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Interactions after death: plant litter controls priority effects in a successional plant community

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Abstract. We performed a field experiment to test whether the presence of litter produced by the dominant species in the first successional year affects the plant community structure in the following year. We removed the litter of *Setaria faberii* (the first-year dominant) in mid-fall, early spring, mid-spring, or late spring. Both the fall and early spring removal increased the biomass of *Erigeron annuus*, which became dominant, and reduced the biomass of *S. faberii*. In the fall-removal treatment more plants of *E. annuus* flowered, while early spring removal increased the biomass of rosettes (non-flowering individuals) at the end of the growing season. In the other treatments and in the control *S. faberii* retained dominance, but its biomass was the highest in mid-spring removal plots. The removal of litter of *S. faberii* in the fall and in early spring allowed *E. annuus* to pre-empt the site and dominate the community. When litter was not removed, it strongly hindered the growth of *E. annuus*, favoring *S. faberii*. These results highlight the importance of litter as a historical factor linking interactions across successive generations, and controlling the community structure.

Key words: Community structure – *Erigeron annuus* – Old-fields – *Setaria faberii* – Interference

Several studies have shown that the relative time at which different populations occupy a site may affect the resulting community structure. The importance of the so-called priority effects has been widely studied in animal communities (e.g., Morin 1984, 1987; Alford and Wilbur 1985; Robinson and Dickerson 1987; Robinson and Edgemon 1988), and to a lesser extent in plant communities (Ross and Harper 1972 and citations therein). Pioneer studies by Sagar and Harper (1961) and Harper (1961, cited in Ross and Harper 1972) showed that even relatively small differences in the time of emergence of different annual plant populations could reverse the outcome of competitive interactions. More recently, Wilson (1988) showed that pre-emption may be important in aerial but not in underground competition. Many successional studies and models incorporate, explicitly or implicitly, pre-emption as an important mechanism affecting the shaping and dynamics of successional communities (e.g., Egler 1954; Connell and Slatyer 1977).

The mechanistic aspects of priority effects in plant communities are not well understood beyond the basic assumptions about the importance of space and/or resource pre-emption. The understanding of the mechanistic aspects of interference is required to expand our perception of how communities are structured (Tilman 1987).

Recently, experimental studies have shown that plant litter may affect the timing of germination and establishment of many plant populations (Facelli and Pickett 1991a, b). Grime (1973, 1979) highlighted the importance of litter accumulation as a mechanism of interference, and discussed its role in the establishment of dominance hierarchies in herbaceous communities (see also Al-Mufti et al. 1977). Experimental manipulations of litter demonstrated its impact on plant community structure and interspecific interactions (e.g., Sydes and Grime 1981; Monk and Gabrielson 1985; Facelli and Pickett 1991a, b; see Facelli and Pickett 1991c for a review).

Previous studies showed that the structure of 1-year-old oldfield communities of the New Jersey Piedmont were strongly influenced by the type and amount of litter (Facelli and Pickett 1991a). Carson and Peterson (1990) demonstrated that the amount of litter and the timing of the removal of litter also affected community structure in a 14-year-old oldfield, although the changes were less marked than those reported by Facelli and Pickett (1991a, b). In this site, the annual grass *Setaria faberii* becomes dominant when fields are disturbed late in spring. In some patches *S. faberii* may remain dominant

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for up to 4 years after the initial disturbance (JMF personal observation). *Setaria faberii* is a fast-growing, highly competitive species (Facelli and Pickett 1991b) that accumulates a dense litter mat. It is frequently replaced as a dominant in those oldfields by *Erigeron annuus*, an annual species that establishes in the fall and flowers in late spring (Bazzaz 1984). Since the end of the life cycle of *E. annuus* overlaps with the beginning of the cycle of *S. faberii*, priority effects may potentially be important in shaping their interaction in the second successional year. Successful establishment of *E. annuus* may create a dense canopy in spring thwarting the establishment of *S. faberii*. Conversely, the accumulation of a thick litter mat by *S. faberii* may prevent the establishment of *E. annuus* in the fall (cf. Facelli and Pickett 1991b).

We report here the results of a field experiment performed in a 1-year-old oldfield, in which we removed the litter of *S. faberii* at different times of the year to assess the effect of litter on community structure.

Methods

A field experiment was carried out at the William L. Hutcheson Memorial Forest Center, East Millstone, New Jersey, USA (40° 30'N, 74° 34'W). Information on successional patterns in the area can be found in Bard (1952), Pickett (1982), Myster and Pickett (1988), and citations therein. The climate is subcontinental, with 1120 mm of precipitation distributed fairly evenly throughout the year. Mean annual temperature is 17.3° C, with monthly temperature ranging from 0.0° C in January, to 24° C in July (Unites States Weather Bureau 1959). Soils are well drained silty loams corresponding to the Penn Silt Loam series (USDA 1976).

The experiment was conducted in a portion of an oldfield that had been under cultivation until 1985. The experimental site was later disked and left fallow in May 1988 and May 1989. After each of those disturbances the community was dominated by *S. faberii*, with *S. glauca*, *Panicum dichotomiflorum*, *Solanum carolinense*, and *Physalis subglabrata* as subdominants (see Facelli and Pickett 1991a). In September 1989 we established the experimental plots in a portion of the area covered by a seemingly homogeneous mat of litter of *S. faberii*. The experiment was a complete block design, with each treatment replicated once in each of six blocks. Each plot was a 0.5-m square, surrounded by 1-m-wide buffer strips. All subsequent measurements were made in the central 30 × 30 cm area. The treatments consisted of the removal of litter at different times of the year: fall removal on 16 October 1989; early spring removal on 19 March 1990; mid-spring removal on 25 April 1990, and late spring removal on 1 June 1990. Each block included a control plot where litter remained undisturbed. The litter was removed with extreme care, avoiding damaging established plants. We immediately returned all the seeds contained in the litter mat to the original plot. This was especially important in the fall removal, when many seeds of *S. faberii* were still attached to the dead plants. The litter was brought to the laboratory, dried at 85° C for 48 h, and weighed. This allowed measurement of the persistence of litter throughout the experiment using blocks as replicates. The litter in the 1-m buffer strips surrounding the plots was left undisturbed.

On several clear days we measured soil temperature at noon (Standard Time) in the upper 5 cm in all plots, using Reotemp soil thermometers, to assess the effect of litter removal on soil temperature. Early in the experiment (1 day after fall removal) we measured soil temperature every 5 cm along transects crossing the center of the plots from which litter had been removed, and 0.5 m across the buffer strips surrounding the plots. The data showed that measuring soil temperature at the center of the plot gave a good characterization of the effect of litter removal.

On 20 April, 4 May, and 25 May, we measured plant cover. We placed a 30 × 30 cm removable frame with a grid of wires spaced every 3 cm. We recorded the identity of the species beneath each of the 100 intersections. We also counted the interceptions on litter and on bare ground, and checked the entire plots for species not censused by the 100 points. Later in the season, this cover measurement became impractical, and probably inappropriate, because of the height and complexity of the canopy.

We counted the number of flowering rosettes of *E. annuus* and other dicotyledons per plot, on 9 August, coinciding with the peak flowering of *E. annuus*. Because flowering rosettes began to senesce shortly afterwards, this variable may be a better estimator of the performance of *E. annuus* than the biomass sampling on 15 September. On that day we harvested all aerial biomass of the plants in all plots, by clipping the material at ground level, and collected the litter remaining in the control plots. The material was brought to the lab, sorted by species, dried at 85° C for 48 h and weighed to the nearest milligram. Biomass values were used to calculate Shannon and Wiener's diversity index (H').

Statistical analyses

Soil temperature, cover, and species richness were analyzed by multivariate repeated-measure ANOVA. When treatment effects were significant ($P \leq 0.01$) we calculated SNK pairwise comparisons ($P \leq 0.05$ after Bonferroni correction by number of comparisons) for each date. The values of cover and species richness were arc sine transformed to increase normality. Number of flowering ro-

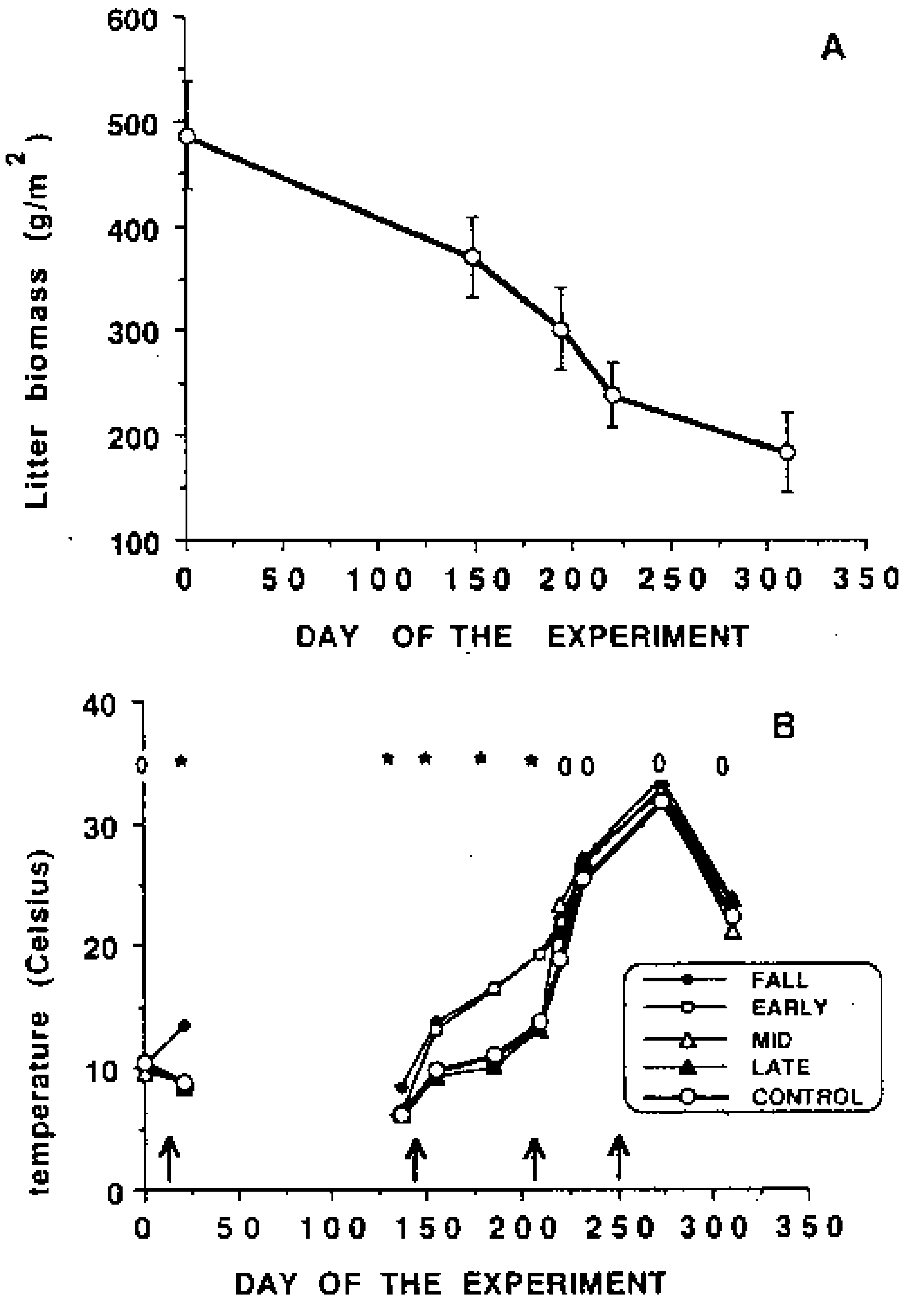

Fig. 1. **A** Amount of litter (mean of six plots, ±1 SD) present in the plots where litter was removed at each date. The last value corresponds to the control plots at the time of the harvest. **B** Soil temperature in plots with litter removed on 16 October (fall), 19 March (early), 25 April (mid), and on 1 June (late), and plot with the litter mat left undisturbed (control). Measurement were not taken during the winter. Stars mark the dates when soil temperature in plots without litter was higher than in those with litter (repeated measures ANOVA, $P < 0.01$). Zeros indicate non significant differences

settes (after arc sine transformation) and species diversity were analyzed by one-way ANOVAs. Biomass data were analyzed by MANOVA (after log transformation) to test for changes in community structure. Since this analysis showed a significant treatment effect on community structure, we performed ANOVAs for each species found in more than 14 plots. For those showing significant treatment effect we calculated SNK pairwise comparisons. All tests were performed using SAS (1986).

Results

The amount of litter collected from the plots at each date decreased throughout the growing season (Fig. 1A), more rapidly in mid-spring. This is usually the period of most rapid litter disappearance because of warm temperatures and high humidity. At all dates up to late spring litter removal increased the soil temperature over the control (Fig. 1B). The effect of the removal on soil temperature was less important as the growing season progressed and the denser canopy (Table 1) intercepted more of the incoming radiation.

The number of species increased consistently throughout the growing season, especially when litter was removed in the fall (Fig. 2A). The removal of litter in the fall and early and mid-spring increased the number of species per plot at the end of the experiment compared to the control and the late-removal treatment ($P<0.01$, Fig. 2A). Species diversity was increased by litter removal, and more so by fall and early spring removal ($P<0.01$, Fig. 2B).

On all three dates that we measured cover (Table 1), the treatments from which litter had been removed had higher total cover of all species (ANOVA, $P<0.01$), with the exception of *Setaria faberii*. The cover of *E. annuus* was always higher in fall and early spring removal (Table 1). Significant differences in the cover of *S. faberii* were first observed on 4 May, when the mid-spring removal treatment had the highest cover. On 25 May, the mid-spring removal treatment still had the highest cover of *S. faberii*, but the late removal and control treatments then had higher cover than the fall and early removal treatments (Table 1).

Fall litter removal increased the number of flowering rosettes of *E. annuus*, while mid-spring removal reduced it (Fig. 3). Early spring removal increased the combined number of flowering rosettes of other dicotyledons: *Erigeron canadensis*, *Oenothera biennis*, and *Aster* spp.

Mid-spring litter removal increased total biomass, and fall removal reduced it ($P<0.01$), though it increased the mass of standing dead material, mostly composed of dead flowering stalks of *E. annuus* (Table 2). The MANOVA showed that the treatments had a significant effect on community structure (Wilk's lambda ap-

Table 1. Cover of dominant species, litter and bare ground on 20 April, 4 May, and 25 May

Species	Treatments				
	Fall	Early	Mid	Late	Control
20 April					
Erigeron annuus	21.8 A	12.2 A	1.8 B	3.2 B	3.8 B
Setaria faberii	0.2	0.3	0.1	0.6	0.1
Allium tricocum	6.3 A	7.7 A	4.3 A	2.5 A	3.3 A
Oenothera biennis	3.3	2.6	1.2	2.4	3.4
Other species	8.7 A	10.0 A	3.5 AB	1.9 B	4.1 AB
Litter	2.0 B	3.5 B	79.8 A	72.2 A	77.8 A
Bare ground	57.7 A	63.8 A	9.3 B	17.2 B	7.5 B
4 May					
Erigeron annuus	40.5 A	30.2 A	3.8 B	9.5 B	8.6 B
Setaria faberii	1.1 B	2.2 B	20.1 A	2.1 B	1.1 B
Allium tricocum	7.8 A	12.8 A	5.2 A	4.3 A	4.8 A
Aster spp.	0.5	3.1	1.1	1.0	0.2
Oenothera biennis	6.9	5.2	10.1	8.6	11.2
Other species	4.4 A	0.3 A	2.3 A	5.4 A	2.3 A
Litter	0.9 B	3.4 B	2.2 A	65.5 A	68.4 A
Bare ground	37.9 A	42.8 A	55.2 A	3.6 B	3.4 B
25 May					
Erigeron annuus	69.0 A	56.0 A	10.3 B	12.1 B	14.1 B
Setaria faberii	8.6 C	8.6 C	50.0 A	29.3 B	23.3 B
Allium tricocum	2.6	1.2	2.8	3.8	1.4
Aster spp.	1.7	2.6	2.1	2.3	3.2
Oenothera biennis	2.1	9.0	2.2	5.2	3.2
Other species	0.8 A	5.4 A	1.8 A	2.6 A	3.9 A
Litter	0.2 B	0.5 B	1.7 B	43.1 A	49.7 A
Bare ground	15.0 B	18.7 B	29.2 A	1.6 C	1.2 C

Same letter for a species within each date means that differences were not significant (ANOVA and SNK, $P>0.05$). Letters are not given for species for which cover was not analyzed (because of large number of zero values)

Table 2. Total biomass (g/m²) and biomass by species at the end of the experiment

Species	Fall	Early	Mid	Late	Control
Erigeron annuus					
Standing dead	191.32 A	27.46 B	14.44 B	26.47 B	25.40 B
Live rosettes	83.71 B	115.02 A	12.93 B	7.11 B	11.93 B
Setaria faberii	100.82 C	83.74 C	313.51 A	245.16 B	234.02 B
Aster spp.	25.40 B	65.58 A	8.93 B	5.29 B	9.93 B
Oenonthera biennis	36.20 A	38.44 A	10.23 A	10.24 A	10.25 A
Physalis subglabrata	2.29 B	1.71 B	24.25 A	2.21 B	2.56 B
Other species	22.25 A	27.20 A	30.82 A	13.76 A	20.15 A
Total biomass	276.98 C	331.69 B	400.27 A	283.95 BC	288.87 BC

The overall community structures were significantly different (Wilk's lambda approximation, $F=2.88$, $P<0.01$). Same letter for a species within each date means that differences were not significant (ANOVA and SNK, $P>0.01$)

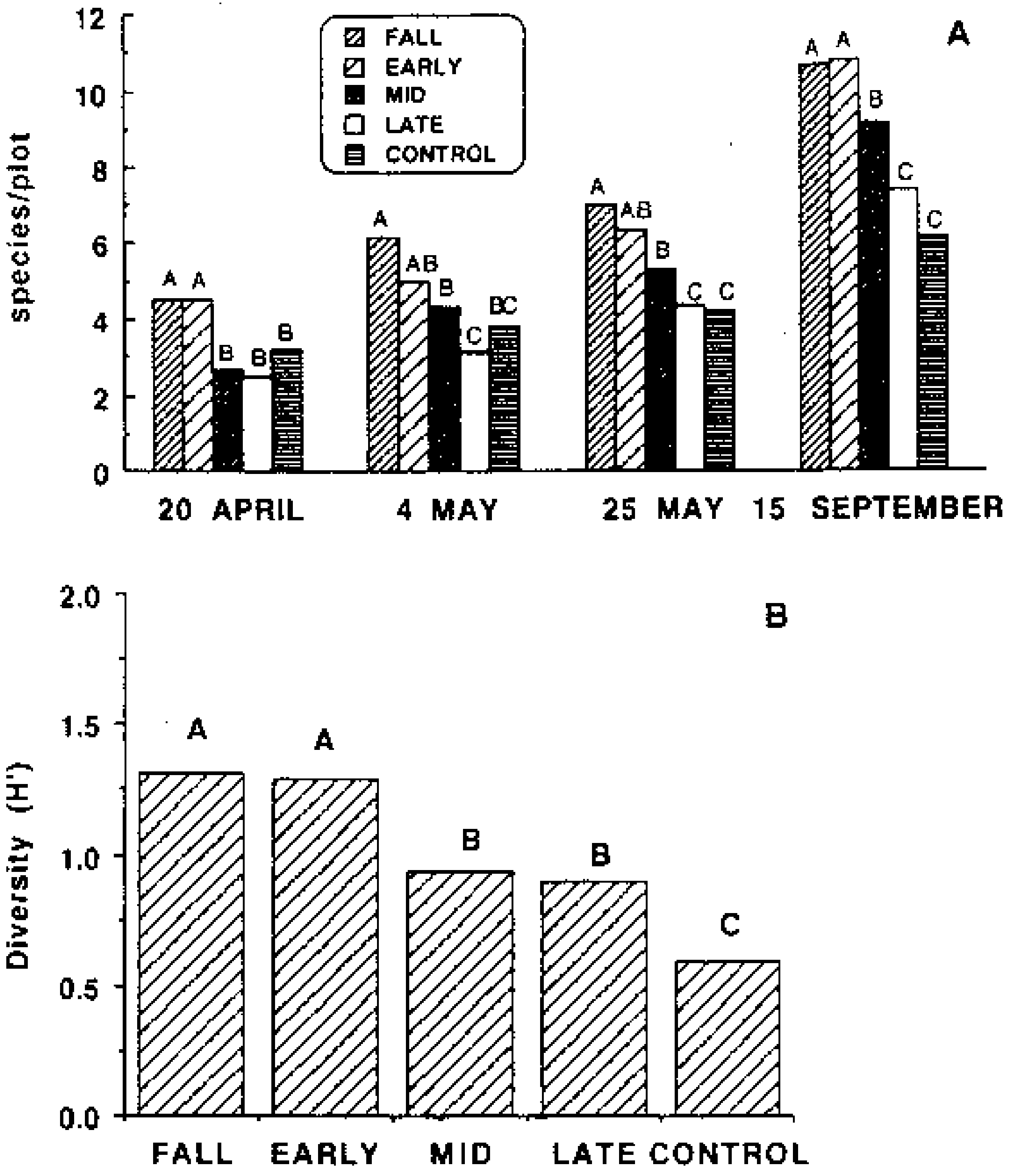

Fig. 2. A Number of species in plots with litter removed on 16 October (fall), 19 March (early), 25 April (mid), and on 1 June (late), and plots with the litter left undisturbed (control). Same letter within the same date indicates that the number of species was not significantly different (repeated measures ANOVA, $P>0.05$). **B** Species diversity calculated by Shannon and Wiener's index using species biomass harvested on 15 September. Same letter indicates that diversity was not significantly different (ANOVA, $P>0.01$)

proximation, $F=2.88$, $P<0.01$). The corresponding ANOVAs showed that the treatments significantly affected the biomass of *E. annuus*, *S. faberii*, *Physalis subglabrata* and *Aster* spp. ($P<0.01$). Pairwise comparisons showed that fall and early spring removal increased the biomass of *E. annuus* and reduced that of *S. faberii* (SNK, $P<0.01$). Early spring removal also increased the biomass of *Aster* spp. Mid-spring removal increased the biomass of *S. faberii* over the late removal and control treatments. The biomass of *P. subglabrata* was also higher in the mid-spring removal plots. There was no significant difference between late removal and control treatments.

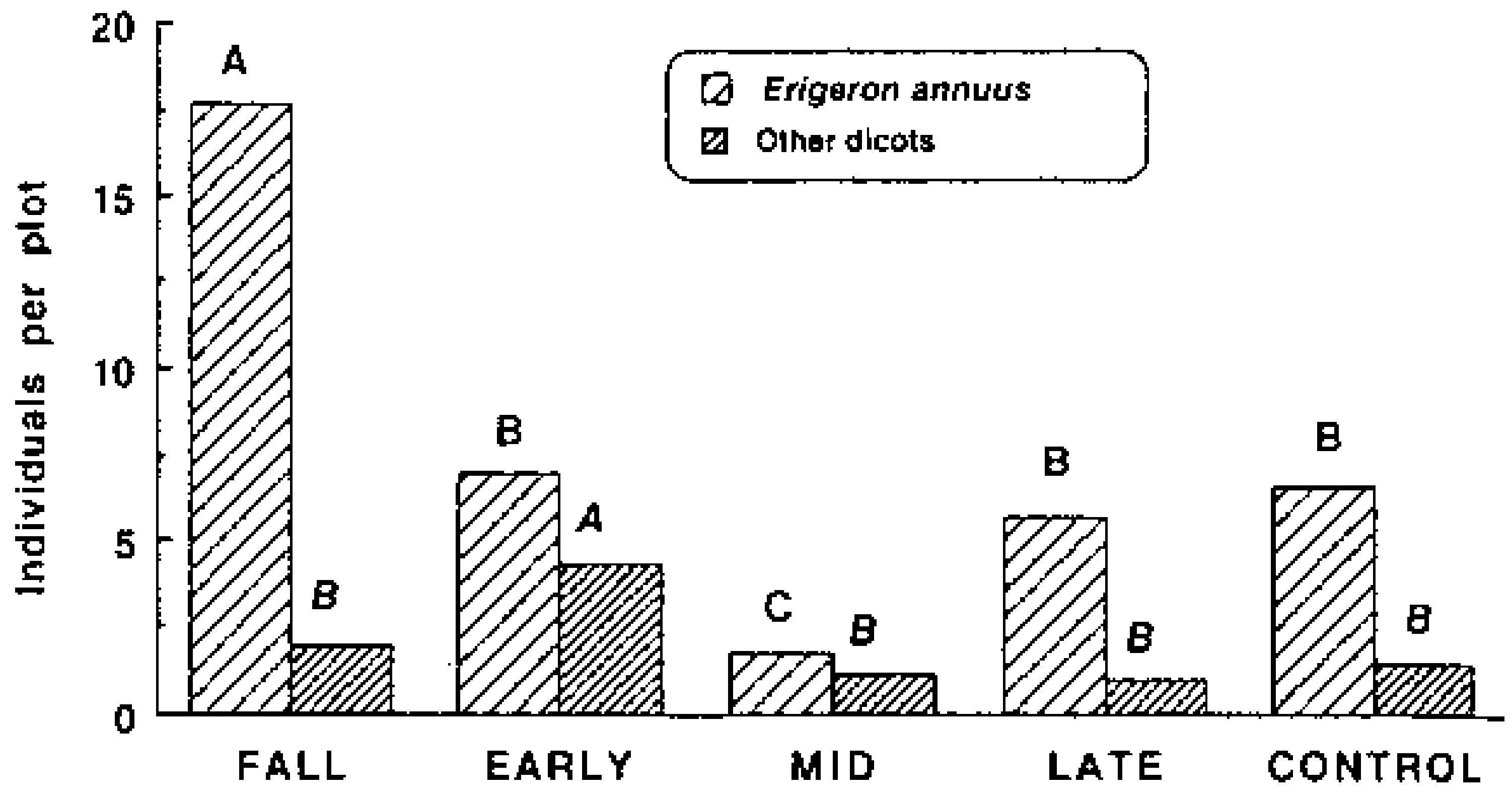

Fig. 3. Number of flowering individuals of *Erigeron annuus* and other dicotyledons (*E. canadensis*, *Oenothera biennis*, and *Aster* spp.) in plots with litter removed on 16 October (fall), 19 March (early), 25 April (mid), and on 1 June (late), and plot with the litter mat left undisturbed (control). Same letter indicates that number of flowering individuals was not significantly different (SNK, $P>0.05$) within each class

Discussion

Our results confirmed previously published results that litter exerts an important effect on successional plant communities (Monk and Gabrielson 1985; Carson and Peterson 1990; Facelli and Pickett 1991a). Furthermore, we showed that timing of removal of litter may produce a complete shift in structure, affecting the identity of the dominant as well as species richness and diversity. The mechanisms involved may be the change of environmental conditions produced by litter that alter the establishment patterns (Facelli and Pickett 1991c).

When litter was removed in the fall, *E. annuus* established better and more individuals flowered in the following spring, probably because higher soil temperatures and light availability allowed them to grow during the winter and very early spring, thus reaching the reproductive stage (Bazzaz 1984). Seedlings of *E. annuus* are able to photosynthesize even at very low temperatures in the winter (Bazzaz 1984). Because the rosettes lie close to the ground, the increased soil temperatures and higher light availability produced by litter removal probably favored the growth of those seedlings. Early spring removal also benefited *E. annuus*, but did not increase the number of flowering individuals, probably because they did not reach minimum reproductive sizes. This suggests that photosynthesis during winter is an important ecological feature in this species, with important effects on individual fitness (Bazzaz 1984). The biomass of *E. annuus* at the end of the growing season was higher in the early spring removal treatment than in the fall removal treatment because of the death of flowering rosettes in the latter. Rosettes that have not flowered can persist during the winter and flower in the following spring (Bazzaz 1984). We did not find any evidence that the litter of *S. faberii* facilitated the establishment of *E. annuus*, as found in a previous study (Facelli and Pickett 1991a). One possible reason is that we started our manipulations in mid-fall, while the facilitation recorded in the previous study was observed early in the fall. Furthermore, Facelli and Pickett (1991a) found increased numbers of very small seedlings of *E. annuus*, but did not follow their fate. The results reported here agree with most others in mesic habitats, where litter usually reduces establishment (Facelli and Pickett 1991a).

Lower cover and biomass of *S. faberii* in the fall and early spring removal was probably due to the improved establishment of *E. annuus* hindering the establishment of the grass by preempting resources. The other possible explanation, that the removal of litter *per se* had a negative effect on *S. faberii*, is unlikely, because litter removal in mid-spring favored its establishment over the control. This result seems to be consistent with previous results, suggesting that litter may have positive indirect effects, even though it may simultaneously exert a negative direct effect (Facelli and Pickett 1991b).

Our results support the idea that litter accumulation may allow some annual species to retain dominance, as proposed by Grime (1979). The mechanism cannot be elucidated here. Release of phytotoxic compounds from decomposing litter, physical obstruction, light interception, or changes in soil temperature may be alternative, although not mutually exclusive, explanations (Grime 1979; Thompson et al. 1977; Facelli and Pickett 1991a, c). Soil temperature is an important factor regulating the establishment of both species (Bazzaz 1984; Baskin and Baskin 1988), and our measurements of soil temperature are compatible with the hypothesis that at least part of the effect of litter on community structure is mediated through its effect on soil temperature.

It is noteworthy that in a previous study (Carson and Peterson 1990) litter removal at different seasons produced only slight changes in community structure and none of the removal produced any shift in the identity of the dominant. The different responses are likely to be due to the initial conditions: the site studied by Carson and Peterson (1990) was dominated by *Solidago* spp., which have a clonal habit that allows sprouting early in the season in spite of the dense litter accumulation. Also, the negative effect of litter of *Solidago* is less strong than that of *S. faberii* (Facelli and Pickett 1991a).

Previous studies (Ross and Harper 1972, and citations therein) showed priority effects in plant communities due to different emergence times. Usually the species that establishes earlier obtains an advantage over later ones, because of resource pre emption (Harper 1977). In our case, litter accumulated in the previous growing season hampers the emergence of the earlier species, and allows the later one to retain dominance. If *S. faberii* establishment or growth is hindered for any reason, or if the litter mat is disturbed, *E. annuus* establishment in the fall would be enhanced, further hindering the re-establishment of *S. faberii* in the next year. The importance of inter-generation interference has already been pointed out by Bergelson (1990), although she studied generations occurring in the same growing season. Here we demonstrate that inter-generation interference may be carried over from one season to the next. This reaffirms the role of litter as a historical factor in the organization of plant communities and stresses the importance of introducing the corresponding temporal component to the study of ecological interactions.

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