Journal of the North Carolina Academy of Sciences, 122(3), 2006, pp. 106–117

AN EXPERIMENTAL STUDY OF THE EFFECTS OF NUTRIENT ADDITION AND MOWING ON A DITCHED WETLAND PLANT COMMUNITY: RESULTS OF THE FIRST YEAR

CAROL GOODWILLIE and WILLIAM R. FRANCH

Department of Biology
East Carolina University
Greenville, NC 27858

Abstract: The effects of nutrients and mowing on plant species composition were investigated at a wetland site in Pitt County, North Carolina. Nutrient levels were manipulated by fertilization, and disturbance was imposed by a fall mowing treatment in a two-factor crossed design. The effects of an existing hydrologic gradient, possibly caused by man-made drainage ditches, was also examined. Diversity was significantly higher in mowed than in unmowed plots. Species diversity was not affected by fertilizer but the interaction of the two main factors was significant, with fertilizer producing a substantial negative effect on diversity only in unmowed plots. The observed patterns suggested a role of competition in reducing diversity. The importance of wetland species was significantly increased by mowing and reduced by fertilization. Abundance of forb species was unaffected by mowing but increased with fertilizer. Diversity was significantly lower in drier plots near a roadside ditch. Trends of these initial data suggested that mowing and human-mediated nutrient enrichment can have important effects on plant community composition and diversity.

Key Words: wetlands; nutrient addition; disturbance; plant community; diversity.

INTRODUCTION

Nutrient availability and disturbance are two key forces that can affect the composition of plant communities. Disturbance provides a source of temporal and spatial variability that can promote species diversity (Huston 1979). Both factors can influence productivity, which in turn can have effects on species richness that are mediated by competitive interactions. Theories of species diversity predict that species rich sites will have intermediate levels of productivity and disturbance, with competitive dominance limiting diversity in sites of high nutrients and productivity and low disturbance (Connell 1978; Huston 1979; Tilman 1988). Ecologists have recognized that, because productivity and disturbance are inherently interrelated, their separate effects can be best studied by experiments that manipulate both variables independently (Wilson and Tilman 1991, 1993).

Studies that address the relationships between disturbance, productivity and diversity of plant communities have often focused on prairies and grasslands (e.g., Silvertown 1980; Wilson and Tilman 1991). Fewer studies have examined their effects in North American wetlands, the results of which have been somewhat inconsistent (reviewed in Bedford et al. 1999). Important functions of wetland ecosystems provide particular motivation for a better understanding of these relationships. Recent studies have focused on increasing rates of human-mediated nutrient enrichment in wetland ecosystems and accompanying declines in diversity and changes in community composition (Morris 1991; Bedford et al. 1999; Pauli et al. 2002).

We report early results of a study that examined the effects of nutrient addition, disturbance and their interaction on plant species composition at a wetland site in eastern North Carolina. Nutrient levels were manipulated by fertilization, and disturbance was applied with a mowing treatment. Likewise, we considered the effects on the plant community of an existing hydrologic gradient, possibly caused by man-made drainage ditches adjacent to the site. We report the effects of these factors on several measures of plant community composition, including species diversity and the relative proportion of forbs versus graminoids. We also examined the effects of the experimental treatments on species that are found predominantly in wetland plant communities. The study serves as a focus for courses in general and plant ecology at East Carolina University and has been carried out entirely by undergraduate biology students.

MATERIALS AND METHODS

Study Site

The experimental site is located within a 235 ha tract of land that was used by the Voice of America (VOA) program for radio broadcasting from the 1950's until the mid 1990's. Located in the central Coastal Plain of North Carolina, the site lies between the Neuse and Tar River basins at one of the highest points in Pitt County, with elevations ranging from 22–25 m. The flat topography and the location between two rivers cause poor drainage, and over 60% of the site has been classified as jurisdictional wetlands. A 1974 soil survey characterized the site as a mosaic of Coxville, Lynchburg, and Goldsboro soils, which are somewhat poorly drained with medium to low fertility and low organic content (USDA 1974).

During the VOA site installation, the land was logged, and a network of drainage ditches was constructed along access roads. The area was maintained as open land for the next several decades by a combination of mowing and burning. Since the VOA's decommission in 1989, the land has been leased from the Department of Education by East Carolina University, where it comprises the West Research Campus (WRC) and serves as a resource for ecological education and research. Several hectares were designated in 2002 for undergraduate ecological studies, on which the current experiment was installed.

The tract supports a rich native flora, with >250 plant species (Chester 2004; B. Sorrie unpublished). Based on reference flora comparisons, the historical plant composition was most likely a mosaic of wet pine flatwood, pine savanna and hardwood communities (Chester 2004). Common species in the herbaceous layer include several grasses (e.g., *Andropogon virginicus* L., *Arundinaria gigantea* (Walt.) Muhl. ssp. *tecta* (Walt.) McClure, *Chasmanthium laxum* (L.) Yates, *Dichanthelium scoparium* (Lam.) Gould), sedges and rushes (e.g., *Rhynchospora inexpansa* (Michx.) Vahl, *Juncus canadensis* J. Gay ex Laharpe), and numerous forbs including *Solidago* spp., *Eupatorium* spp. and *Smilax* spp. Several carnivorous plants (e.g., *Sarracenia*

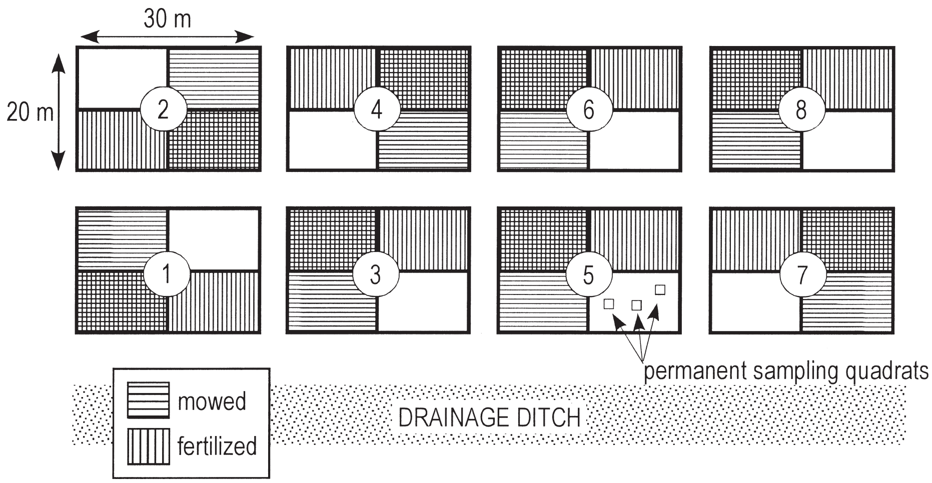

FIG. 1. Schematic of experimental design. Each treatment plot contains three 1 m^2 permanent sampling quadrats.

purpurea L., *Drosera rotundifolia* L.) are also found at the site. Currently, the woody component of the flora is dominated by sweet gum (*Liquidambar styraciflua* L.) and black gum (*Nyssa sylvatica* Marsh.), with a few remnant trees of longleaf pine (*Pinus palustris* P. Mill.). Ninety-five of the 250 species found at the site were sampled in the experimental plots. Approximately half of these are classified on the USDA plants database as obligate or facultative wetland species in North Carolina (http://www.plants.USDA.gov).

Experimental Design and Sampling

The study area was last burned in March 2002 and mowed and tilled in October 2002 to remove existing vegetation. The experimental treatments were initiated in February 2003. Four experimental treatments were replicated on eight 20 × 30 m blocks in a randomized block design adjacent to a drainage ditch (Fig. 1). Federal regulations for jurisdictional wetlands prohibit soil disturbance, which was necessary for installation of the experiment. A permit from the Army Core of Engineers limited the area available for experimental use to the presumed zone of influence of a drainage ditch. Mowing and fertilization were applied in a two factor full-factorial design to yield four treatments: 1) no mowing, no fertilizer; 2) no mowing, fertilizer; 3) mowing, no fertilizer; and 4) mowing, fertilizer. For logistical reasons, fertilizer treatments and mowing treatments were placed in contiguous plots within each replicate block (Fig. 1), and treatments were randomly assigned to plots within that constraint. Three permanent one m^2 quadrats were established for vegetation sampling at randomly-generated coordinates within each plot. Quadrats were placed at least 1.5 m away from each treatment plot perimeter in order to avoid edge effects and to create an effective buffer zone between treatments. Pellet fertilizer (NPK composition of 10-10-10) was applied by broadcast spraying in February, June and October 2003 and February and June 2004 at a concentration per application of

28 kg per ha. Mowing was performed in October 2003 with a bush hog mower, and clippings were left on the soil surface.

Thirteen undergraduate biology students sampled the area in August 2004. Teams of three or four students recorded the abundance of each plant species as both stem count and percentage cover in each of the 96 permanent one m^2 quadrats (8 blocks × 4 treatments × 3 quadrats). Soil moisture levels were measured in March 2005 at seven randomly chosen locations in each of the 32 plots (8 blocks × 4 treatments). Soil moisture data in the four treatment plots were pooled to yield a total of 28 samples per block. Moisture was quantified with a Soil Moisture Meter (Lincoln Irrigation, Inc; Lincoln, NE 68505), which gave a qualitative measure, ranging from 0 (dry) to 10 (fully saturated with water).

Analysis

Analysis of variance (ANOVA) was used to test the effect of the treatments on plant community variables, with fertilizer and mowing as fixed factors and block as a random factor. Dependent variables included species diversity, the proportion of wetland species, the relative importance of forbs vs. graminoids, and total percentage cover. Using cover data, a Shannon-Wiener diversity index was calculated for each quadrat as

$$H' = \sum_{i=1}^{n} p_i * \ln p_i$$

where p_i is the proportion of the i_{th} species. The importance value of each species was calculated for each quadrat as the average of relative density (stem count/total stem count for all species) and relative cover (percentage cover/total percentage cover of all species). The proportion of wetland species was calculated in each quadrat by summing importance values for all species having obligate or facultative wetland status. The relative proportion of forbs and graminoids was calculated by summing the importance values of forb species and dividing by the total importance value of forbs and graminoids. The total percentage cover was calculated by summing cover values for all species. This measure is likely to be related to aboveground biomass. Individual analyses for 10 species with high overall importance values were also performed. The proportional community variables did not meet all assumptions of the ANOVA model, and standard transformations did not improve the data's fit. However, ANOVA has been shown to be robust to moderate violations of model assumptions (Lindman 1974). Moreover, the qualitative results were not sensitive to data transformations.

Spatial heterogeneity in soil moisture and plant composition was evident, and observations suggested that a major gradient occurred perpendicular to the road and ditch (Fig. 1). Analysis of variance with row (proximity to ditch) as a main factor and blocks nested within rows was used to test whether soil moisture differed in blocks near to versus away from the ditch. Additional analyses of plant community variables that included row as a factor in the model, with blocks nested within rows, were performed to investigate the effects of ditch proximity on plant diversity, proportion of wetland species, proportion of forbs, and total percentage cover.

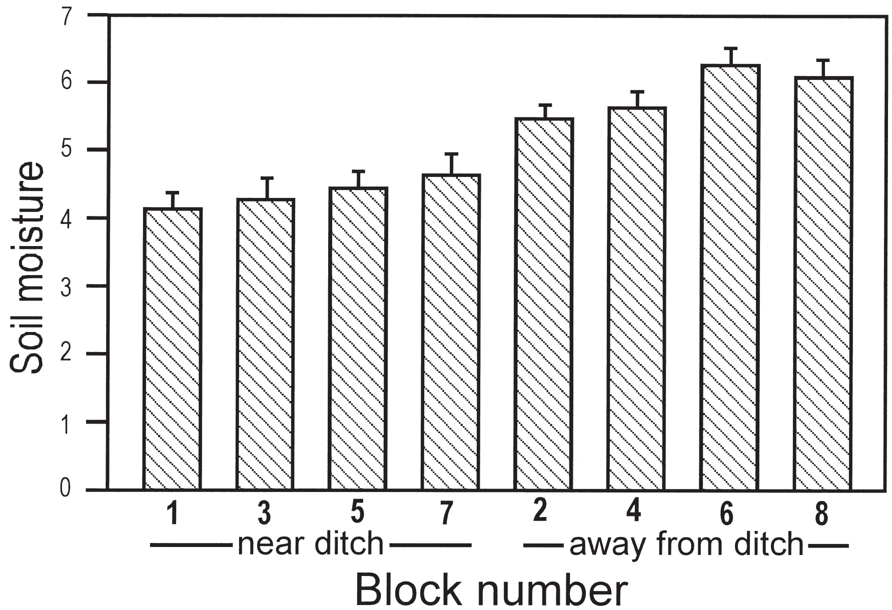

FIG. 2. Moisture levels in experimental blocks. Each bar represents the mean of 28 moisture readings, seven in each treatment plot per block. Soil moisture is expressed in unitless values, with zero indicating completely dry soil and 10 indicating saturated soil. Error bars = 1 SE.

RESULTS

Soil moisture was significantly lower in the row of blocks adjacent to the ditch ($F = 61.2$, $P < 0.0001$) and did not vary significantly among blocks within rows ($F = 0.698$, $P = 0.652$, Fig. 2).

The three-way interaction (fertilizer × mowing × block) was not significant for any dependent variable and, therefore, was not included in the models. Interactions between main treatments and block were non-significant for all variables except for the proportion of forbs (Table 1). Analysis of variance of species diversity (Shannon-Wiener index) revealed a significant effect of mowing; diversity was greater in mowed than unmowed treatments in seven of eight blocks (Table 1, Fig. 3). Species diversity was not affected by fertilizer alone. However, the interaction of the two main factors was significant, with fertilizer showing a negative effect on diversity in unmowed treatments and a positive effect in mowed treatments (Fig. 4). Variation in diversity among blocks was significant, and inspection of the means revealed a pattern of lower diversity in the row of blocks adjacent to the drainage ditch (Fig. 1, Fig. 3). Adding row (proximity to ditch) as a factor in the ANOVA, the results for fertilizer, mowing and their interaction were qualitatively unchanged from the basic model, but diversity was significantly lower in the row near the ditch ($F = 55.56$, $P < 0.001$). Moreover, blocks within rows were not significantly different, indicating that most of the variation among blocks in the main model was found between rows.

The proportion of wetland species was significantly affected by mowing, with greater importance of wetland species in mowed than in unmowed treatments for all plots (Table 1, Fig. 3). The proportion of wetland species was smaller in fertilized

Table 1. Analysis of variance of treatment effects on several measures of plant community composition. Diversity was calculated using the Shannon-Wiener index. See text for details on calculations of other dependent variables. Fertilizer and mowing were fixed effects; block was treated as a random variable.

Measure of composition/ Effect	df	MS	*F*	*P*
Diversity				
Fertilizer	1	0.237	2.641	0.108
Mowing	1	1.359	15.163	<0.001
Block	7	0.814	9.077	<0.001
Fertilizer × mowing	1	1.302	14.527	<0.001
Proportion wetlands species				
Fertilizer	1	0.200	21.490	<0.001
Mowing	1	0.060	6.462	0.013
Block	7	0.079	8.479	<0.001
Fertilizer × mowing	1	0.012	1.253	0.266
Proportion forbs				
Fertilizer	1	0.099	6.963	0.033
Mowing	1	0.001	0.001	0.977
Block	7	0.008	0.240	0.959
Fertilizer × mowing	1	0.006	0.470	0.495
Fertilizer × block	7	0.014	1.183	0.323
Mowing × block	7	0.029	2.446	0.026
Total cover				
Fertilizer	1	10,853.443	5.234	0.025
Mowing	1	2,079.016	1.003	0.320
Block	7	2,444.167	1.179	0.324
Fertilizer × mowing	1	4.928	0.002	0.961

than in unfertilized treatments in seven of eight plots, and the overall effect was significant (Table 1, Fig. 3). The main treatments did not interact significantly to affect the importance of wetland species, but variation among blocks was significant. Despite differences in soil moisture, when the row factor was added to the ANOVA model, blocks adjacent to and away from the ditch did not differ significantly in the proportion of wetland species ($F = 0.34$, $P = 0.58$), and variation among blocks within rows remained significant ($F = 4.15$, $P = 0.04$).

The proportion of forb species was significantly affected by fertilizer, with greater forb abundance in fertilized than in unfertilized treatments for seven of the eight blocks (Table 1, Fig. 3). The main effect of mowing on the proportion of forbs and graminoids was not significant, and there was significant variation among plots in the response to mowing. Total cover was significantly greater in fertilized than in unfertilized subplots (mean = 175.9 and 154.6, respectively). The main effect of mowing was not significant.

Individual species responded differently to the two main treatment factors (Fig. 5). Of the 10 species having large overall importance values, six were significantly affected by fertilizer. *Solidago microcephala* (Greene) Bush and *Rhexia mariana* L. increased with fertilizer, whereas *Aristida virgata* Trin., *Arundinaria gigantea* ssp. *tecta*, *Rhynchospora inexpansa* and *Smilax glauca* Walt. were less abundant in fertilized blocks. Two of the 10 species analyzed (*Arundinaria gigantea*

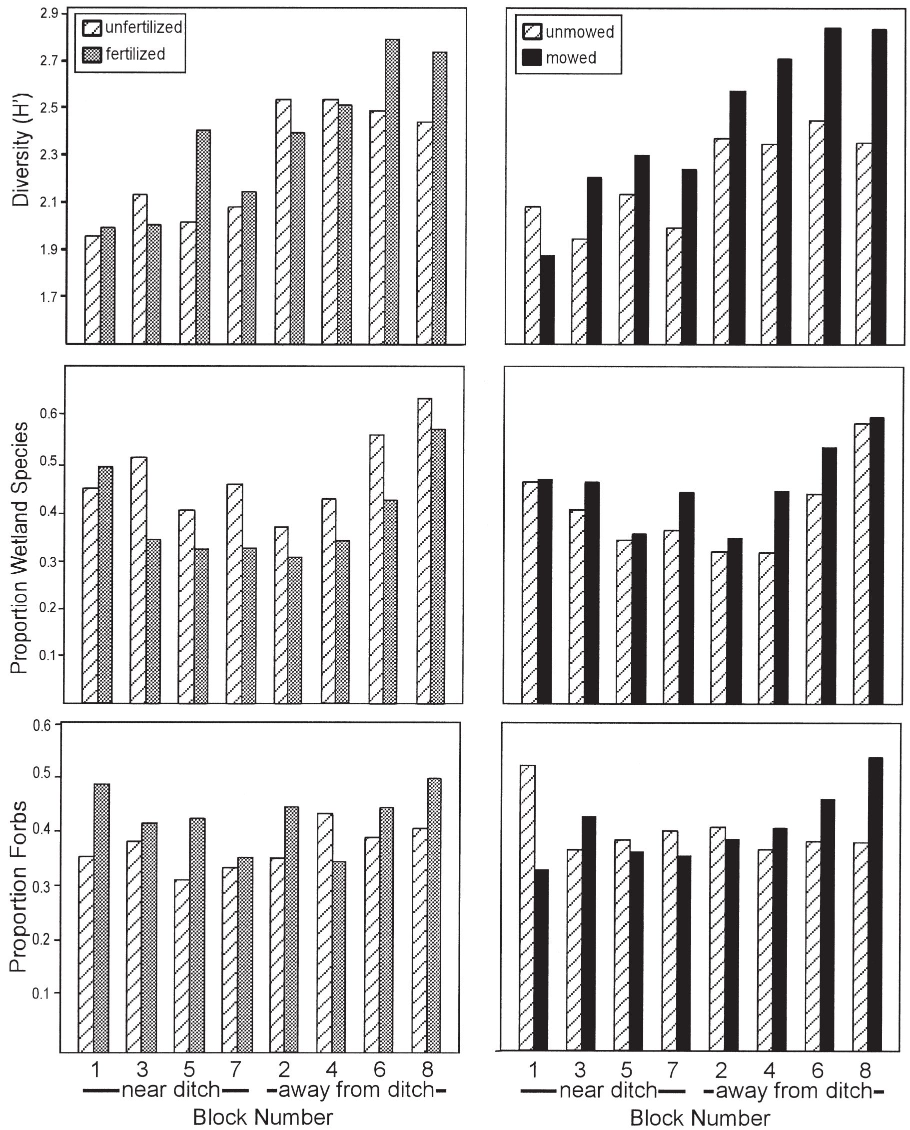

FIG. 3. Effects of mowing and fertilizer on several measures of plant community composition. Diversity is quantified using the Shannon-Wiener index. See text for detailed information on the calculation of dependent variables.

ssp. *tecta* and *Packera tomentosus*) increased significantly with mowing; none showed significant reductions with mowing. Abundances for four species were significantly different in rows near to versus away from the ditch (Fig. 5).

DISCUSSION

Higher diversity was found in mowed than in unmowed plots. Ecologists have long recognized the role of disturbance in structuring ecological communities (Connell 1978; Huston 1979; Pickett 1980). Classic ecological models predicted that

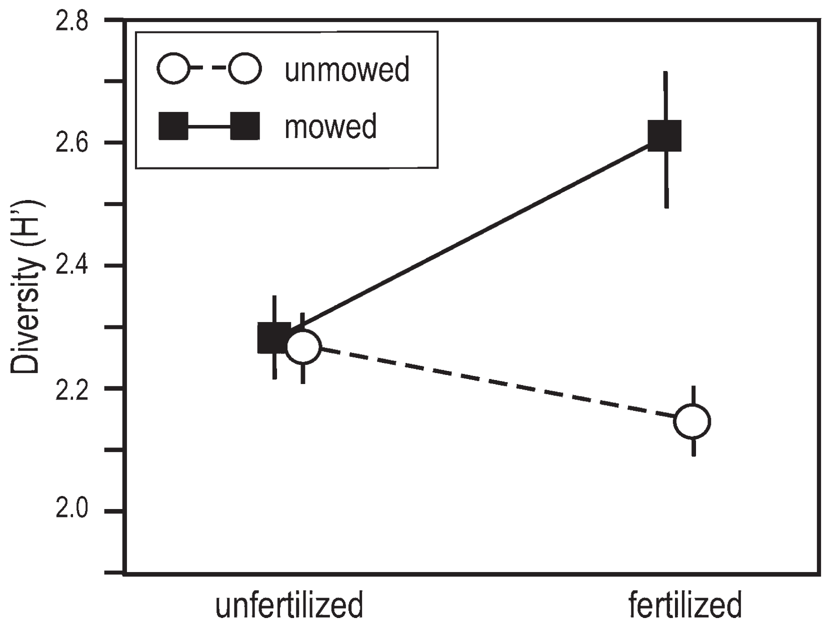

FIG. 4. Interacting effects of mowing and fertilizer on plant species diversity, as quantified using the Shannon-Wiener index. The interaction is significant at $P = 0.001$ (Table 1). Bars indicate one standard error of the mean.

intermediate levels of disturbance would promote high diversity (Huston 1979). Only rapidly colonizing species are expected to persist with intense and frequent disturbance; on the other hand, low disturbance may permit a few species with superior competitive abilities to dominate. Studies of plant communities have yielded variable outcomes, providing some support for these theories but also suggesting that the effects of disturbance on community structure may depend on the nature and timing of the disturbance and the biology of competitive dominant species (Armesto and Pickett 1985; Pickett and White 1985; Collins 1987; Luken et al. 1992). This study with only two levels of disturbance—mowed vs. unmowed—did not provide a direct test of the intermediate disturbance hypothesis. Nevertheless, the finding of higher diversity in mowed than in unmowed plots is consistent with the idea that some disturbance is necessary to maintain community diversity.

Prior to European settlement, the most important source of disturbance at the site was likely to have been wildfires. This is reflected by the presence of a substantial number of fire-dependent or fire-associated species at the WRC (Chester 2004; B. Sorrie, unpublished). Mowing in our study mimics the effects of fire in the sense that it destroys aboveground, but not belowground, plant tissue, but other potentially important effects of fire, such as litter removal and its role in nutrient dynamics, may not be provided by mowing. This limits the extent to which we can interpret our results with respect to fire frequency and suppression.

Ecological studies have provided support for hypothesized relationships between species diversity and productivity, with low diversity expected in both very high and low biomass habitats (Grime 1979; Wheeler and Giller 1982). A corollary of this relationship is that nutrient availability can affect community diversity. Areas with

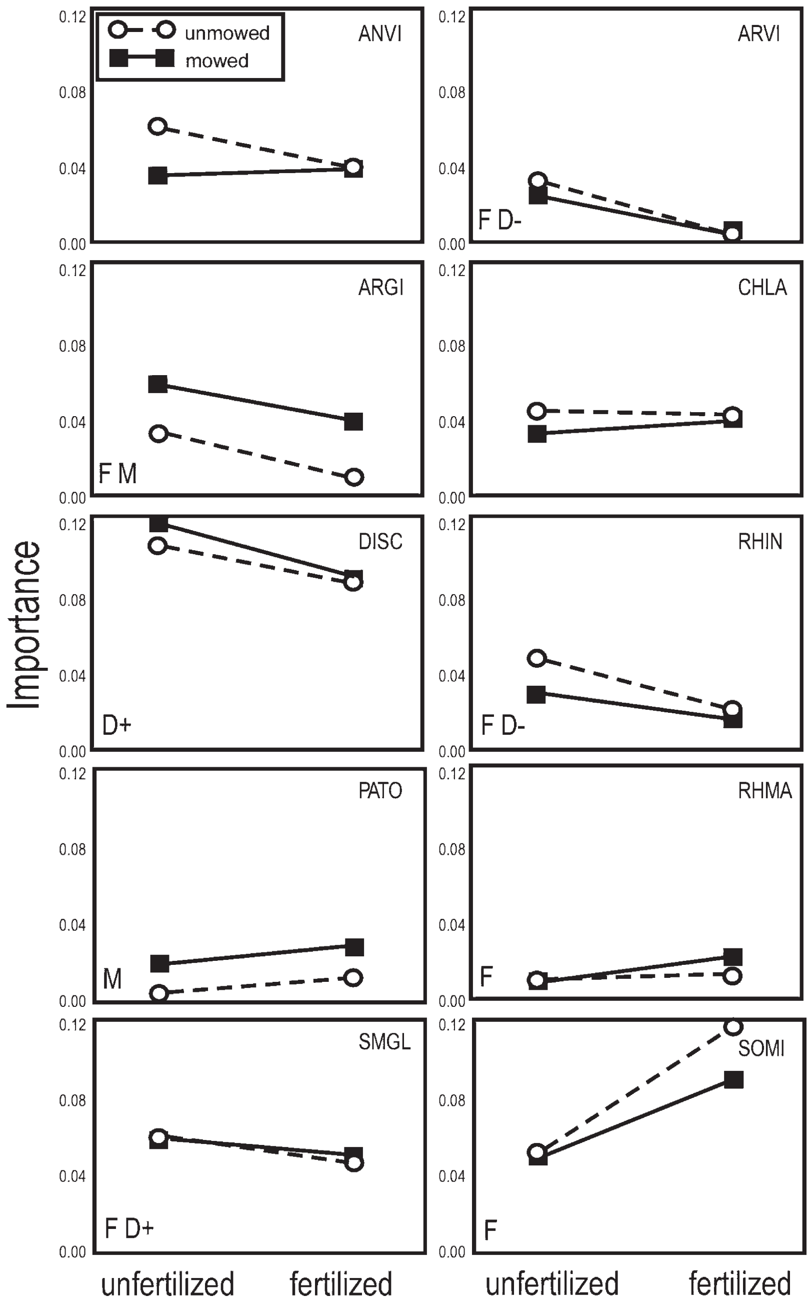

FIG. 5. Responses of ten abundant species to mowing (open circles versus filled squares) and fertilizer (left versus right). See text for details on the calculation of importance. ANVI = *Andropogon virginicus*, ARVI = *Aristida virgata*, ARGI = *Arundinaria gigantea* ssp. *tecta*, CHLA = *Chasmanthium laxum*, DISC = *Dichanthelium scoparium*, RHIN = *Rhynchospora inexpansa*, PATO = *Packera tomentosus*, RHMA = *Rhexia mariana*, SMGL = *Smilax glauca*, SOMI = *Solidago microcephala*. Letters at lower left indicate effects that are significant at $P < 0.05$. F = fertilizer, M = mowing. D+ and D− indicate that the species was significantly more abundant in the blocks near to or away from the ditch, respectively.

high nutrient availability and productivity are expected to experience low plant diversity because of the dominance of strong competitors. This effect has been evident in a number of nutrient enrichment studies of grasslands (Reed 1977; Wilson and Shay 1990), including the classic Park Grass Experiment, in which fertilization has resulted in dramatic loss of species richness over the course of decades (Silvertown 1980). Nutrient enrichment herein resulted in an increase in total plant cover by all plant species, suggesting that productivity was higher in fertilized than in unfertilized plots. However, fertilization had no statistically significant overall effect on diversity (Table 1).

Bedford et al.'s (1999) review of studies of North American wetland communities found general congruence with the results for other types of ecosystems; species richness was often shown to decline as nutrient availability increased. Other studies of wetlands have yielded conflicting results, however; Bowman et al. (1993) found that nutrient addition changed the composition, but not the diversity, of a wet alpine meadow. Our results are similar in that community composition, as reflected in the relative abundance of forbs versus graminoids and wetlands versus upland plants, was significantly altered by fertilization, although diversity was unchanged.

Competition is the mechanism that is thought to explain why both high nutrient availability and low disturbance can lead to low diversity (Grime 1973). Our finding of a significant interaction between fertilization and mowing is consistent with this idea. Fertilization reduced species diversity in the absence of mowing, whereas in mowed plots fertilizer had a positive effect on diversity (Fig. 4), suggesting that disturbance may have alleviated the competitive interactions that were intensified by fertilization in unmowed treatments. We found congruence with a study of disturbance and nutrient addition to a 30-year old field, where fertilizer was found to decrease diversity only in the undisturbed plots (Wilson and Tilman 1991). Similarly, grazing was found to reduce the negative effects of nutrient enrichment on diversity in a calcareous grassland (Jacquemyn et al. 2003).

Mowing had significant positive effects on the importance of wetland species. Wetland species showing substantially higher abundance in mowed treatments included *Rhexia virginica* L., *Dichanthelium lucidum*, *Solidago stricta* Ait., and *Arundinaria gigantea* ssp. *tecta*. Fertilization decreased the relative importance of wetland species, with large negative effects seen in *Cyrilla racemiflora* L., *Gratiola pilosa* Michx., *Clethra alnifolia* L., *Aristida virgata*, and *Calamagrostis coarctata* (Torr.) Eat. Plants that are tolerant of disturbance and low nutrient wetland soils may experience a trade-off in lower competitive ability (Grime 1979). Thus, reduced abundance of wetland species in fertilized and unmowed plots may reflect competitive dominance of upland plant species. Alternatively, higher nutrient levels may be detrimental to the growth of some wetland species. Future experimental studies will be designed to distinguish between these alternative hypotheses.

An unexpected confounding factor in this experiment was spatial variation in soil moisture. Blocks adjacent to the ditch (blocks 1, 3, 5, 7) had significantly lower soil moisture levels than those farther away (Fig. 2), suggesting an effect of ditch drainage. However, a more subtle increase in soil moisture is also evident in a comparison of blocks 2, 4, 6 and 8, which appears to reflect a microelevational gradient. Thus, variation in soil moisture may result from both human-mediated and natural effects. Regardless of its cause, the effects of soil moisture on plant diversity appear to be dramatic. The drier near-ditch blocks had significantly lower species diversity. In contrast to our results, wetter areas in an alluvial wetland in France experienced lowered diversity than did drier areas (Touzard et al. 2002). However, wetter soils were associated with intense flooding in that study, which appears to limit diversity. Although blocks adjacent to and away from the ditch in our study did not differ significantly in the proportion of wetland species, many individual wetland species, including some sedges and rushes, were found almost exclusively in blocks away from the ditch. Their pattern may have been obscured in the statistical analysis by the dominance of *Dichanthelium scoparium* (Lam.) Gould, a facultative wetland species, in blocks 5 and 7 near the ditch.

Substantial effects on a wetland plant community of the Coastal Plain were noted after a single year of nutrient addition and mowing. By examining the effects of disturbance and nutrients in the same experiment, we found that the combined effect of the two factors cannot be predicted from the application of either treatment alone. In future work, we will complement the study with experiments to elucidate some of the species interactions underlying the patterns we observed. We will also assess the effect of treatments on plant biomass, a direct measure of productivity. The effects of each of the factors explored in our experiment—disturbance, nutrient addition and variation in soil moisture—have implications for human impacts on wetland communities. Although our projected long-term experiment is in the early stages, initial results suggest that these factors can influence plant community composition.

Acknowledgments: We thank the members of the 2004 vegetation sampling and analysis course (B. Cahoon, J. Dieterle, K. Harper, Z. Harrison, J. Kincaid, N. Norwood, A. Pegram, K. Powers, G. Riddick, M. Silverman, J. Vaughan, N. Walter) for plant data collection and helpful discussions, L. Clough and D. Knowles for development of the project, the Stiller family for assistance with fertilizing, the ECU grounds crew for mowing, and the spring 2005 general ecology students for collection of soil moisture data. The manuscript was substantially improved by editing and insightful comments of two anonymous reviewers and the editor. This research was supported by National Science Foundation Award DUE-126824 to C.G., L. Clough and D. Knowles.

LITERATURE CITED

ARMESTO, J. J., AND S. T. A. PICKETT. 1985. Experiments on disturbance in old-field plant communities: impact on species richness and abundance. Ecology 66:230–240.

BEDFORD, B. L., M. R. WALDBRIDGE, AND A. ALDOUS. 1999. Patterns in nutrient availability and plant diversity of temperate North American wetlands. Ecology 80:2151–2169.

BOWMAN, W. D., T. A. THEODOSE, J. C. SCHARDT, AND R. T. CONANT. 1993. Constraints of nutrient availability on primary production in two alpine tundra communities. Ecology 74:2085–2097.

CHESTER, R. E. 2004. Floristic assessment of a wet mineral flat at the East Carolina University West Research Campus and investigation of influential, human-mediated factors on the plant community. MS thesis, East Carolina University, 121 p.

COLLINS, S. L. 1987. Interaction of disturbances in tall grass prairie: a field experiment. Ecology 68:1243–1250.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199:1302–1310.

GRIME, J. P. 1973. Competitive exclusion in herbaceous vegetation. Nature 242:344–347.

———. 1979. Plant Strategies and Vegetation Processes. Chichester, UK: John Wiley and Sons, 222 p.

HUSTON, M. 1979. A general hypothesis of species diversity. Am. Nat. 113:81–101.

JACQUEMYN, H., R. BRYS, AND M. HERMY. 2003. Short term effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. Biol. Cons. 111:137–147.

LINDMAN, H. R. 1974. Analysis of Variance in Complex Experimental Designs. San Francisco: W. H. Freeman, 352 p.

LUKEN, J. O., A. C. HINTON, AND D. G. BAKER. 1992. Responses of woody plant communities in power-line corridors to frequent anthropogenic disturbance. Ecol. Appl. 2:356–362.

MORRIS, J. T. 1991. Effects of nitrogen loading on wetland ecosystems with particular reference to atmospheric deposition. Annu. Rev. Ecol. Syst. 22:257–279.

PAULI, D., M. PEINTINGER, AND B. SCHMID. 2002. Nutrient enrichment in calcareous fens: effects on plant species and community structure. Basic Ecol. Appl. 3:255–266.

PICKETT, S. T. A. 1980. Non-equilibrium coexistence of plants. B. Torrey. Bot. Club 107:238–248.

———, AND P. S. WHITE. 1985. The Ecology of Natural Disturbance and Patch Dynamics. Orlando, FL: Academic Press, 472 p.

REED, F. C. P. 1977. Plant species number, biomass accumulation and productivity of a differentially fertilized Michigan old-field. Oecologia 30:43–53.

SILVERTOWN, J. 1980. The dynamics of a grassland ecosystem: botanical equilibrium in the Park Grass Experiment. J. Appl. Ecol. 17:491–504.

TILMAN, D. 1988. Plant Strategies and the Dynamics and Structure of Plant Communities. Princeton, NJ: Princeton Univ. Press, 360 p.

TOUZARD, B., B. CLEMENT, AND S. LAVOREL. 2002. Successional patterns in a eutrophic alluvial wetland of Western France. Wetlands 22:111–125.

UNITED STATES DEPARTMENT OF AGRICULTURE. 1974. Soil Survey of Pitt County, North Carolina. U.S. Government Printing Office, Washington, DC.

WHEELER, B. D., AND K. E. GILLER. 1982. Species richness of herbaceous fen vegetation in Broadland, Norfolk in relation to the quantity of above-ground plant material. J. Ecol. 70:179–200.

WILSON, S. D., AND D. TILMAN. 1991. Interactive effects of fertilization and disturbance on community structure and resource availability in an old-field plant community. Oecologia 88:61–71.

———, AND ———. 1993. Plant competition and resource availability in response to disturbance and fertilization. Ecology 74:599–611.

———, AND J. M. SHAY. 1990. Competition, fire and nutrients in a mixed-grass prairie. Ecology 71:1959–1967.

Received 27 June 2006