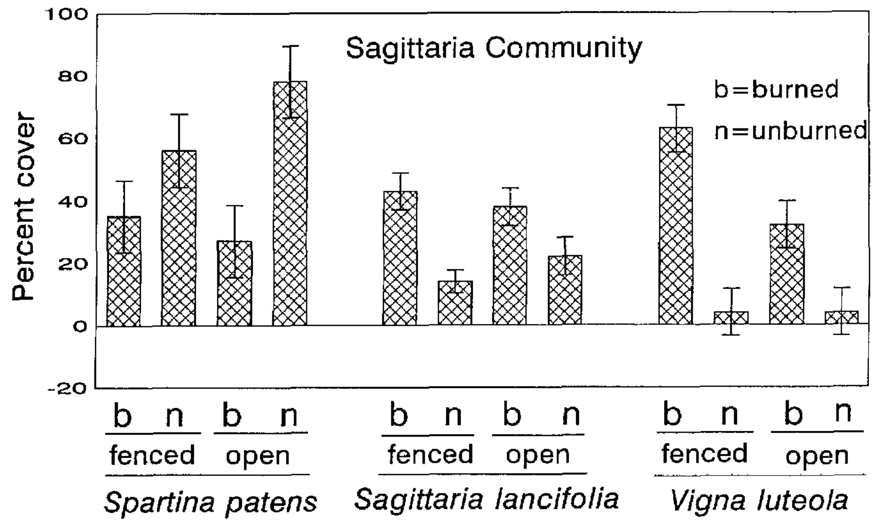

Figure 4. Effects of burning and fencing on plant cover of *Spartina patens, Sagittaria lancifolia,* and *Vigna luteola* in the *Sagittaria* community. (b=burned, n=unburned). Error bars represent ± 1 standard error.

densities of nutria can lead to significant reductions of plant biomass. After excluding herbivores for 2 years, biomass of *Sagittaria lancifolia* and *Ammannia coccinea* Rottboell increased significantly on the Atchafalaya Bay islands (Fuller et al. 1985). Results from exclosure studies conducted in mesohaline marshes by Chabreck (1959) indicated that plots protected from herbivory possessed 40% greater standing crop than unprotected plots. In an earlier study of the Pearl River (Taylor and Grace 1995), biomass increased 30% in plots protected from herbivory in fresh, oligohaline, and mesohaline marshes. Since that earlier study, which took place in 1990–91, our observations indicate that populations of nutria and wild boar (*Sus scrofa* L.) have increased substantially. We hypothesize that the increase in nutria has resulted from decreased trapping. Wild boar appear to be recently introduced to the Pearl River, and it is possible that their increased activity is associated with a post-introduction population increase. Regardless of the cause, it appears that the impact of herbivores has tripled (based on the percentage of biomass increase resulting from fencing) in the Pearl River marshes.

Comparatively few studies have documented the effects of burning on Gulf coastal marshes (Chabreck 1982, Mendelssohn et al. 1988). In this study, burning led to a one-third reduction in biomass, much of which appeared to result from removal of senescent tissues

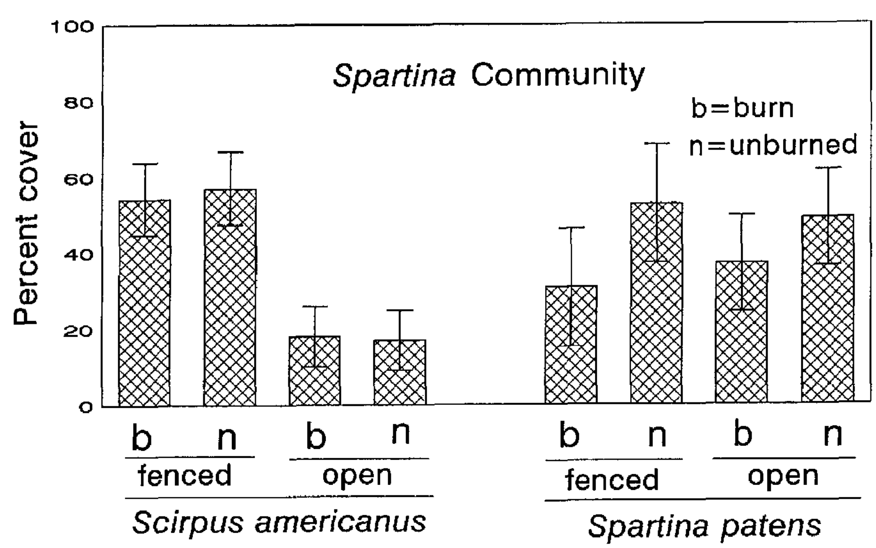

Figure 5. Effects of burning and fencing on plant cover of *Spartina patens* and *Scirpus americanus* in the *Spartina* community. (b=burned, n=unburned). Error bars represent ± 1 standard error.

and litter. This effect was generally similar across habitats even though fire intensity appeared to vary among communities. In addition, burning had a significant effect on the cover of dominant species in the *Sagittaria* community. In the *Sagittaria* marsh, *S. patens* cover was reduced while cover of *S. lancifolia* and *V. luteola* increased (Figure 4). Mendelssohn et al. (1988) found that burning could suppress one species, particularly *S. patens,* while allowing a species that was otherwise an inferior competitor to increase. While it was expected that burning might increase herbivory due to a preference by herbivores for regrowth (Lynch 1941, Kays 1956, Smith and Kadlec 1985), there is no indication of such an effect in this study.

Species density was enhanced primarily by the combination of burning and fencing (Figure 2). The greatest increase took place in the *Sagittaria* community, where species density increased from 8 to 13 species (Figure 2) while the effect was rather weak in the *Panicum* community. Taylor et al. (1994) found no evidence for an interactive effect between herbivory and fire on species density in a degenerating brackish marsh, in contrast to our results where the combination of burning and fencing enhanced species density considerably. The reason for this difference is not known. However, the current study examined the effects of treatments over two years while the study by Taylor et al. (1994) included only a single growing season, suggesting that experiment duration might contribute to the difference.

It might be expected that fire and herbivory would affect species density in coastal marshes. Schmalzer et al. (1991) found that species density increased one year after fires in *Juncus roemerianus* Scheele and *Spartina bakeri* Merr. marshes. This change was primarily due to an increase in minor species. Such a result is not surprising since fire opens up the canopy, increases nutrient cycling (Hoffpauir 1961, Vogel 1977, Wright and Bailey 1982), removes litter, increases ash deposits, has little negative impact on seed survival, and therefore, often initiates or stimulates new growth (Kays 1956, Vogel 1977, Wright and Bailey 1982). In this case, restricting herbivores from burned areas appears to have created a special set of conditions suitable for enhanced species density.

While the results reported here are not entirely consistent, along with other published findings, they suggest a general hypothesis about how fire and herbivory control the community structure of Gulf coastal marshes in which *Spartina patens* is a significant component (Figure 6). The main elements of this hypothesis are (1) that fire impairs *S. patens* more than it does other species, (2) that herbivory impairs other species more than it does *S. patens,* and (3) that the competitive balance between *S. patens* and other species is influ-

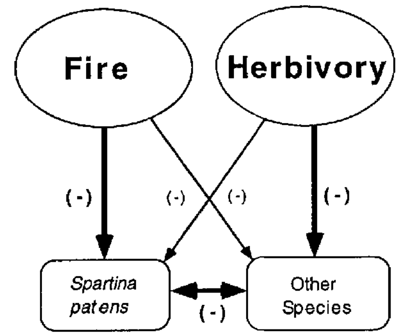

Figure 6. Hypothesized general effects of fire and herbivory on community structure. Thick lines indicate a strong effect and thin lines a weaker effect.

enced by burning and herbivory. In the model presented in Figure 6, a pathway represented by a thin line and a minus symbol is a weak, negative pathway while a pathway represented by a bold line and minus symbol is a strong, negative pathway.

The model described here is generally supported by previous literature. Several authors have found that following fire, *Spartina patens* is slower to regrow than other dominant species (Lynch 1941, Chabreck 1982, Mendelssohn 1988, Taylor et al. 1994). At the same time, *S. patens* is considered to be quite unpalatable to most wildlife (Lynch et al. 1947, Kays 1956, Linscombe et al. 1981). For these reasons, prescribed burning is often recommended as a means of reducing the relative abundance of *S. patens* and increasing the relative abundance of other plant species with a resulting benefit to wildlife populations (Chabreck 1988).

The role of competition in determining the relative abundance of *Spartina patens* has received little study. Grace et al. (1992, 1993) found in greenhouse pot experiments that *S. patens* transplants were relatively weak competitors and, depending on the competition index used, ranked either sixth or fourth in competitive ability out of six common marsh species (the other species being *Eleocharis macrostachya, Solidago sempervirens* L., *Scirpus validus* Vahl, *Scirpus robustus* Pursh, and *Sagittaria lancifolia*). In a one-year field study of competition conducted at the Pearl River, Taylor et al. (1997) found that when protected from herbivory, *S. patens* transplants were more affected by competition than those of either *Panicum virgatum* or *Spartina alterniflora* Loiseluer. Unpublished greenhouse competition experiments involving transplants of *S. patens* and *Scirpus americanus* showed *Scirpus americanus* to be a better competitor than *S. patens* (Keough, Guntenspergen, and Grace unpublished). Thus, there is some evidence to indicate that young *S. patens* plants are weak competitors, particularly in fresh marsh conditions. However, these results do not indicate that *S. patens* is a weak competitor over longer time periods. Field studies of mature vegetation have shown that given sufficient time, *S. patens* produces a dense persistent canopy that can result in strong competitive suppression of other marsh species (Brewer and Grace 1990, Grace and Pugesek 1997). Overall, this information suggests that *S. patens* may be a weak competitor when small but a more formidable competitor when mature.

To date, virtually all investigations of the effects of fire on Gulf coastal marshes have focused on mesohaline marshes where *Spartina patens* and *Scirpus americanus* occur. The emphasis on this habitat type has been driven by the high wildlife value of *Scirpus americanus,* a species that is often favored by fire and generally restricted to mesohaline conditions (Chabreck 1982, Mendelssohn et al. 1988). In this study, we have examined the effects of fire and herbivory over a range of marsh types. While the abundance of *S. patens* was greatest in the *S. patens* marsh type, it was a significant component in all three communities studied here and is known to have an extremely broad ecological amplitude.

In the *Panicum* community at the Pearl River, the combined treatments of burning and excluding herbivores resulted in a substantial shift in the relative abundances of *Spartina patens* and *Panicum virgatum,* with *S. patens* being reduced and *P. virgatum* being enhanced (Figure 3). Further, the reduction in *S. patens* in the burned plus fenced treatment suggests that under these conditions, *P. virgatum* competitively dominated over *S. patens.* When fenced but not burned, there was no evidence that *P. virgatum* was competitively dominant. These results are consistent with the model in Figure 6.

In the *Sagittaria* community, burning led to a reduction in *Spartina patens* and a substantial increase in *Sagittaria lancifolia* and *Vigna luteola* (Figure 4). As in the *Panicum* community, *S. patens* was reduced when burned and fenced compared to its growth when unburned and unfenced. *Sagittaria lancifolia* and *Vigna luteola* showed exactly the opposite pattern to *S. patens.* Thus, the results for this marsh are consistent with the proposed model.

In the *Spartina* community, the patterns were similar to those from the other communities, but the magnitudes of effects on *S. patens* were less. As a result, the cover of *S. patens* was not significantly affected by burning or fencing (although *Scirpus americanus* was enhanced by fencing). Thus, in this community, burning and fencing did not significantly shift the balance between the dominant species.

Overall, therefore, two of the three communities studied here showed results consistent with the proposed hypothesis. However, the results from the *Spartina* community did not clearly support our hypothesis. One possible reason that *Spartina patens* did not show a significant response to burning and fencing in this marsh may be the high levels of herbivory occurring there. Field observations showed that this marsh type was difficult to burn during both years because of the small fuel load and its discontinuous nature. When comparing marshes, it was found that fencing led to increases of approximately 65, 100, and 250% in biomass in the *Panicum, Sagittaria,* and *Spartina* communities, respectively. Thus, it seems that herbivory effects were substantially greater in the *Spartina* community compared to the other communities. However, further work is needed to determine if the model would hold generally for *Spartina* marshes where there was sufficient fuel for a hot fire. The evidence available from Taylor et al. (1994) suggests that this would be the case since their results from a *Spartina* marsh in coastal Louisiana fit the proposed model. However, we feel that further tests are needed to determine how generally the model proposed in Figure 6 applies to Gulf coastal marshes. In particular, the interaction between herbivory intensity and fire intensity deserves further study.

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