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Experimental test of the role of mammalian herbivores on old field succession: Community structure and seedling survival[1]

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CADENASSO, M.L., S.T.A. PICKETT (Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545) AND P.J. MORIN (Department of Ecology, Evolution, and Natural Resources, 14 College Farm Road, Cook College, Rutgers University, New Brunswick, NJ 08901). Experimental test of the role of mammalian herbivores on old field succession: community structure and seedling survival. J. Torrey Bot. Soc. 129:228–237. 2002.—When elucidating plant community dynamics, investigators have focused on plant-plant and plant-environment interactions and on the characteristics of individual plants. The role of animals has been relatively neglected. Herbivory may affect vegetation dynamics by altering community composition and structure and by influencing the performance of species. Therefore, herbivory can be an important factor in succession. We experimentally tested the role of mammalian herbivores in two fields at the Hutcheson Memorial Forest Center in central New Jersey. Both fields were released from active cultivation, one at the beginning of the experiment and the other 17 years earlier. Large exclosures (5 × 5 m) were used to exclude mammalian herbivores, and open units of the same size were used as controls. The effect of herbivore exclusion on the structure and composition of the plant community was analyzed. In addition, tree seedlings of three species—*Acer rubrum*, *Cornus florida*, and *Juniperus virginiana*—were planted in the experimental units in both fields. These species typically invade early- to mid-successional old fields. The survival of these individuals was calculated and, using height as an indicator, their performance assessed. Herbivore exclusion primarily influenced the structure of the plant community rather than its composition. Percent cover of species and species richness of all plants were not affected by herbivory, but in one field the relative cover of exotics was greater in the exclosures. The height profile of the plant community in the exclosures was significantly taller than the community in the open plots. The survival and growth of planted *A. rubrum* and *C. florida* seedlings was significantly greater when protected from herbivores. In contrast, the survival and growth of *J. virginiana* seedlings was not affected by herbivores. Growth and survival of *J. virginiana* did differ by the field they were planted in, suggesting that physiological constraints may be more important than herbivory for this species. These results reenforce that herbivorous mammals play a key role in old field succession, particularly in the pivotal shift of dominance from herbaceous to woody cover.

Key words: Succession, herbivory, seedling survival, community composition, community structure, exotic species, mammalian herbivores, Hutcheson Memorial Forest Center, New Jersey.

By the mid 1800's, the landscape of the northeastern United States had been dramatically altered by clearing deciduous forests to create agricultural fields (Russell 1997). Many of these agricultural fields have since been released from active cultivation and allowed to revert to deciduous forests through succession. Several approaches have been used to describe changes in plant communities and to understand what factors influence the rate and direction of those changes. Primary approaches have included the study of plant-plant interactions (Keever 1950), plant-environment interactions (Bazzaz 1979; Vitousek and White 1981), and life history strategies or traits of individual plant species (Gleason 1926; Drury and Nisbet 1973; Noble and Slatyer 1980; Peet and Christensen 1980). However, remarkably little research has investigated the impact of animals on successional processes (Bowers 1993; Bazzaz 1996). We conducted a long-term exclosure experiment to determine the impact of mammalian herbivores on old field succession and the key transition from herbaceous to woody dominance.

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It has been widely suggested that herbivores influence the composition and structure of plant communities (e.g. reviewed by Huntly 1991). Specifically, herbivory has been shown to lead to a decrease in plant biomass (Huntly and Inouye 1988; Crawley 1989) and to cause a change in the relative abundance of species (Crawley 1989; Gutierrez et al. 1997). These effects may be direct, through selective foraging (Huntly 1991; Augustine and McNaughton 1998; Olff and Ritchie 1998). Indirect pathways include altering resource availability including space, light, and nutrients (Vitousek and White 1981; Huntly and Inouye 1988; Inouye et al. 1991; Hobbs 1996; Augustine and McNaughton 1998) or altering competitive hierarchies (Huntly 1991; Bowers 1993). Herbivore impacts on plant communities may vary with field age or stage of succession (Armesto and Pickett 1985; Huntly 1991; Davidson 1993).

A pivotal event in old field succession is establishment of woody species with the subsequent development of a tree canopy. The shift in community composition and structure from predominantly herbaceous to woody canopy dominance may be greatly influenced by herbivory (Davidson 1993; Weltzin et al. 1997). The primary mechanism by which herbivores influence the rate of this shift is by preventing or greatly slowing the establishment of tree species in the fields (Inouye et al. 1994). Assuming herbivores are present, the primary determinants of herbivore impacts to seedling populations and, consequently, establishment of the woody canopy are the selectivity of the herbivore and the response of the plant to damage (Cadenasso and Pickett 2000). These two factors can work together to determine the composition of the first woody canopy and the time that canopy closes.

Two main questions motivated this experiment: 1) do mammalian herbivores influence the composition and structure of herbaceous old field communities? and 2) do mammalian herbivores influence the survival and performance of invading tree seedlings? The experiment was conducted in two fields of different successional stages. This design does not allow us to determine how the influence of mammalian herbivory on vegetation dynamics alters or changes during succession. However, exclosures and open control plots were replicated in each field, allowing us to determine the influence of mammalian herbivory on vegetation dynamics within a field.

Succession, or more generally vegetation dynamics, is determined by three factors: 1) site availability, 2) differential species availability, and 3) differential species performance (Pickett et al. 1987). Because all experimental units were established in the same manner in each field, it was assumed that site availability was similar within each field. Also, within each field, there was no difference among the units in species availability as propagules could freely disperse into each unit. This assumption does not hold for species dispersed primarily by mammals. By eliminating differences in site availability and species availability, this experiment tested the differential performance of species and the impact of herbivores on that performance (*sensu* Pickett et al. 1987). This addressed question one. To address question 2 and to determine herbivore impact on the transition from herbaceous to woody dominance, identical numbers and species of seedlings were planted in all units. Unfortunately, no data on vegetation structure and composition were available from the beginning of the experiment. The data presented here were collected more than a decade after the experiment was initiated in 1984. Therefore, we are evaluating the net, long-term effects of herbivory on community composition and structure, and on seedling survival and performance.

Materials and Methods. SITE DESCRIPTION. The experiment was conducted at the Hutcheson Memorial Forest Center (HMFC) of Rutgers University. The Center is 14 km east of New Brunswick in Somerset County (40° 30′N, 74° 34′W) on the New Jersey Piedmont. The soils are well drained loams derived from the underlying Brunswick red shale (Robichaud and Buell 1973). Local climate is subcontinental temperate, with an average annual precipitation of 116 cm distributed evenly throughout the year, increasing slightly during the 240-day growing season (Robichaud and Buell 1973). The maximum temperatures, mean of 24° C, occur in July and the minimum temperatures, mean of 0° C, occur in January (Robichaud and Buell 1973).

EXPERIMENTAL DESIGN. The experiment began in 1984 in both fields, each approximately 0.5 ha. One field, hereafter referred to as Field 1, was plowed and disked at the start of the experiment. The other, Field 2, had last been plowed and disked 17 years earlier in 1967. During those 17 years the field was undergoing succession. Therefore, at the start of this experiment, there was no plant establishment in Field 1. Field 2 had an established plant community consisting of herbaceous and woody species, including scattered saplings of tree species.

The effect of mammalian herbivores on old field succession was tested by comparing plant community composition and structure between exclosures and open controls. Four exclosures and four open controls were established in each field. The experimental units were 5 × 5 m, located in the center of the field, and were more than 10 m apart. The exclosures were designed to exclude the primary mammalian herbivores, which are white-tailed deer (*Odocoileus virginianus*), cottontail rabbits (*Sylvilagus floridanus*), and meadow voles (*Microtus pennsylvanica*). Exclosures were constructed using four wooden corner posts with supporting horizontal beams and diagonal braces. Galvanized sheet metal was wrapped around the perimeter of the exclosures and was buried 0.5 m below and extended 1 m above the soil surface. Wire mesh, of a 10 cm grid, was riveted to the sheet metal and extended an additional 3 m in height. Around the perimeter of the exclosures, 1 cm diameter holes were drilled in the sheet metal at the soil surface to prevent water from pooling along the perimeter and to facilitate movement of any surface water through the exclosures. Open units were constructed with the same wood framing as the exclosures but without the caging material. The perimeters of the open plots were ditched and refilled to control for the effect of construction. A single strand of wire encircled the top of both the exclosures and the open units to allow for similar seed input from bird defecation into all the units.

Vegetation in the units was sampled in July 1995 in Field 1 and in July 1996 in Field 2. Four 0.5 × 2.0 m plots were established in the center of each unit (Fig. 1). The plots were established in the center to avoid influences from unit construction that were presumed to be restricted to the perimeter of the unit. In each plot, the percent cover of all species was estimated visually. Taxonomy follows Gleason and Cronquist (1991). In Field 1 the maximum height of each species was also measured in the plots.

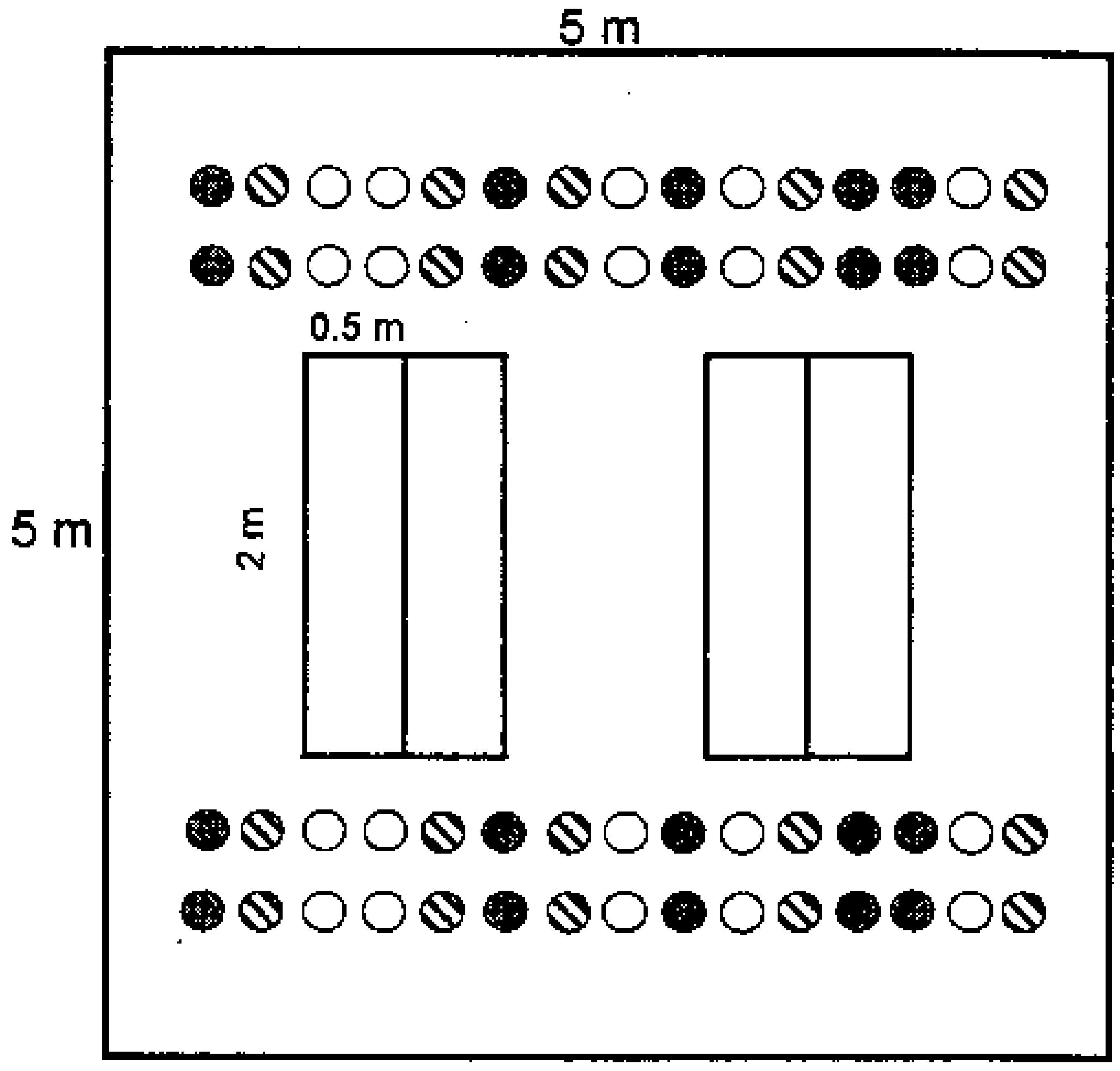

Fig. 1. Sampling Design. In the center of each experimental unit, four 1 m^2 plots measuring 0.5 × 2.0 m were established to sample species cover and height. A buffer zone was left in the middle of the unit for samplers to move about. Sixty seedlings were planted on two opposing sides of each unit. Twenty individuals of *Acer rubrum* (●), *Cornus florida* (○), and *Juniperus virginiana* (⊘).

The impact of mammalian herbivores on the survival and growth of tree seedling species was tested by planting seedlings into the experimental units. Seeds of *Acer rubrum* L., *Cornus florida* L., and *Juniperus virginiana* L. were collected in the spring and fall of 1985 at HMFC. The seeds were stratified and germinated in a greenhouse at Rutgers University. Seedlings were grown to 15–20 cm in height and planted into the experimental units in September 1986. They were planted in pairs by species and pairs of all 3 species were arrayed randomly in groups of six seedlings. These groupings were repeated 5 times on opposing sides of each experimental unit (Fig. 1). The height of all surviving seedlings was measured and, subsequently, the percent survival of the planted seedlings was calculated.

STATISTICAL ANALYSES. *Composition and Structure of Old Field Communities.* Data from Field 1 and Field 2 were analyzed separately as a difference in community composition and structure is expected between fields of different successional stages. Our research questions focus on the effects of herbivory on old field communities and, therefore, all analyses compared protection from and exposure to herbivory (exclosed vs. open units) within each field. The effect of exposure to herbivory on the relative percent cover of each life form—tree, shrub, vine, herb, and grass—was analyzed using a single factor multivariate analysis of variance (MANOVA). If the MANOVA was significant then results from the univariate single factor ANOVAs were considered to determine which life form contributed to the significant result. Proportional cover was used so as to consider the contribution each taxon or functional group made to the total plant cover. The effect of exposure to herbivory

Table 1. MANOVAs and univariate ANOVAs for effects of herbivory on total plant cover and on the relative cover of exotic species for Field 1 and Field 2.

	Source	df	Wilks' λ	*F*	*P*
Field 1					
(a) Multivariate analysis	Herbivory	2, 5	0.1417	15.14	0.0076
	Source	df	ss	*F*	*P*
(b) Univariate analyses					
Total cover	Herbivory	1	41.0645	0.05	0.8237
	Error	6	4546.2305		
Relative exotic cover	Herbivory	1	1077.3879	36.18	0.0010
	Error	6	178.6593		
	Source	df	Wilks' λ	*F*	*P*
Field 2					
(a) Multivariate analysis	Herbivory	2, 5	0.7334	0.91	0.4606

on the relative cover of exotic species was also tested using a single factor MANOVA.

The effect of exposure to herbivory on species richness of all plants and species richness of each life form was analyzed using a single factor MANOVA. Differences in species richness of exotic and native species relative to exposure to herbivory were also tested for using a single factor MANOVA.

Patterns in community composition were further evaluated using dominance-diversity curves produced for each herbivore treatment in each field as a synthetic measure of species richness and total percent cover. These curves illustrate evenness—the distribution of cover across all species present in the community. Evenness was calculated for each experimental unit as the inverse of the Simpson Index of diversity (Barbour et al. 1987) and was analyzed using an ANOVA to test for the effect of herbivore exposure.

The structure of the plant communities in the open units and the exclosures in Field 1 was evaluated by considering the height profiles of the community in each unit. The maximum height of each species was measured in the units in Field 1 only. An ANOVA was used to test for the effect of herbivore exposure on the height profile of the community using the average height of the tallest 5 species in each unit. The 5 tallest species were not necessarily the same species in each experimental unit. The identity of the species was irrelevant because the focus of this analysis was on the height profile of the plant community not on the height responses of individual species.

Survival and Performance of Tree Seedlings. There was no expected difference in the herbivore community between Field 1 and 2, so field was included in the analyses as a factor. Therefore, the effect of herbivore exposure and field on the survival and height of seedlings planted into the units was analyzed using two factor MANOVAs for each seedling species. Survival of each species was calculated as the percentage of the 20 individuals initially planted in each unit that were present at the time of sampling. If the MANOVAs were significant then the results from the two factor ANOVAs were considered to determine which of the two factors—herbivore exposure or field—contributed to the significance.

Results. Eighty-two species were found in the two fields, including 51 native species, 28 exotic species, and 3 species identified only to genus making it impossible to determine whether the plant was native or exotic. Forty two species were found in both fields, 56 species were in Field 1 and 68 were in Field 2.

Composition and Structure of Old Field Communities. Exposure to herbivory did not affect the relative cover of tree, shrub, vine, grass, or herb species in either field (Field 1 p = 0.58, Field 2 p = 0.98). However, in Field 1, the relative cover of native and exotic species differed significantly between the open plots and the exclosures (Table 1). In Field 1, the relative cover of native species was greater in the open units than in the exclosures and the relative cover of exotic species was greater in the exclosures than in the open units (Fig. 2).

Exposure to herbivory did not affect total plant species richness or species richness of different life forms in either field (Field 1 p = 0.54, Field 2 p = 0.75). In both fields, the average

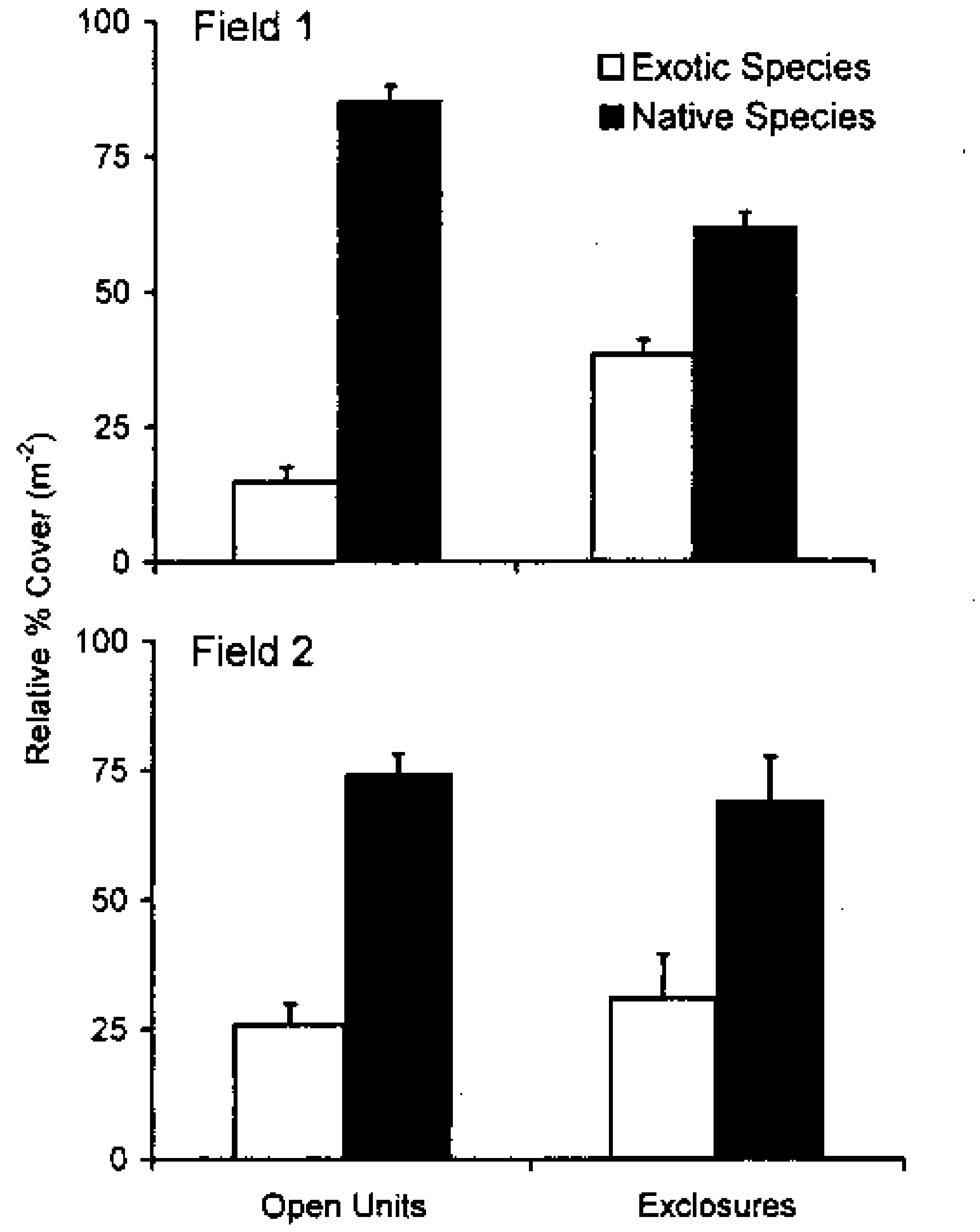

Fig. 2. Relative percent cover (m^{-2}) of exotic and native species in open units and exclosures in both fields. Open bars show the relative cover of exotic species while the relative cover of native species is indicated by the solid bars. Each bar represents the average across the four replicate treatment units ± 1S.E.

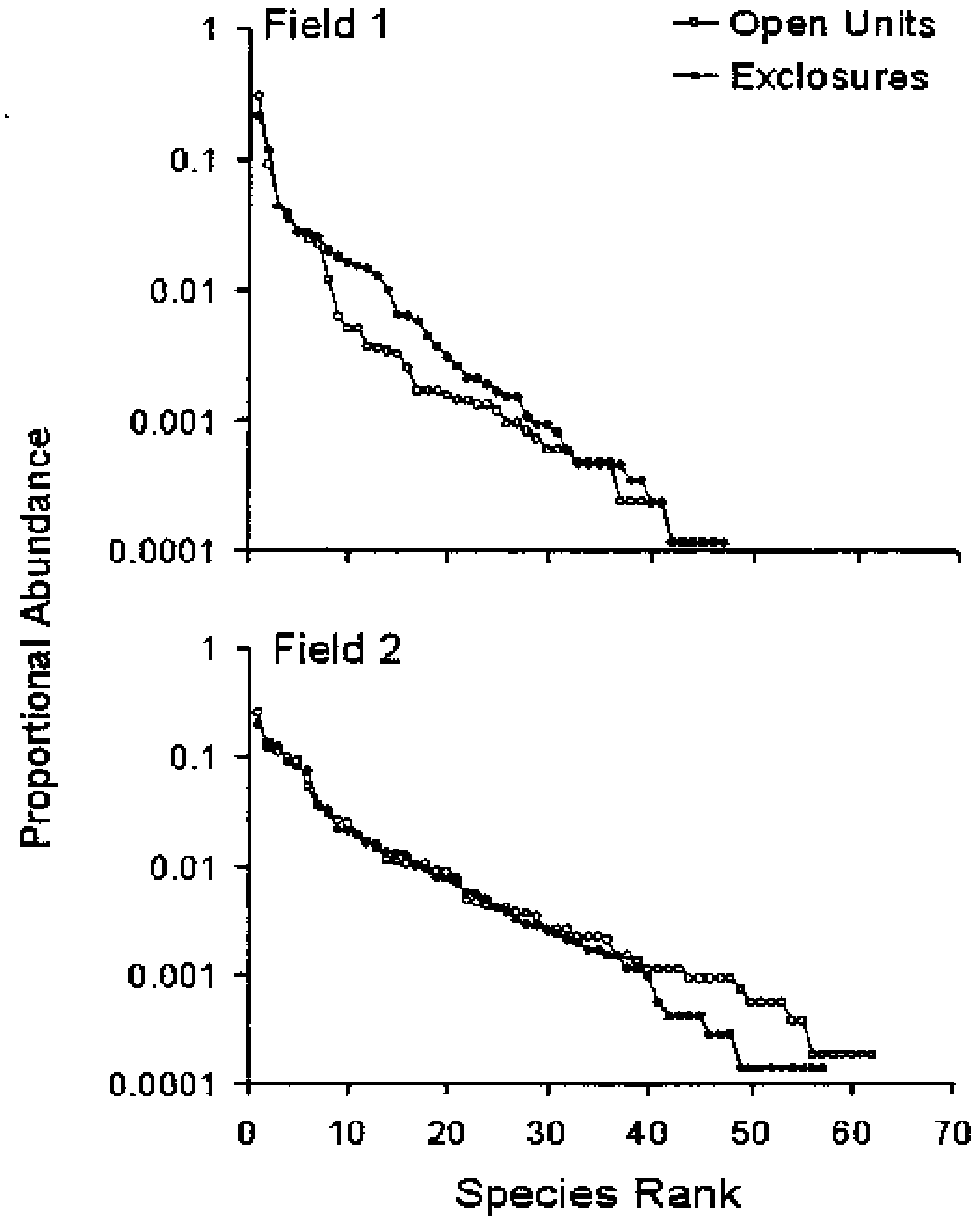

Fig. 3. Dominance-diversity curves for species recorded in the plots. Species are ranked along the *x* axes from most abundant to least abundant.

species richness of native plants was greater than that of exotic plants regardless of herbivore exposure, but this was not statistically significant (Field 1 $p = 0.11$, Field 2 $p = 0.87$).

The integrative measure of evenness showed a trend ($p = 0.08$) in Field 1 towards greater evenness in the exclosures ($\bar{X} = 5.05 \pm 1.96$) compared to the open plots ($\bar{X} = 2.90 \pm 0.65$). No pattern of evenness and exposure to herbivory was found in Field 2 ($p = 0.68$; Fig. 3).

The height profile of the community in Field 1, which was represented by the average height of the 5 tallest species in each experimental unit, varied significantly with exposure to herbivory ($p = 0.04$). In the open units, the average height profile was 114.45 cm and ranged between 67 and 158 cm. In the exclosures the average height profile was 145.55 cm and ranged between 90 and 275 cm. These species were important contributors to the total plant cover in the open units and the exclosures. In the open plots the cover of the 5 tallest species ranged from 66 % to 85 % of the total plant cover and in the exclosures the cover of the 5 tallest species ranged from 59 % to 87 % of the total plant cover.

SURVIVAL AND PERFORMANCE OF TREE SEEDLINGS. MANOVAs for *A. rubrum* (Table 2) and *C. florida* (Table 3) seedlings indicated that

Table 2. MANOVA and the univariate ANOVAs for effects of field and herbivore treatments on height and percent survival of *Acer rubrum*. Treatment is the only significant factor in the MANOVA and is, therefore, the only factor considered in the ANOVAs.

a) Multivariate analysis	Source	df	Wilks' λ	*F*	*P*
	Field	2	0.8303	1.12	0.3596
	Treatment	2	0.2681	15.01	0.0007
	Field*Treatment	2	0.8967	0.63	0.5491
b) Univariate analyses	**Source**	**df**	**ss**	***F***	***P***
Height	Treatment	1	5.2975	9.10	0.0107
	Error	12	6.9840		
Percent Survival	Treatment	1	11826.5625	31.94	0.0001
	Error	10	4418.7500		

Table 3. MANOVA and the univariate ANOVAs for effects of field and herbivore treatments on height and percent survival of *Cornus florida*. Treatment is the only significant factor in the MANOVA and is, therefore, the only factor considered in the ANOVAs.

a) Multivariate analysis	Source	df	Wilks' λ	*F*	*P*
	Field	2	0.9306	0.41	0.6735
	Treatment	2	0.2552	16.05	0.0005
	Field*Treatment	2	0.9296	0.42	0.6693
b) Univariate analyses	Source	df	ss	*F*	*P*
Height	Treatment	1	6.7401	17.51	0.0013
	Error	12	4.6201		
Percent Survival	Treatment	1	14101.5625	34.06	0.0001
	Error	12	4968.7500		

the herbivore treatment significantly affected both tree seedling survival (Tables 2 and 3, Fig. 4) and height (Tables 2 and 3, Fig. 5); there was no effect of field (Tables 2 and 3). Seedlings of *A. rubrum* and *C. florida* had greater survival and grew taller in the exclosures regardless of the field they were planted in (Tables 2 and 3, Figs. 4 and 5). In contrast, the survival and growth of *J. virginiana* seedlings did not differ between herbivore treatments but did differ significantly between fields (Table 4). *Juniperus virginiana* seedlings had greater survival and grew taller in Field 2 (Figs. 4 and 5).

Discussion. HERBIVORY AND COMMUNITY COMPOSITION AND STRUCTURE. This long term experiment suggests that mammalian herbivory primarily influences the structure of the plant community, not its composition. Species richness, total cover (Table 1) and the relative cover of each life form present in the community were unaffected. This is surprising, given the literature suggests herbivory either speeds up or slows down succession depending on the successional age or stage of the field (Davidson 1993). If herbivores were speeding up succession, cover of woody species in these fields

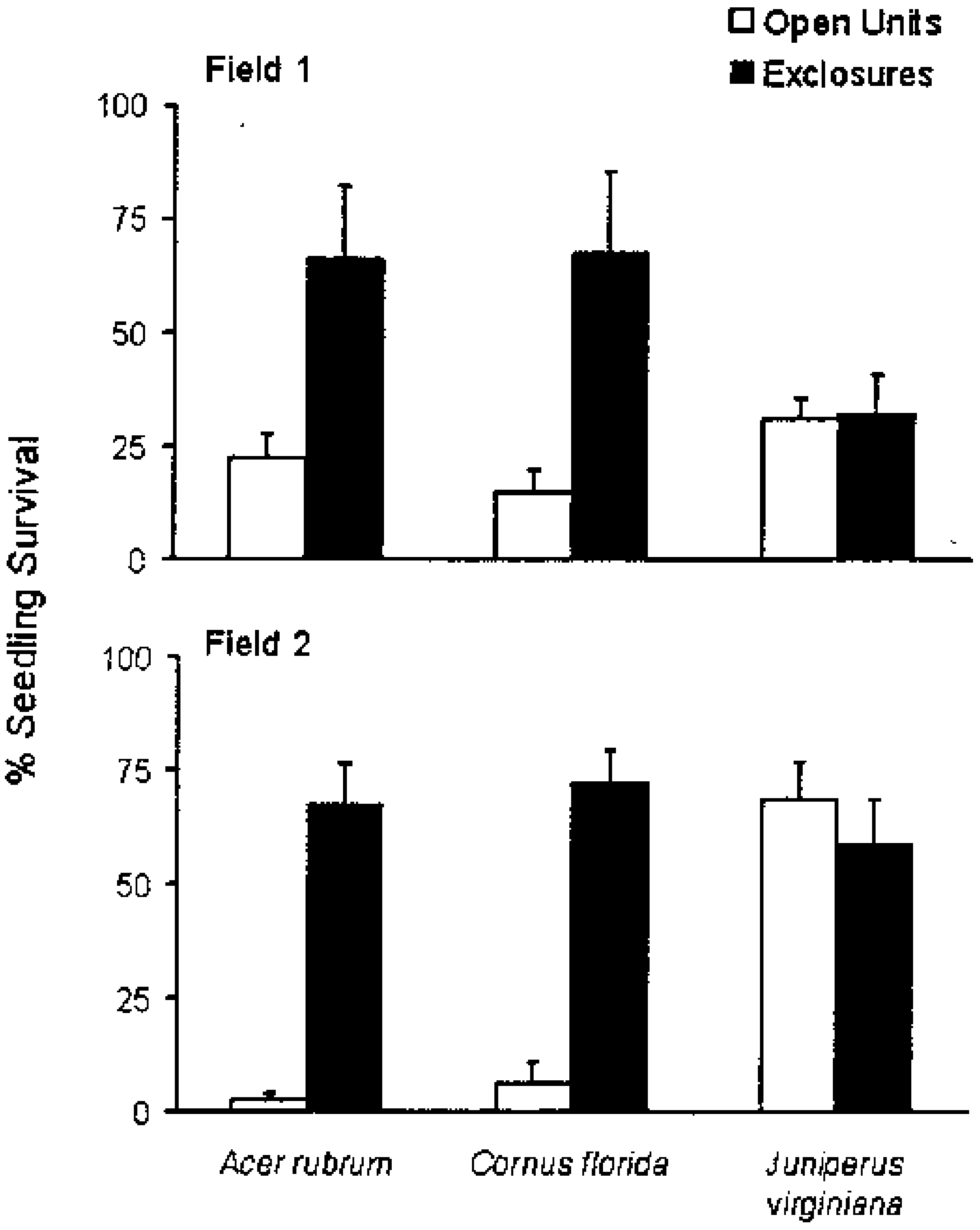

Fig. 4. Seedling survival by species in open units and exclosures in Field 1 and Field 2. Survival was calculated as the % of seedlings planted at the start of the experiment that were present when resampled 11 (Field 1) and 12 (Field 2) years later. Each bar represents the average of the four replicate units ± 1S.E.

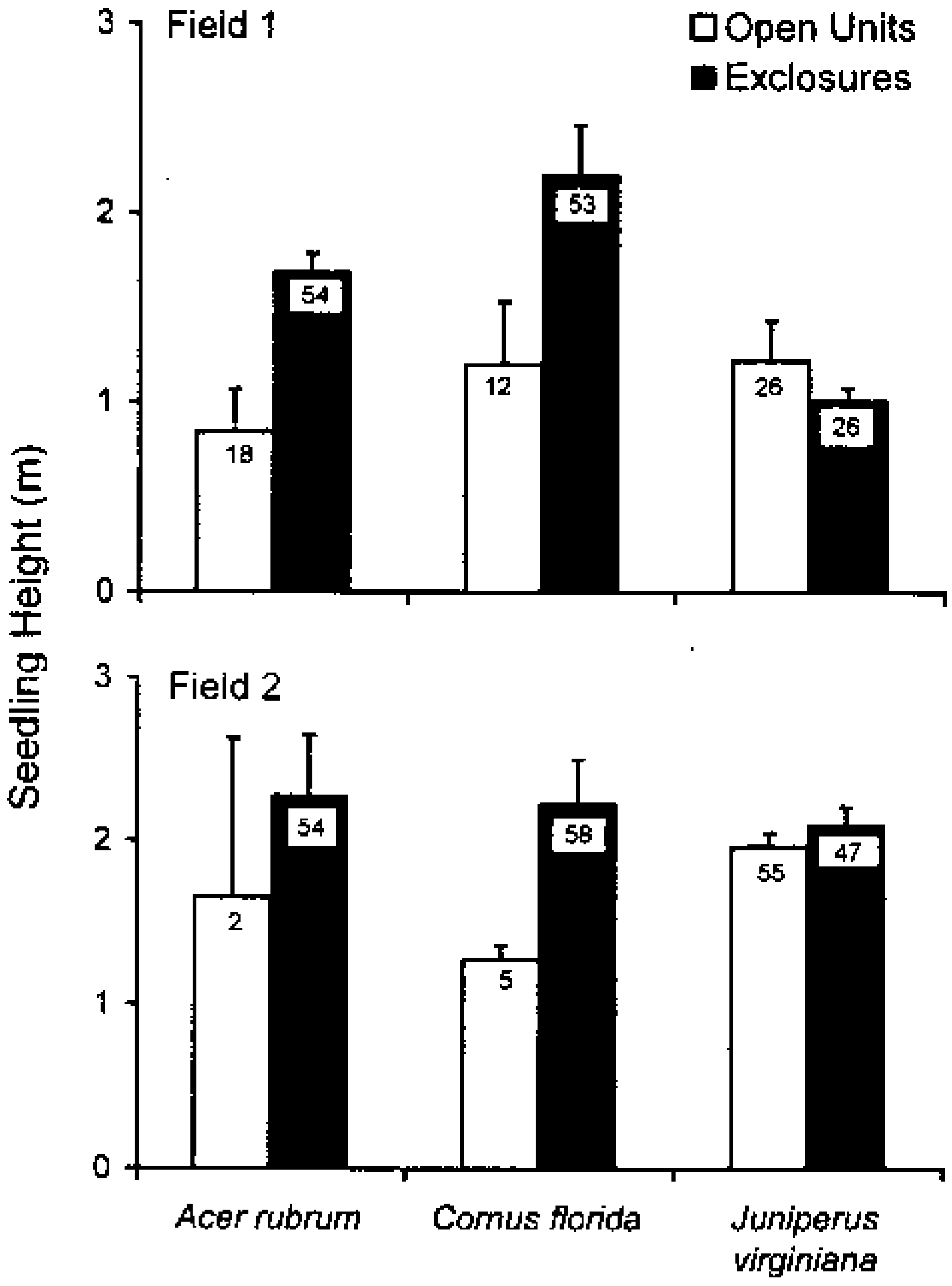

Fig. 5. Seedling height (m) by species in the open units and exclosures in Field 1 and Field 2. Each bar represents the average of all seedlings found in the four replicate units ±1S.E. The number of seedlings used in the calculation is indicated in the bar and is variable due to differential survival.

Table 4. MANOVA and the univariate ANOVAs for effects of field and herbivore treatments on height and percent survival of *Juniperus virginiana*. Field is the only significant factor in the MANOVA and is, therefore, the only factor considered in the ANOVAs.

a) Multivariate analysis	Source	df	Wilks' λ	*F*	*P*
	Field	2	0.1950	22.7043	0.0001
	Treatment	2	0.9761	0.1345	0.8756
	Field*Treatment	2	0.7242	2.0951	0.1695

b) Univariate analyses	Source	df	ss	*F*	*P*
Height	Field	1	3.3508	49.36	0.0001
	Error	12	0.8146		
Percent Survival	Field	1	5064.0625	15.57	0.0019
	Error	12	3131.2500		

would be greater in the open units compared to the exclosures. Alternatively, if herbivores were slowing down succession, cover of woody species would be greater in the exclosures compared to the open units. No such patterns were found in these fields after 11 and 29 years, respectively, of succession.

We expected exposure to herbivory would shift plant cover in favor of exotic species. In general, success of exotic species is greater in disturbed communities (Fox and Fox 1986) or in communities where the native species are disrupted, creating space for invasive species (Baker 1986; Burke and Grime 1996). In addition, exotic species commonly out-compete native species for resources (Bazzaz 1986; Orians 1986; D'Antonio 1993) suggesting that exotic species should rebound faster following herbivore damage. For example, damage by native herbivores was greater to a native *Lonicera* vine species than to an exotic congenor (Schierenbeck et al. 1994). Furthermore, once vines were damaged, the exotic species had a greater ability for compensatory growth (Schierenbeck et al. 1994). Results from one field in this study, however, are contrary to the expectation that herbivory causes a shift toward exotic species. In Field 1, the relative cover of exotic species was significantly greater in the exclosures where the community was protected from herbivory. No difference was found in the number of exotic species between the open units and the exclosures indicating that exotic species were able to disperse and establish into both treatments. Exposure to herbivory did not affect the relative cover of exotic species in Field 2.

Although protection from herbivory impacted the performance of exotic species as a whole in Field 1, the enhanced cover of exotics in the exclosures was specifically due to the abundance of *Daucus carota*, *Rosa multiflora*, and *Rumex acetocella*. All other exotic species differed little in cover between the two herbivore treatments. The differential response of exotic species to herbivory illustrated through our experiment and other research such as the *Lonicera* study (Schierenbeck et al. 1994) emphasizes that the ecology of individual species must be known to understand the role of exotics in communities and ecosystems. In addition, these results suggest that herbivory impacts one of the causes of succession—differential plant performance.

The effect of herbivory on plant performance is further supported by the strong influence of herbivory on the height profile of the plant community in Field 1. Plant height is one measure of performance. In the exclosures where plants were protected from herbivory they were significantly taller than plants in the open units. As argued in the statistical analyses section, species identity is irrelevant to this analysis, and the 5 tallest species were not always the same species. Frequently though the tallest species included *Solidago* spp and *Rosa multiflora*. What is relevant is that the 5 tallest species in each of the experimental units contributed greatly to the total plant cover. This alteration of the height profile may have additional implications on the ability of species to germinate and establish into the community or it may alter plant- animal interactions or the performance of other individuals present in the community.

HERBIVORY AND SEEDLING SURVIVAL AND GROWTH. The survival of planted *A. rubrum* and *C. florida* seedlings was strongly controlled by herbivores in both fields (Fig. 4, Tables 2 and 3). An earlier study conducted at HMFC concluded that herbivory was the primary control of woody seedling establishment (Myster and McCarthy 1989). Herbivory has also been shown in other systems to influence seedling establishment and growth (Howe 1991; Inouye et al. 1994). The outcome of herbivory on plant community structure and composition is dependent on herbivore selectivity and species tolerance (Augustine and McNaughton 1998). In addition, the ability of a seedling to survive following herbivore damage may depend on the herbivore causing the damage or on the ability of the seedlings to resprout (Cadenasso and Pickett 2000). Of the seedlings that survived the greater than 10 years of the experiment, those exposed to herbivory were significantly shorter than individuals of the same species in the exclosures (Fig. 5, Tables 2 and 3). Seedlings in the open units were most likely subjected to repeated damage by herbivores and, consequently, remained in a size class susceptible to browse for a longer time. When protected from herbivory, these fast growing species may be able to escape herbivory by rapidly growing to a size where they are no longer vulnerable to herbivore damage. The dramatic decrease in survival and growth of *A. rubrum* and *C. florida* seedlings when exposed to herbivory indicates that, in this system, mammalian herbivores slow growth and decrease survival of these two species. The robustness of these results is indicated by their consistency across fields despite differences in the successional age and, consequently, vegetation structure between them.

In contrast to *A. rubrum* and *C. florida*, the survival and growth of *J. virginiana* seedlings were not influenced by herbivores (Figs. 4 and 5, Table 4). *Juniperus virginiana* has been found to be unpalatable to herbivores relative to *A. rubrum* and *C. florida* (Myster and Pickett 1992; Meadows unpublished data). Evergreen trees store more of their carbon and nitrogen reserves in their leaves than deciduous trees (Bryant et al. 1991). Consequently, browsing may be more damaging to evergreens; and leaves of evergreens are generally better defended against browsing than deciduous tree leaves (Bryant et al. 1991). *Juniperus virginiana* employs both mechanical and chemical defenses against herbivores. The foliage of this species is spinescent, especially in the juvenile stage (Kozlowski 1971) which may effectively deter herbivores. The foliage also contains volatile oils which inhibit the growth rates of deer rumen microorganisms (Schwartz et al. 1980a; Meyer and Karasov 1991). In feeding trials, deer preference has been inversely linked to the concentration of volatile oil content in *Juniperus* foliage (Schwartz et al. 1980b). Feeding trials conducted in the same young field used in this experiment support these generalizations (Meadows, unpublished data). In these trials, 4 tree species were used—*J. virginiana*, *A. rubrum*, *C. florida* and *Quercus rubrum*. No *J. virginiana* seedlings were damaged and *C. florida* and *Q. rubra* were the most heavily damaged. Our results support the generalization that unpalatable species will dominate a community when herbivore pressure is great (Myster and Pickett 1992; Davidson 1993; Pastor and Cohen 1997; Augustine and McNaughton 1998). In addition, our results provide a mechanism for the common observation that *J. virginiana* is the first woody species to dominate old fields in the New Jersey Piedmont (Robichaud and Buell 1973).

The field they were planted in significantly affected survival and growth of the planted seedlings. The primary difference between the two fields was age and, consequently, structure of the vegetation. Though field age is not replicated in this experiment and cannot be confirmed as a cause of differential survival and growth, field age can be implicated. The greater survival and growth of *J. virginiana* in Field 2, the older field, may potentially be due to the already established woody saplings in this field, which ameliorated abiotic conditions or concealed the planted seedlings from large herbivores. However, the insignificant effect of exposure to herbivory and significant effect of field suggests that the survival and growth of *J. virginiana* are controlled by physiological limits rather than by herbivores.

CONCLUSIONS. Results of our long term experiment show the influence of herbivores on differential species performance, one of the causes of old field succession. Both native and exotic species responded individually. However, the influence appears to be on the architecture of the community, not on its composition or other characteristics such as percent cover. Our clear experimental results suggest herbivores greatly influence survival and growth of invading woody species. As a result, herbivores may slow succession towards woody canopy development, although this was not shown at the community level in either the newly abandoned or older field after 11 and 29 years, respectively, of succession. Successional rates and pathways may depend on the selectivity of the herbivores for particular species and the response of individual species to herbivory.

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