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Bulletin of the Torrey Botanical Club, Vol. 118, No. 1 (Jan. - Mar., 1991), 62-66.

Bulletin of the Torrey Botanical Club 118(1), 1991, pp. 62–66

Heterogeneity of plant litter accumulation in successional communities[1]

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ABSTRACT

FACELLI, J. M. AND W. P. CARSON (Department of Biological Sciences, Rutgers University, P.O. Box 1059, Piscataway, NJ 08855). Heterogeneity of plant litter accumulation in successional communities. Bull. Torrey Bot. Club 118: 62–66. 1991.—We sampled the litter accumulated in five seral sites (aged 5, 15, 23, 29, and 47 yr) and in an oldgrowth forest in early spring and fall. We collected and weighed all the litter in twelve 0.24 m^2 quadrats per field, arranged in three parallel transects. In the four younger sites, the transects were 12, 24, and 36 m distant from a forest edge. Total litter was lower in the four younger fields than in either the older site or in the forest. Litter composition in the four younger fields was rather similar, and mostly composed of herb litter. In the 47 yr site and in the forest, litter of tree leaves and wood were the main components. Spatial heterogeneity in the litter layer was high, specially in the 23 and 29 yr oldfields. In the four younger fields, the composition of the litter was significantly affected both by the age of the field and by the distance from the forest edge.

Key words: detritus, heterogeneity, New Jersey, oldfields, patchiness, succession, temperate forest.

The amount of accumulated plant litter varies greatly in both space and time (Facelli and Pickett 1991). Differential production and decomposition of litter (Olsen 1963), and episodic deposition and removal (Orndorff and Lang 1981) may introduce significant spatial variation in litter biomass and composition. Litter can alter the soil moisture and temperature, and the light profile close to the soil surface (e.g., Walsh and Voight 1977; Grime 1979; Hamrick and Lee 1987), and decomposing litter releases nutrients and phytotoxins (e.g., Stinner *et al.* 1984; see Facelli and Pickett 1991, for a review on the ecological effects of litter). The intensity of the effect of litter will depend upon the quantity and composition of the litter. Because different types of litter may differentially affect species performance (e.g., Gross and Werner 1982; Goldberg and Werner 1982; Fowler 1986; Sydes and Grime 1981) the properties of the litter mat may impact community structure and dynamics (Monk and Gabrielson 1985; Carson and Peterson 1990; Facelli and Pickett 1991; in press).

Little information on litter accumulation through succession is currently available (Facelli and Pickett 1991). Furthermore, few studies report variations in composition and spatial heterogeneity of the litter mat in successional communities. The objective of this study is to characterize the amount, composition, and spatial heterogeneity of the litter layer in seral habitats. We did not intend to analyze the litter dynamics (i.e., litter inputs and outputs) but rather we wanted to characterize differences in the composition of the litter mat that may alter successional dynamics (Facelli and Pickett 1991; in press; Carson and Peterson 1990).

Methods. We sampled five successional sites aged 4, 15, 23, 29 and 47 years, and a relatively undisturbed oldgrowth forest. The four younger sites and the oldgrowth forest were located at the William L. Hutcheson Memorial Forest Center (HMF), East Millstone, New Jersey (40°30′N, 74°34′W). The oldgrowth forest is a relict of the typical mixed oak forest of central New Jersey (Frei and Fairbrothers 1963). The oldfields are part of the long term Buell Successional Study (Pickett 1982; Myster and Pickett 1988). The mentioned studies suggest that all the oldfields in the area are ecologically homogeneous. Each of the four oldfields was approximately 100 ×

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[1] E. D'Angela helped to sort the litter. The advice of B. C. McCarthy, C. J. Peterson, and S. T. A. Pickett improved this manuscript. JMF acknowledges support from Consejo Nacional de Investigaciones Cientificas y Técnicas de la República Argentina, and a 1987 Summer Research Grant from the William L. Hutcheson Memorial Forest Center.

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Received for publication October 11, 1989 and in revised form May 17, 1990.

50 m in size, and had a side bordered by a forest. The other seral site was an undisturbed 47 yr woodlot located 1 km north of HMF, and dominated by a dense, continuous canopy of *Acer rubrum*. Bard (1952) found that early succession at this site was similar to fields at HMF. All the sites were on the same soil series: the Penn Silt Loam (USDA 1976). We assume that the main differences among sites were due to different successional ages, and that the space-for-time substitution allows one to infer general successional trends (Pickett 1989). Litter accumulation during succession at HMF was studied previously by Lang (1973), but at that time the stress was placed on litter dynamics rather than on litter composition and heterogeneity.

We sampled all sites twice in 1987: early spring (9–15 March), and late fall (just after the first major killing frost, 10–11 December). These dates correspond, approximately, to peaks in minimum and maximum litter accumulation in oldfields and forests (Odum 1960; Lang 1973). At each site we established three 40 m long parallel transects, 12 m apart from each other. In the four younger fields, the transects were placed 12, 24, and 36 m distant from the forest edge. We collected all the litter in four quadrats (60 × 40 cm each) randomly placed along each transect. We sorted the litter into (1) herbs (any piece of herbaceous material more than 2 cm long); (2) perennial vines (mostly dead stems of *Lonicera japonica* and *Rubus* spp.); (3) leaves of trees (entire leaves or pieces larger than 2 cm in diameter); (4) wood (twigs and branches with diameter between 3 mm and 15 cm; and (5) detritus (any plant remain of small size whenever we were able to identify it as a plant tissue). We did not collect organic material integrated into the soil (A_0 Horizon). After sorting, all the material was oven dried at 85°C for 48 hr and weighed.

We tested for differences among sites in the total amount of litter accumulated by separate ANOVA's for the spring and fall data. To increase normality, we used log transformed data. When ANOVA's showed significant differences ($P < 0.05$), we calculated Least Significant Differences (LSD, $P < 0.05$). To analyze the effects of age of the site and distance with respect to the forest edge on the composition of the litter mat we performed two-way ANOVA's, and LSD's, for the three main litter components in the four oldfields (herbs, leaf and wood litter). To assess the overall patchiness of the litter layer we calculated the index of horizontal heterogeneity proposed by Facelli *et al.* (1987):

$$D_b = \sum_{i=1}^{n} \left(p_i \sum_{j=1}^{r} p_{ij}^2 \right)$$

where n is the number of components (5), r the number of quadrats in the site (12), p_i is the proportion of the i^{th} component in the total litter of the site and p_{ij} the proportion of the i^{th} component found in the j^{th} frame.

Results. Overall, total litter was higher at the wooded sites than at the oldfield sites (Fig. 1). Total litter on the wooded areas was maximum in spring, and minimum in the fall, while on the four oldfields the contrary was true (Fig. 1). Thus, in the fall there were only small differences in total litter at oldfields and woodlots. We found no significant difference in total litter among the four oldfields ($P > 0.25$; Fig. 1).

The composition of the litter mat in the four oldfields was quite similar (Fig. 1). As expected, the amount of herb and tree leaf litter was higher in fall than in spring, but the differences between maxima and minima diminished with field age. Wood litter was more abundant in spring than in fall. Detritus and vine litter were minor components of the litter (Fig. 1).

The heterogeneity of litter distribution (as measured by the D_b index) increased from the youngest field to mid-aged fields, and then declined in the woodlot and in the oldgrowth forest (Table 1). Similar trends were observed in spring and fall. Litter heterogeneity in the oldfields had a definite pattern. Distance from the forest significantly ($P < 0.01$) affected the amount of herbs, leaves and wood litter (Table 2). In all cases, the effect of the forest edge depended upon the age of the field (significant interaction, $P < 0.01$). Herb litter decreased with distance away from the forest edge in the 5 and 15 yr oldfields, but it showed the opposite trend in the 23 and 27 yr sites (Table 2). In the transect closer to the forest edge, leaf and wood litter increased with age ($P < 0.01$, Table 2), but only slight effects of age were detected in the transects 24 and 36 m distant from the forest edge.

Discussion. The pattern of litter accumulation suggested by the values of total litter we measured agree with the model by Olsen (1963) and with observations by Odum (1960), Golley (1965) and Lang (1973). The evidence suggests a period of net accumulation immediately following disturbance, followed by a dynamic equilibrium and a further pulse of accumulation, after tree invasion. Our data also suggest that changes in

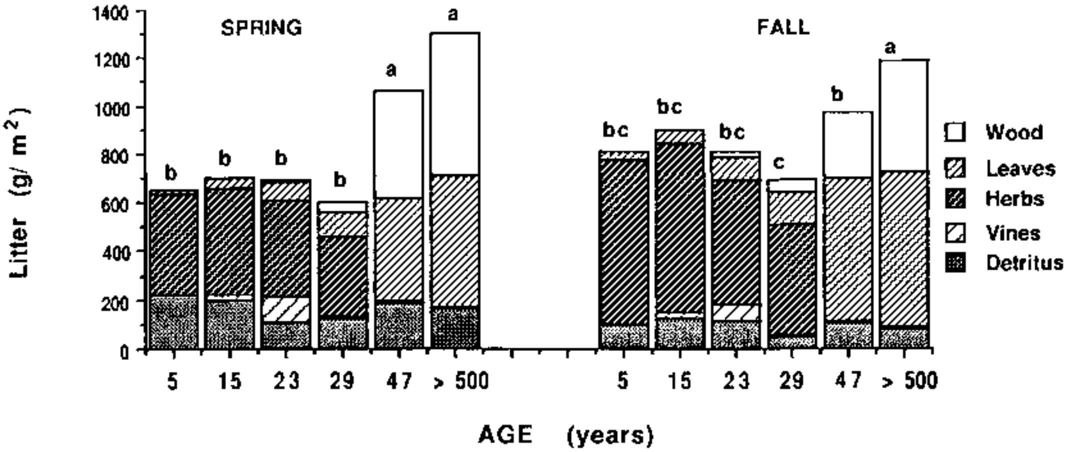

Fig. 1. Composition of the litter accumulated in four oldfields (5, 15, 23 and 29 yr old), a 47 yr successional woodlot, and a oldgrowth forest in the spring and fall 1987. Same letter within each season indicates that differences in total accumulated litter are not significant ($P > 0.05$).

litter composition may also be sudden. A complete change in litter composition seems to have occurred in the period between age 29 yr and 47 yr (Fig. 1). The small changes that happened in the previous 20 yr seem to be determined by the spatial arrangement of the field respective to forested areas (see below). Though our study was not planned to analyze the dynamics of litter through succession, the observed patterns allow one to establish working hypotheses for future studies.

The seasonal patterns observed for herb and leaf litter contrasted with the patterns observed for wood litter. Herb and leaf litter accumulation closely follow organ death, whereas wood accumulation may depend upon the mechanical damage to branches (dead or alive) by frost heaving or heavy winds during winter (Christensen 1975). The larger seasonal variation in total litter in the two youngest oldfields could be due to higher litter production and faster decomposition in early oldfield communities (Odum 1960; Golley 1965).

Table 1. Spatial heterogeneity (calculated by the D_b index) in five oldfields of different ages and in an oldgrowth forest, in the spring and fall 1987.

Successional age (yr)	Season	
	Spring	Fall
5	0.091	0.096
15	0.112	0.103
23	0.183	0.162
29	0.141	0.137
47	0.139	0.127
>500	0.124	0.130

In the four oldfields, both age and distance to the forest edge affected litter composition and accounted for a significant proportion of the observed heterogeneity. Because the younger site had no trees, leaf litter accumulation there was due to wind deposition of leaves from the forest. Shure and Phillips (1987) showed that leaf litter deposition in large forest gaps was nearly as large as the in situ production. In the older fields, a proportion of the leaf litter was produced in situ by the trees that first invade areas close to the forest edges (JMF personal observation). Low values of herb litter close to the forest edge in those fields may be attributed to suppression of herbs by the invading trees (Grime 1979).

The heterogeneous litter distribution in oldfields may respond to both random and deterministic causes. We were able to discriminate the distance to forest edges as an important variable affecting litter accumulation. Distance to forest edge acts on litter accumulation both through the movement of litter across the boundary (cf. Orndorff and Lang 1981; Shure and Phillips 1987) and through faster tree invasion close to the forest.

Litter at the levels we found in our oldfields was found to alter plant abundance (Hamrick and Lee 1987; Watt 1970; Goldberg and Werner 1982; Fowler 1986) and successional dynamics (Monk and Gabrielson 1985; Carson and Peterson 1990). In experiments conducted in oldfields at HMF, amounts of tree leaves within the range we found in the younger oldfield dramatically altered plant community structure (Facelli and Pickett in press), and favored the establishment

Table 2. Amount of litter of herbs, tree leaves and wood (in g/m^2) in four oldfields of different ages, and at different distances from a forested border, in the spring and in the fall 1987. Same letter indicates that differences are not significant ($P < 0.05$).

	Spring 1987			
	Age (years)			
Distance (m)	5	15	23	29
Herbs				
12	552.21 A	535.25 A	112.96 C	6.83 D
24	384.83 AB	471.50 AB	454.21 AB	570.04 A
36	296.75 B	326.79 B	610.21 A	412.08 AB
Leaves				
12	24.67 C	88.92 B	181.83 A	218.33 A
24	15.08 C	17.08 C	26.88 C	76.90 B
36	10.04 C	9.21 C	5.71 C	17.63 C
Wood				
12	0.00 C	5.42 C	44.50 B	104.50 A
24	0.00 C	3.00 C	1.88 C	9.67 C
36	0.00 C	0.75 C	2.25 C	1.66 C

	Fall 1987			
	Age (years)			
Distance (m)	5	15	23	29
Herbs				
12	791.27 A	836.21 A	138.40 D	121.43 D
24	592.50 B	512.53 C	559.08 BC	612.66 B
36	643.36 B	719.36 B	835.08 A	623.93 B
Leaves				
12	58.29 BC	105.42 B	226.79 A	258.63 A
24	29.96 CD	47.08 BC	25.75 CD	90.79 B
36	9.71 D	12.58 D	15.25 CD	36.29 C
Wood				
12	1.71 C	6.67 C	51.08 B	134.58 A
24	0.00 C	0.63 C	8.01 C	12.92 C
36	0.00 C	0.00 C	1.67 C	9.67 C

of tree seedlings (Facelli unpublished). Thus, the heterogeneity in both litter amount and composition we recorded is likely to influence the vegetation patchiness. Random sources of litter variation will superimpose microenvironmental patchiness (Facelli and Pickett 1991) to that already existing, while deterministic factors will reinforce the existing patchiness in the system.

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