Plant Litter: Light Interception and Effects on an Old-Field Plant Community

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PLANT LITTER: LIGHT INTERCEPTION AND EFFECTS ON AN OLD-FIELD PLANT COMMUNITY[1]

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Abstract. We studied the effects of litter of the annual grass *Setaria faberii*, the perennial herb *Solidago* spp. (mostly *S. canadensis*), and leaves of the hardwood tree *Quercus alba* on a successional plant community. We also assessed light interception by these litter types in the laboratory. Light extinction followed the Beer-Lambert exponential law. *Solidago* litter had the highest transmittance constant and *Quercus* litter the lowest. The three types of litter produced different light mosaics at the microsite (0.8 cm diameter) scale. In the field, all three litter types affected community structure, but the effect of *Quercus* was the strongest. Litter reduced the density of the two dominant grasses, *Setaria faberii* and *Panicum dichotomiflorum*. *Quercus* and *Setaria* litter resulted in biomass compensation (i.e., fewer but larger individuals) by *S. faberii* but not by *P. dichotomiflorum*, which probably was always outcompeted by *S. faberii*. *Solanum carolinense*, the main dicot in the community, was unaffected by litter addition. *Setaria* and *Solidago* litter enhanced the establishment of *Erigeron annuus*, but *Quercus* litter reduced it. Litter reduced the number of flowering individuals of *S. faberii* and the number of seeds per plot; *Quercus* litter increased the production of seeds per individual. We conclude that species-dependent effects of litter on plant populations may significantly alter interspecific interactions and change plant community structure through direct and indirect effects.

Key words: community structure; Erigeron annuus; *establishment; light interception; microsites;* Panicum dichotomiflorum; *patches; reproductive output;* Setaria faberii; Solanum carolinense.

INTRODUCTION

Litter accumulation during succession has been traditionally considered an ecosystem process with significant impact on carbon (Odum 1960, Golley 1965, Mellinger and McNaughton 1975) and nutrient cycles (Stinner et al. 1984, Holland and Coleman 1987). In addition to being the substrate for the detritus food web and a nutrient reservoir, litter deeply alters the microenvironment and may affect the structure and dynamics of plant communities. Litter accumulation may be considered as part of the successional "reaction" (Clements 1916, cf. Roberts 1987), i.e., environmental changes produced by the action of the colonizing organisms.

While several studies have examined population level effects of litter (e.g., Schlatterer and Tinsdale 1969, Werner 1975, Hamrick and Lee 1987), few have focused on the effects of litter on the structure of successional communities (but see Monk and Gabrielson 1985, Carson and Peterson 1990). Several studies have examined the phytotoxic effects of litter (Grime 1979, see Rice 1979 for a review). No attempts have been made to link physical properties of different litter types with their effects on plant communities.

Litter accumulation during succession is spatially heterogeneous because of vegetation heterogeneity, redistribution of litter, and uneven decomposition (Shure and Phillips 1987, Facelli and Carson, *in press*, Facelli and Pickett 1991). Heterogeneous distribution of litter may result in patchy microenvironmental conditions (reviewed by Facelli and Pickett 1991). Litter reduces light at the soil surface (Weaver and Rowland 1952, Knapp and Seastedt 1986), alters soil temperature (Watt 1970, Beatty and Sholes 1988), and affects soil water and nutrient dynamics (Fowler 1986, Knapp and Seastedt 1986). Those environmental changes may differentially affect germination and establishment of several different species within a plant community (Thompson et al. 1977, Grime 1979, Goldberg and Werner 1983, Hamrick and Lee 1987). Litter, together with standing vegetation, defines the presence of gaps available for colonization (Goldberg and Werner 1983, Silvertown and Smith 1989, Bergelson 1990).

Here we report results of two studies: an experiment testing the effects of three types of litter on an early old-field community, and a laboratory study examining light interception by these litter types. The field experiment addressed two main questions: (1) How do

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the different types of litter affect density and biomass of the dominant plant populations? (2) How do the different types of litter affect reproductive output of the dominant plant species? The laboratory study addressed two questions: (1) How does light interception change with the type and amount of litter? (2) How do the type and amount of litter affect the distribution of light microsites at the ground level? Our goal was to assess the effects of different types of litter in a successional plant community, and to analyze how light interception properties of the litter related to these community-level impacts.

MATERIALS AND METHODS

Litter collection

In both studies we used litter of three species: the annual grass *Setaria faberii*, the perennial herb *Solidago* spp. (mainly *S. canadensis*), and the hardwood tree *Quercus alba*. Generic names (*Setaria, Solidago,* and *Quercus*) will be used henceforth to identify litter types. *Setaria faberii* and *Solidago* spp. dominate very young and midaged old fields, respectively, in the New Jersey Piedmont. They accumulate dense litter mats, ranging from 200 to 600 g/m². *Quercus* leaves are deposited by wind into the old fields, and form patches reaching 200 g/m² (Facelli and Carson, *in press*). We collected *Setaria* litter from a 1-yr old field, *Solidago* litter from a 15-yr old field, and *Quercus* litter from an old-growth forest. All sites were adjacent to the field where the experiment was conducted. All the litter was collected in mid-April, the time when most species are germinating or sprouting. *Setaria* litter was a mixture of stems and blades. The litter of *Solidago* consisted of stems (0.5–1 m long), the only material that persists into the spring. For *Quercus* litter we collected entire leaves without signs of advanced decomposition. The litter was air-dried, weighed, and bagged to prepare samples to be used in both studies.

Laboratory study of light extinction

For each type of litter we used seven amounts representative of the range of biomass found for each litter type in old fields at the field site (Facelli and Carson, *in press*). The amounts were 10, 25, 50, 75, 100, 125, and 150 g/m² of *Quercus* litter; 25, 50, 100, 150, 200, 300, and 400 g/m² of *Setaria* litter; and 50, 100, 150, 200, 300, 400, and 600 g/m² of *Solidago* litter. We used 10 samples of each amount for each litter type. Each sample was dropped from 50 cm onto the central 40 × 40 cm portion of a 1 × 1 m plexiglass sheet, to simulate the natural structure of the litter mat in the field. The only light source in the laboratory was a 3000 W day-light reflector bulb placed 1 m above the plexiglass. We used a LI-COR LI 185B photo-radiometer (LI-COR, P.O. Box 4425, Lincoln, Nebraska) to measure the transmitted radiation (photon flux) with a rubber eye cup attached to the sensor to minimize the effect of diffuse radiation. Measurements were taken at nine equidistant points (5-cm spacing) previously marked in a 100-cm² square in the center of the plexiglass frame. The percent Relative Illumination (RI) for each point was calculated as: 100 × (radiation transmitted by the plexiglass with litter)/(radiation transmitted by the plexiglass).

We defined two scales of heterogeneity: the "patch" and the "microsite" level. For the patch level we considered the mean RI of the nine points beneath each litter sample as the experimental unit ($N = 10$ for each litter type and amount). We used the least square regression method (Model I) to fit the data to the equation of the Beer-Lambert exponential extinction law (cf. Fitter and Hay 1987):

$$\mathrm{RI} = 100e^{bM}$$

where M is the amount of litter (in grams per square metre), and b the transmittance constant of the litter. We tested the null hypothesis that there were no differences among the transmittance coefficients (b) of the three kinds of litter by testing for homogeneity of all three possible pairs of slopes, and evaluated the fitness of the model by the determination coefficients (r^2) of each equation (Sokal and Rohlf 1981). At the "microsite" level we considered the individual point sampled by the 0.8 cm diameter sensor as the sample unit. We used the 90 measurements (9 points × 10 samples) taken for each type and amount of litter to construct the frequency distribution of RIs. We tested for homogeneity of the frequency distributions using the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). To reduce the number of pairwise comparisons, we only tested for differences across litter types at the amounts of each type of litter that produced patches with RI ≈ 30 and 60%.

Field experiment on litter effects

The study was carried out at the William L. Hutcheson Memorial Forest Center (HMF), East Millstone, New Jersey, USA (40°30′ N, 74°34′ W). The climate is subcontinental, with 1120 mm of precipitation evenly distributed throughout the year. Mean monthly temperatures range from 0.0°C in January to 24° in July (United States Weather Bureau 1959). The soil is a well-drained silty loam, derived from the Triassic red shales of the Brunswick Formation and corresponds to the Penn Silt Loam series (USDA 1976).

The experimental site was cultivated until 1985, when it was left fallow. On 9 June 1987 we cleared the vegetation and rototilled the soil to 5 cm depth. The experiment was conducted as a complete block design, with each treatment replicated in one 60 × 40 cm plot in each of 20 blocks. The four treatments were: (a) no litter added, henceforth Control, (b) 100 g/m² of *Quercus* litter added, (c) 400 g/m² of *Solidago* litter added, and (d) 400 g/m² of *Setaria* litter added.

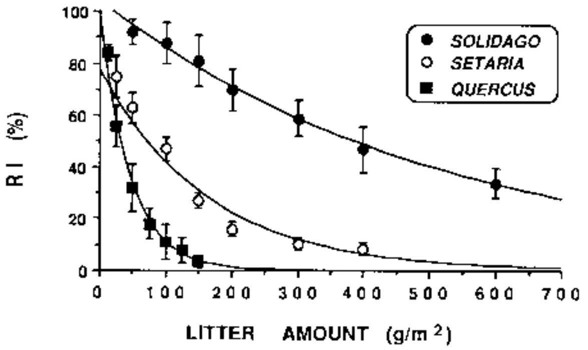

FIG. 1. Light extinction curves for layers with different amounts of litter of *Quercus* ($b = -0.0237$; $r^2 = 0.866$, $P < .01$); *Setaria* ($b = -0.0059$; $r^2 = 0.919$, $P < .01$); and *Solidago* ($b = -0.0018$; $r^2 = 0.962$, $P < .01$). All three transmittance coefficients (b) were significantly different from each other ($P < .01$). Each symbol represents $\bar{X} \pm 1$ SD Relative Illumination (RI) of 10 samples.

The amounts selected for each litter type represent the values commonly found in old fields at HMF (Facelli and Carson, *in press*). The litter was homogeneously distributed on the plots, and a cage (3 cm high) of galvanized wire (5-cm mesh) was placed on each plot, including controls, to prevent wind from removing the litter. Data were taken from the central 40 × 20 cm area of each plot to reduce border effects. Between plots, 50 cm wide corridors were maintained clear of vegetation.

On 6 July, 22 July, and 11 August we visually estimated plant cover, approximating to the nearest 5%. Top soil temperatures just before sunrise (0530) and at early afternoon (1330) were also measured, with dial-head thermometers inserted to 5 cm depth at the center of each plot. On 6 July we counted the independently rooted stems (considered to be individuals) of each species in all plots. We harvested 10 randomly selected blocks on 11 August and the other 10 on 5 October. We clipped the plants at the soil surface and counted the stems of each species. The material was oven-dried for 48 h at 85° and weighed. On both dates we also collected, dried, and weighed the litter remaining on the plots.

Differences in plant community structure were tested by multivariate analyses of variance (MANOVAs), using the PROC GLM in Statistical Analysis System (SAS 1986). The independent variables were either density or biomass of the four species present in at least 75% of the plots (*Setaria faberii, Panicum dichotomiflorum, Solanum carolinense,* and *Erigeron annuus*). We transformed density data as $(\text{individuals} + 1)^{1/2}$, and biomass data as $\log_{10}(\text{biomass} + 1)$ to enhance their normality. When MANOVA rejected the null hypothesis of no difference in community structure ($P \leq .01$), we performed separate analyses of variance (ANOVAs) for each of the four species. Least significant difference (LSD, $P \leq .01$) pairwise comparisons were calculated only when ANOVA declared the effect of treatments significant ($P \leq .01$). The significance level for all tests was set at a conservative level because we performed some nonindependent comparisons.

On 5 October we measured reproductive output of the dominant species (*Setaria faberii*). We counted the number of flowering individuals and weighed the seeds produced per plant. We used mean seed mass, calculated over 10 samples of 100 seeds taken from the total pool of seeds (from all plots), to estimate the mean number of seeds per plot and per plant. A preliminary analysis showed that neither litter treatment nor individual variation within treatment affected seed mass (nested ANOVA; $P = .24$ and $P = .49$, respectively).

RESULTS

Light extinction characteristics of litter

Light transmittance by the three types of litter fitted well the Beer-Lambert model (Fig. 1). The three litter types had significantly different transmittance coefficients (b) (Fig. 1). *Quercus* litter had the lowest transmittance, and that of *Solidago* the highest.

When present at amounts producing the same RI at the patch level, the three types of litter created different mosaics of light microenvironment (Fig. 2). Patches

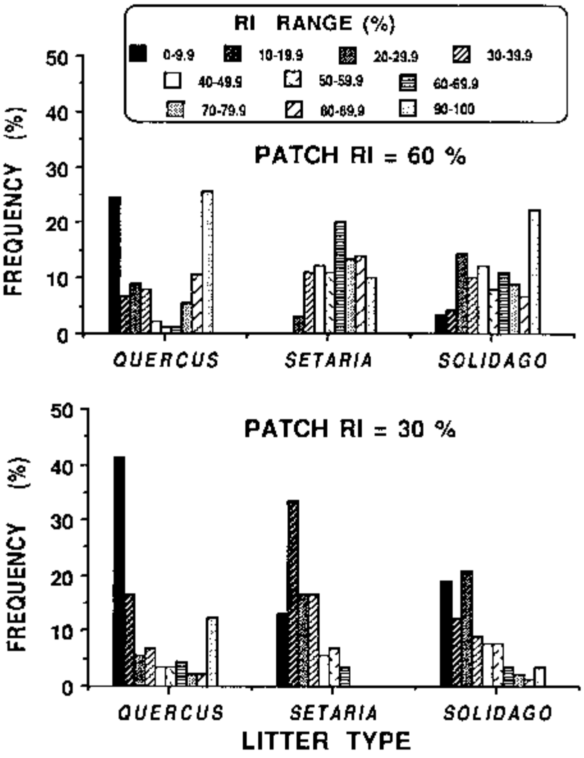

FIG. 2. Frequencies of Relative Illumination (RI) at microsites in light mosaics created by mats of litter of *Solidago, Setaria,* and *Quercus* reducing the light intensity to ≈60 and 30% of the incident radiation in 40 × 40 cm patches. The three types of litter created different frequency distributions of RI (Kolmogorov-Smirnov test, $P < .01$) at both levels of patch RI.

TABLE 1. Soil temperature (in degrees Celsius) just before sunrise and in the early afternoon on 6 July, 22 July, and 11 August in plots with litter of *Solidago, Setaria,* and *Quercus.* Same letter in each column indicates that differences are not significant (ANOVA/LSD, $P > .01$).

	6 July		22 July		11 August	
	Sunrise	Noon	Sunrise	Noon	Sunrise	Noon
Control	18.8 A	33.3 A	20.2 A	39.7 A	18.7 A	29.8 A
Solidago	20.4 A	31.4 AB	19.3 A	38.4 A	21.0 A	30.2 A
Setaria	19.6 A	28.7 BC	21.8 A	35.6 B	19.5 A	31.5 A
Quercus	20.5 A	25.6 C	20.2 A	32.1 C	22.1 A	28.9 A

with 25 g/m^2 of *Quercus* litter, 50 g/m^2 of *Setaria* litter, or 300 g/m^2 of *Solidago* litter reduced the radiation to ≈60% of incident radiation (Fig. 1), but they formed different light mosaics (Fig. 2). A similar outcome was yielded by litter mats that produced patches with RI = 30% (Fig. 2). *Quercus* litter created mosaics with a high proportion of both high and low RI microsites, and low frequencies of intermediate RI sites (Fig. 2). In contrast, litter of *Setaria* or *Solidago* formed rather unimodal mosaics, with larger proportions of sites with intermediate RIs.

Effects of litter on plant community structure

All three types of litter had relatively high persistence. Mass losses by 11 August and 5 October were, respectively, 33 and 46% for *Setaria* litter, 17 and 32% for *Quercus* litter, and 16 and 22% for *Solidago* litter. Soil temperature at sunrise was not affected by litter on any of the three dates, but *Quercus* and *Setaria* litter reduced soil temperature at noon on the first two dates (Table 1). The lack of treatment effect on 11 August suggests that at that time light interception by the canopy had become more important than interception by litter (see Table 2). The plant community in the plots was very simple, with only four species (*Setaria faberii, Panicum dichotomiflorum, Solanum carolinense,* and *Erigeron annuus*) consistently present in most plots. Those four species combined accounted for 85–95% of the total number of plants and 83–99% of the total biomass in all treatments. In all, only 15 species were recorded, and plots typically contained fewer than five species (Table 2). *Setaria* was the dominant, and *Panicum* and *Solanum* the subdominants, in all treatments. *Erigeron* reached high densities but scarcely contributed to the community biomass. *Setaria, Panicum,* and *Erigeron* established exclusively by germination. Almost all *Solanum* shoots originated from sprouting underground organs.

Litter significantly reduced total plant cover (Table 2). The strongest effect was exerted by *Quercus* litter, and the least by *Solidago* litter (Table 2). The hypotheses of no effect of litter on density and biomass were rejected by MANOVA for all three dates (Table 3). Total plant density was always lower in the litter treatments (Fig. 3). The strongest effect was produced by *Quercus* litter and the weakest by *Solidago* litter; however, differences between the effects of *Solidago* and *Setaria* litter at 6 July and 11 August were not significant (Fig. 3). Total plant biomass was significantly reduced by all three types of litter, most strongly by *Quercus* (Fig. 3).

The density of *Setaria,* the dominant species, was reduced by litter addition, but there was no significant difference between the effect of *Solidago* and *Setaria* litter at any time (Fig. 4). Litter also reduced the density of *Panicum,* the species with the second highest density in the control plots (Fig. 4). Although the effect of the three litter types on *Panicum* did not differ significantly

TABLE 2. Mean total cover, mean number of species per plot (±SD) and number of species in all plots on 6 July, 22 July, and 11 August. For total cover, same letter indicates that differences between treatments are not significant (ANOVA/LSD, $P > .01$).

	Treatment			
	Control	*Solidago* litter	*Setaria* litter	*Quercus* litter
		6 July		
Total cover (%)	12.0 A	9.5 A	4.7 B	3.0 B
Species/plot	4.4 ± 1.3	3.5 ± 1.2	3.2 ± 1.4	2.8 ± 1.1
Species in all plots	13	7	11	8
		22 July		
Total cover (%)	61.3 A	37.8 B	32.0 B	21.2 C
Species/plot	4.5 ± 1.1	4.4 ± 1.0	4.2 ± 0.9	2.5 ± 1.3
Species in all plots	13	8	9	10
		11 August		
Total cover (%)	77.3 A	59.1 B	41.4 BC	37.1 C
Species/plot	3.8 ± 1.3	3.7 ± 1.6	3.5 ± 1.3	3.1 ± 1.3
Species in all plots	12	9	11	8

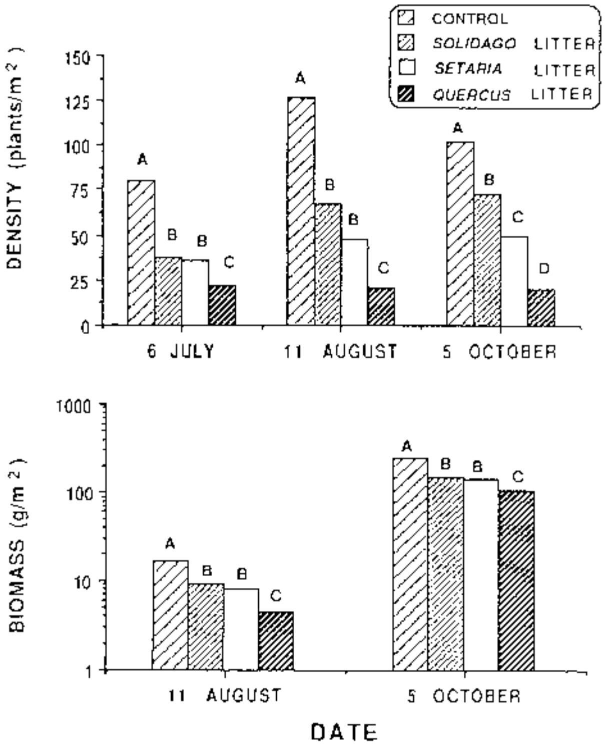

FIG. 3. Total plant density on 6 July, 11 August, and 5 October (above), and total biomass on 11 August and 5 October (below), in plots without litter (Control), and with litter of *Solidago*, *Setaria*, and *Quercus*. Same letter means that differences between treatments are not significant (ANOVA/LSD, $P > .01$).

on 6 July, *Quercus* litter had a significantly stronger effect than *Solidago* litter on 22 July and 22 August. *Solanum*, the principal dicot (by biomass) in the community, was unaffected by the litter treatments (Fig. 4). The density of *Erigeron* was low on 6 July; most germination occurred in late summer and early fall (cf. Bazzaz 1984). *Erigeron* density was increased by litter of *Solidago* and *Setaria*, but was reduced by *Quercus* litter (Fig. 4).

Litter, particularly that of *Quercus*, reduced the biomass of *Setaria* on 11 August (Fig. 5); however, by 5 October no litter treatment showed a significant effect. In contrast, the significant negative effect of litter on *Panicum* persisted until the end of the season (Fig. 5).

TABLE 3. Results of MANOVAs testing for the null hypotheses of no effect of litter on community structure for density and biomass, at three dates. Biomass was not assessed on 6 July.

Date	Density		Biomass	
	F*	P	F*	P
6 July	5.22	<.0001	···	···
11 August	7.45	<.0001	7.76	<.0001
5 October	5.18	<.0001	2.97	<.0017

* Calculated by Wilk's criterion.

Litter of *Quercus* significantly increased the mean plant size of *Setaria*, but not that of *Panicum* on 5 October (Table 4). Biomass of *Solanum* was unaffected by litter addition (Fig. 5), and it replaced *Panicum* as the second species (by biomass) in the plant community in the litter treatments.

The number of flowering plants of *Setaria* was closely correlated with *Setaria* plant density in the last harvest ($r = 0.98$, df = 39, $P < .01$), and was significantly reduced by the three types of litter (ANOVA, $P < .01$). Mean estimated number of *Setaria* seeds per plot was significantly reduced by all litter treatments (Fig. 6). Mean number of seeds per individual was unaffected

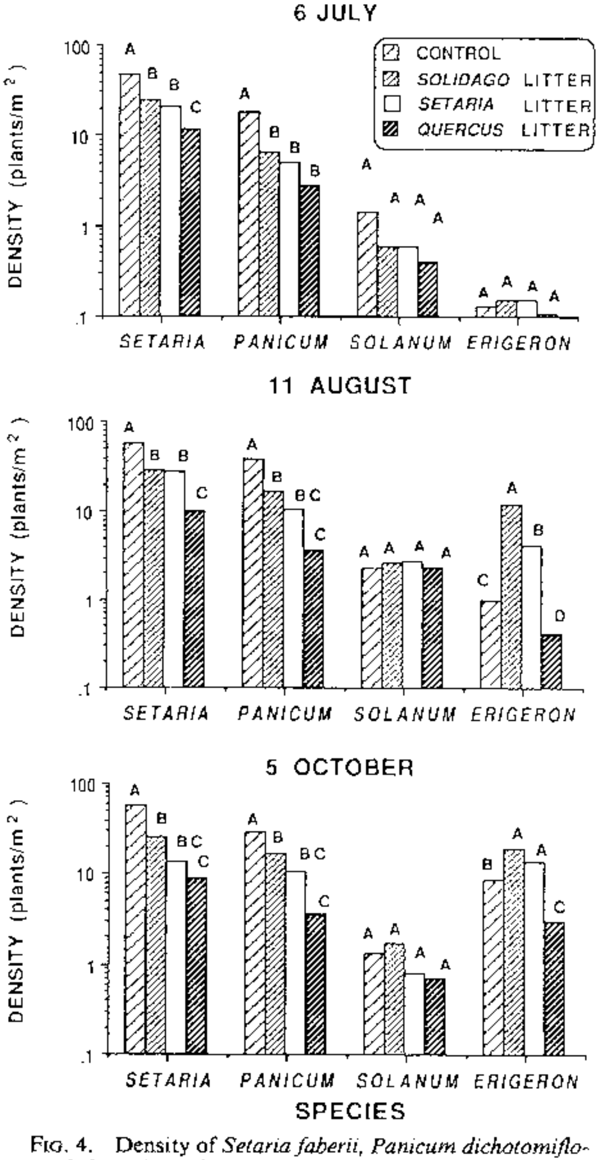

FIG. 4. Density of *Setaria faberii*, *Panicum dichotomiflorum*, *Solanum carolinense*, and *Erigeron annuus* on 6 July, 11 August, and 5 October, in plots without litter (Control), and with litter of *Solidago*, *Setaria*, and *Quercus*. Same letter within each date indicates that species means are not significantly different (ANOVA/LSD, $P > .01$).

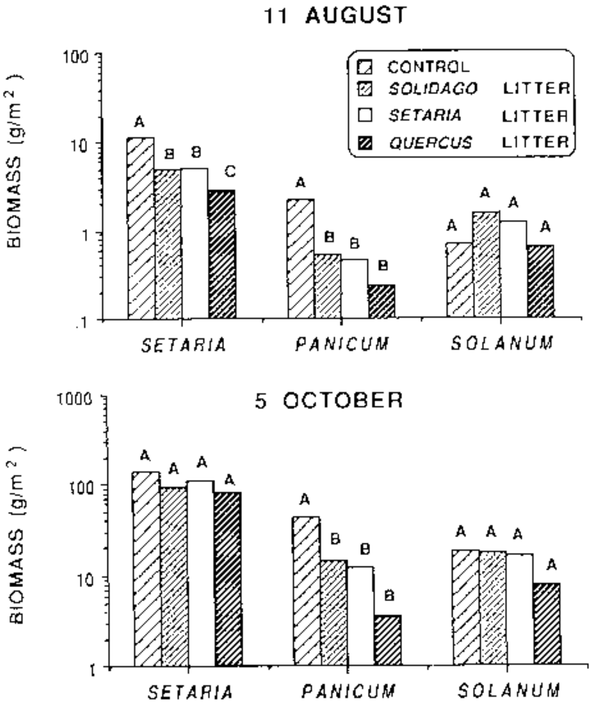

FIG. 5. Biomass of *Setaria faberii*, *Panicum dichotomiflorum*, and *Solanum carolinense* on 11 August and 5 October, in plots without litter (Control), and with litter of *Solidago*, *Setaria*, and *Quercus*. Same letter indicates that differences between treatments are not significant (ANOVA/LSD, $P > .01$).

by *Solidago* and *Setaria* litter, but was significantly increased by *Quercus* litter (Fig. 6).

DISCUSSION

Light extinction characteristics of litter

Our results show that variation in both amount and identity of litter can strongly affect the soil surface light environment at the two scales studied. Relatively small amounts of *Quercus* or *Setaria* litter reduced the radiation at the ground surface to low levels. In contrast, *Solidago* litter produced RI < 50% only when present in amounts close to or above those typically found in old fields at HMF (Facelli and Carson, *in press*). The heterogeneous distribution of hardwood leaf litter carried by the wind from forests into old fields (Shure and Phillips 1987, Facelli and Carson, *in press*) may affect old field community structure because of the strong shading effect of the litter (cf. Baskin and Baskin 1988, Silvertown and Smith 1989).

A focus on litter as mass accumulated per area characterizes studies of carbon or nutrient cycles (e.g., Odum 1960, Golley 1965, Mellinger and McNaughton 1975). Recent insights into the impact of litter on community structure and dynamics (e.g., Goldberg and Werner 1983, Monk and Gabrielson 1985, Beatty and Sholes 1988) emphasize the need to assess the structural properties of the litter layer. Previous studies on the effects of different litter types focused on differences in chemical composition (see Rice 1979 for a review). Differences in physical structure may result in different ecological effects because of differences in light interception and mechanical impediment (Facelli and Pickett 1991).

TABLE 4. Estimated mean plant size of *Setaria faberii* and *Panicum dichotomiflorum* at 5 October in plots without litter (Control), and with litter of *Solidago*, *Setaria*, and *Quercus*. Same letter within each species indicates that differences between treatments are not significant (ANOVA/LSD, $P > .01$).

	Mean plant size (g/plant)			
Species	Control	*Solidago* litter	*Setaria* litter	*Quercus* litter
Setaria	3.45 B	3.49 B	6.11 AB	8.26 A
Panicum	1.92 A	0.68 A	1.17 A	0.86 A

Effects of litter on plant community structure

Litter reduced the establishment of two annual grasses (*Setaria* and *Panicum*), both of which have dormant seeds requiring high temperatures and light to germinate (Baskin and Baskin 1988). Field measurements suggest that soil temperature did not limit the germination of *Setaria* (Bazzaz 1984), although it is possible that temperature fluctuation by itself may affect ger-

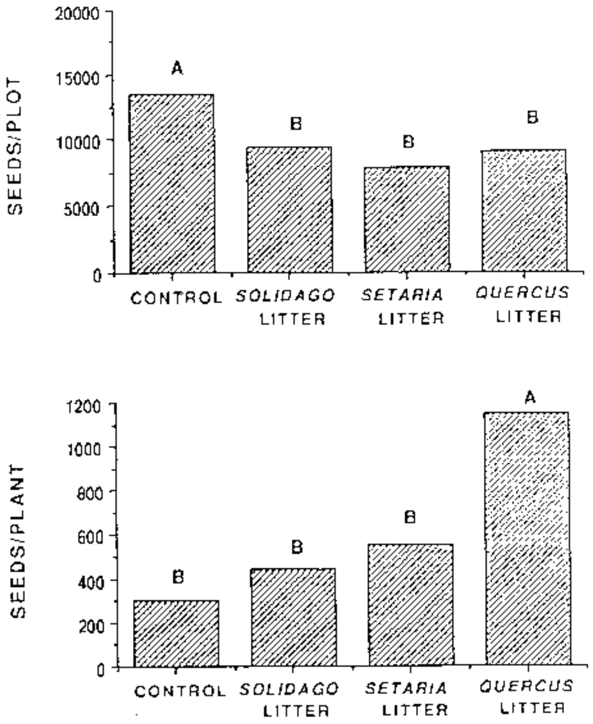

FIG. 6. Effect of litter addition on the reproductive output of *Setaria faberii* (estimated number of seeds produced per plot and per plant). Same letters indicate that differences are not significant (ANOVA/LSD, $P > .01$).

mination (cf. Thompson and Grime 1983). In a greenhouse experiment (J. M. Facelli and S. T. A. Pickett, *unpublished manuscript*), where differences in soil temperature are unlikely, *Quercus* litter reduced both *Setaria* germination and the number of *Setaria* seedlings emerging from the litter. Light deprivation and mechanical impediment to emergence may have been the main factors limiting *Setaria* density in this study.

The reduction in number of individuals had different consequences for *Setaria* and *Panicum*. *Setaria* reached the same biomass in all treatments at the end of the growing season, in spite of the different densities. Individual size distributions of *Setaria*, therefore, may be regulated principally by intraspecific competition (Weiner and Solbrig 1984). *Panicum* did not compensate for the lower densities by increasing individual biomass, probably because individuals of *Panicum* were always outcompeted by *Setaria*.

All litter treatments strongly affected the reproductive output of *Setaria*. Litter reduced both the number of flowering plants and the number of seeds per plot, even though total biomass of *Setaria* was not affected by the treatments. This suggests that reproductive output per plot was limited by population density rather than by total biomass. Although the much larger plants of *Setaria* in the *Quercus* litter plots produced twice as many seeds as individuals in the other treatments, their aggregate seed production remained low due to the reduced plant density. These patterns illustrate the differences between responses observed at the population and individual levels, and the importance of phenotypic plasticity in the organization of early successional communities (Bazzaz 1987).

Neither density nor biomass of *Solanum*, the dicot with highest biomass, was affected by litter. Dicots had been previously shown to be less affected by litter than grasses (Sydes and Grime 1981, but see Monk and Gabrielson 1985). The perennial habit of *Solanum*, which sprouts from subterranean organs after disturbance, confers tolerance to litter because sprouts have more energy reserves than seedlings (Grime 1979, Knapp and Seastedt 1986). It is still possible, however, that litter may have had a negative effect on *Solanum*, and that this was mitigated by reduced competition from grasses. In the presence of *Quercus* litter *Solanum* replaced *Panicum* as the second species by biomass in the community hierarchy. Thus, differential species responses to litter addition can change interspecific interactions and the community structure. We predict that the impact of litter on community organization decreases through succession as annual species are replaced by perennial species, less dependent on establishment from seeds (but see Carson and Peterson 1990).

The increased density of *Erigeron annuus* over time in the *Solidago* and *Setaria* litter treatments may have been caused by the accumulation of its wind-dispersed seeds in the litter or by an increased number of safe sites. Germination and establishment occur shortly after seed dispersal and probably are the most critical life stages for the species (Bazzaz 1984). In arid environments litter usually enhances establishment because of reduced desiccation (e.g., Fowler 1986). In mesic habitats, however, litter usually reduces germination and establishment (Schlatterer and Tinsdale 1969, Werner 1975, Hamrick and Lee 1987, see Facelli and Pickett 1991 for a review). Only *Quercus* litter reduced the establishment of *Erigeron*, possibly by mechanically preventing the seeds from reaching the soil (Fowler 1986, Hamrick and Lee 1987). *Erigeron* usually replaces *Setaria* as dominant in the 2nd or 3rd yr of succession in the study site (J. M. Facelli, *personal observation*). The positive effect of *Setaria* and *Solidago* litter on *Erigeron* density suggests facilitation by litter.

Litter can significantly influence plant community structure both through direct effects on different species, and through the resulting indirect effects. Because the amount and composition of litter in a given patch result from past events affecting litter production and decomposition in situ, and may be affected by redistribution of litter from neighboring areas (Shure and Phillips 1987, Facelli and Carson, *in press*), litter is a vector of plant–plant interactions through time and space (Bergelson 1990, Facelli and Pickett 1991).

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