

# The role of litter in an old-field community: impact of litter quantity in different seasons on plant species richness and abundance

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**Summary.** We studied the effect of removing and adding plant litter in different seasons on biomass, density, and species richness in a *Solidago* dominated old-field community in New Jersey, USA. We removed all the naturally accumulated plant litter in November (658 g/m<sup>2</sup>) and in May (856 g/m<sup>2</sup>) and doubled the amount of litter in November and May in replicated plots (1 m<sup>2</sup>). An equal number of plots were left as controls. Litter removal and addition had little impact on total plant biomass or individual species biomass in the growing season following the manipulations. Litter removal, however, significantly increased plant densities but this varied depending upon the season of litter removal, species, and life history type. Specifically, the fall litter removal had a much greater impact than the spring litter removal suggesting that litter has its greatest impact after plant senescence in the fall and prior to major periods of early plant growth in spring. Annual species showed the greatest response, especially early in the growing season. Both spring and fall litter removal significantly increased species richness throughout the study. Litter additions in both spring and fall reduced both plant densities and species richness in June, but these differences disappeared near the end of the growing season in September. We concluded that in productive communities where litter accumulation may be substantial, litter may promote low species richness and plant density. This explanation does not invoke resource competition for the decline in species richness. Finally, we hypothesize that there may be broad thresholds of litter accumulation in different community types that may act to either increase or decrease plant yield and diversity.

**Key words:** Disturbance – Litter – Old-field – Plant density – *Solidago canadensis*

Litter is an important component of most plant communities (Facelli and Pickett in press). Most studies of litter

have focused on inputs and outputs of litter, litter nutrient dynamics and rates of litter decomposition (e.g., Weigert and McGinnis 1975; Abbot and Crossley 1982; Vitousek 1982; Seastedt 1988). Less attention has focused on how plant litter may affect species diversity and plant abundance. In this study, we investigate the role of litter in the organization of an old-field plant community.

Spatially variable rates of litter input or decomposition can create an array of microhabitats which may favor different plant species (Al-Mufti et al. 1977; Sydes and Grime 1981a; Monk and Gabrielson 1985). A series of studies have verified that a given quantity of litter may promote or inhibit the performance of particular plant species (e.g., Barrett 1931; Gross and Werner 1982; Gross 1984; de Jong and Klinkhamer 1985; Fowler 1986, 1988; Hamrick and Lee 1987; Cheplick and Quinn 1987). With the exception of extensive work in North American prairies (see below) only a few studies have investigated the effect of litter on the entire community (Heady 1956; Monk and Gabrielson 1985; Beatty and Sholes 1988).

Litter accumulation is a major structuring force in prairies. In tallgrass prairies, fire works as an agent that removes the litter layer thereby increasing yield and altering species diversity and composition (Dyksterhuis and Schmutz 1947; Weaver and Roland 1954; Old 1969; Hulbert 1969; Knapp and Seastedt 1986). Knapp and Seastedt (1986) concluded that the impact of litter on key ecological processes made the tall grass prairie unique among North American vegetation types. Watt (1971, 1974) observed similar effects of litter on grassland vegetation in England. In contrast, in dryer less productive grasslands, litter may help to conserve soil moisture and thus increase yield and plant diversity (Willms et al. 1986; Fowler 1986; but see Fowler 1988).

Only a few studies have examined the impact of litter on terrestrial communities other than grasslands. In any community where production is high or decomposition rates are low or both, litter accumulation may alter community dynamics (e.g., Grime 1979). For example, in a deciduous forest community in England, Sydes and Grime (1981a) found that the distribution of understory

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herbs was closely correlated with the quantity of leaf litter (see also Beatty and Sholes 1988; Monk and Gabrielson 1985).

The role of herbaceous litter in structuring old-field communities is virtually unexplored (but see Monk and Gabrielson (1985) for the effects of tree leaf litter), even though herbaceous litter has been shown to effect the germination and survivorship of several old-field species (e.g., Werner 1975; Gross and Werner 1982; Goldberg and Werner 1983). Old-field communities often have high rates of annual net primary productivity (e.g., Bazzaz and Mezga 1973; Carson and Barrett 1988) resulting in large amounts of accumulated litter (e.g., Odum 1960; Weigert and McGinnis 1975). Furthermore, many old-fields have served as model systems to test theories of resource competition and community organization via multiple year nutrient enrichment experiments (most recently e.g., Tilman 1987; Carson and Barrett 1988). These studies have reported decreases in species richness following fertilization and interpreted these decreases in terms of resource competition. They generally have not considered that substantial litter accumulation may also lead to lower levels of species richness and plant density.

On the piedmont of New Jersey where we conducted this study, litter levels in old-fields are quite patchy ranging from 400–900 g/m<sup>2</sup> (Facelli and Carson 1990). Similar levels of litter in grasslands have been shown to either have no impact or to decrease community biomass, density and species richness (Penfound 1964; Willms et al. 1986). Much lower levels of leaf litter reduced total biomass in British woodlands and promoted forbs at the expense of grasses (Sydes and Grime 1981 a, b). For this study, we addressed two questions: (1) what is the short term impact of litter on plant biomass, density and species richness and (2) does this impact vary with litter quantity and season? To answer these questions, we either added or removed plant litter in replicated plots in spring and fall in a *Solidago* dominated old-field community.

## Materials and methods

### Study site and experimental design

We conducted this study in a 14 yr old-field at the William L. Hutcheson Memorial Forest Center (HMF) located 14 km west of New Brunswick, New Jersey, USA. The soil is a well drained loam derived from the Brunswick red shale formation (Ugolini 1964). The climate is subcontinental with a mean annual rainfall of 115 cm distributed fairly evenly through the year. The growing period generally extends from late March to mid-November and the frost free period extends from late April to mid-October (Robichaud and Buell 1973). *Solidago* spp. (primarily *S. canadensis* and secondarily *S. rugosa*) accounted for about 70% of the biomass in this old-field; *S. graminifolia*, and *Aster pilosus* were also present in the canopy. *Fragaria virginiana* was the dominant species in the subcanopy. Nomenclature follows Gleason and Cronquist (1963).

In November 1985, we established 100, 1.0 m<sup>2</sup> experimental plots in a 10 × 10 array within this old-field. All plots were 1.5 m apart. We had five treatments: fall litter removal, fall litter addition, spring litter removal, spring litter addition, and a control.

Treatments were randomly assigned to each plot. On 19 November 1985 we conducted the fall litter removal; all litter and standing dead within 20 replicate plots was removed, dried for 48 h, and weighed to the nearest 0.1 g. Immediately thereafter, this litter was used for the fall litter addition treatment. We determined the mean weight of the litter removed per plot and then spread this amount evenly throughout each of 20 fall litter addition plots using the litter that we had just removed. This approximately doubled the average amount of litter within each plot. On 15 April 1986, we conducted a spring litter removal and addition exactly as described for the fall treatments. Thus, there were five different treatments, each replicated 20 times. We made every effort not to disturb the soil surface during our removal treatments. We chose not to remove and then immediately replace the litter in the control plots (thus strictly controlling for potential experimental artifacts) because this would have severely altered the natural structure (e.g., compaction) of the litter.

### Vegetation analysis

We randomly selected ten of the twenty replicate plots from each treatment for sampling on 29 May–1 June 1986. First, we measured plant density in 100 cm<sup>2</sup> subplots in the center of each 1 m<sup>2</sup> plot. Then we determined above-ground biomass for each species by harvesting in 0.25 m<sup>2</sup> plots located at the center of each replicate plot. This same sampling procedure was repeated in the remaining plots (10 plots per treatment) on 10–14 September 1986.

### Statistical analysis

We used an analysis of variance (ANOVA) for a completely randomized design and Student-Newman-Keuls multiple comparison tests to determine significant treatment effects within each sample date (SAS Institute 1985). Analyses were done on species richness, biomass and density of the common species and life history types. A t-test was used to compare the amount of litter between November and April. Because the means of some data were not normally distributed, all data were log-transformed before analysis (Sokal and Rohlf 1981). We excluded one significant outlier (Dixon's test  $p < 0.01$ ) from the spring litter addition treatment sampled in May in the analysis of the density of annuals (Sokal and Rohlf 1981; Snedecor and Cochran 1989).

## Results

### Biomass

Litter biomass was significantly higher in the spring than in the fall (t-test,  $p < 0.001$ ). We removed a mean of 657.7 g/m<sup>2</sup> in November of 1985 and 855.7 g/m<sup>2</sup> in April of 1986. These differences likely reflected litter deposition into the plots from surrounding standing dead vegetation coupled with the further senescence of leaves and stems during the winter. Therefore, litter removals and additions were not equivalent between the two seasons (Table 1). Our litter manipulations had their intended effects; litter was significantly lower in the removal plots and significantly higher in the addition plots compared to the control plots (Table 1).

Removal and addition treatments never significantly altered total plant biomass or the biomass of species other than *Solidago* in either May or September (Table 1). The fall litter addition significantly reduced the

**Table 1.** The effect of litter manipulations on plant litter and biomass (g/0.25 m<sup>2</sup>). C=Control, SR=Spring removal, FR=Fall removal, SA=Spring addition, FA=Fall addition. Asterisks indicate the significance level of the ANOVA (\*= $p < 0.05$ ; \*\*= $p < 0.01$ ; \*\*\*= $p < 0.001$ ). Treatment means were separated by an S-N-K multiple comparison test. The absence of letters indicates that all treatments were statistically equivalent. All statistical comparisons are among treatments within a sampling date

	Removals			Additions	
	C	FR	SR	FA	SA
<b>BIOMASS</b>					
Litter (May)***	188.4a	53.0b	6.7c	402.2d	481.6e
Litter (Sept)***	165.1a	65.3b	16.2c	318.8d	414.3e
Total plant biomass (May)	79.7	85.5	61.8	82.3	69.1
Total plant biomass (Sept)	156.0	170.9	160.2	162.4	134.7
<i>Solidago canadensis</i> (May)	45.8	38.2	38.1	45.1	41.1
<i>Solidago canadensis</i> (Sept)*	110.2a	99.9ab	92.2ab	71.1ab	49.6b
<i>Solidago rugosa</i> (May)	4.7	4.5	2.1	5.7	8.3
<i>Solidago rugosa</i> (Sept)**	1.8a	21.2b	21.8b	42.2b	42.2b
<i>Fragaria virginiana</i> (May)	3.6	2.4	2.0	3.2	1.7
<i>Fragaria virginiana</i> (Sept)	2.9	2.2	3.5	4.3	2.3
Non- <i>Solidago</i> spp. (May)	8.6	10.1	8.5	7.5	6.5
Non- <i>Solidago</i> spp. (Sept)	7.9	7.2	13.3	9.7	8.8

**Table 2.** The effect of the litter manipulations on total density and the density of annuals, biennials and perennials. Values represent means for 10 × 10 cm subplots. Abbreviations as in Table 1. All statistical comparisons are among treatments within a sampling date. Total densities will not equal the sum of perennials, biennials, and annuals because numerous small individuals could not be accurately identified

	Removals			Additions	
	C	FR	SR	FA	SA
Total density (May)***	10.2a	56.9b	22.2a	3.0c	4.4c
Total density (Sept)***	3.0a	23.2b	7.5c	2.6a	3.3a
Annuals (May)**	0.7bc	10.2a	1.5b	0.1bc	0.0c
Annuals (Sept)*	0.0a	1.4b	1.2b	0.0a	0.0a
Biennials (May)**	0.3a	3.3b	2.1ab	0.0a	0.0a
Biennials (Sept)	0.0	4.7	0.5	0.0	0.0
Perennials (May)***	4.3a	10.3b	5.6a	2.5a	3.0a
Perennials (Sept)***	2.7a	11.7b	3.5a	2.6a	3.1a

biomass of *S. canadensis* relative to the control treatment in September. *S. rugosa* had significantly lower biomass in the control treatment relative to any other treatment.

#### Plant densities

Litter manipulations had their most pronounced effects on plant densities (Tables 2 and 3). The magnitude of this effect, however, varied with season of removal. The fall removal significantly increased both total plant density and the density of annuals and perennials over all other treatments in the May sampling (Table 2). In the September sampling, the fall removal had significantly greater total density and density of perennials than all other treatments. Overall, the spring litter removal produced less of an effect; only annuals and total plant density were significantly higher by September relative to controls. The only major effect of the litter additions

**Table 3.** Densities for the common species in May and September for each treatment. Values represent means for 10 × 10 cm subplots. Full species names are in the text. Statistical analysis, significance levels, and abbreviations as in Table 1, except that P=Perennial, B=Biennial, A=Annual

		May				
		C	FR	SR	FA	SA
<i>Fragaria</i>	(P)	0.2	0.6	0.4	0.1	0.3
<i>Oxalis</i> ***	(P)	0.5a	5.8b	0.9a	0.2a	0.0a
<i>Barbarea</i> ***	(B)	0.2a	3.4b	2.1b	0.0a	0.0a
<i>Oenothera</i> **	(B)	0.1a	0.9b	0.0a	0.0a	0.0a
<i>Ambrosia</i> **	(A)	0.0a	0.8b	0.1a	0.0a	0.0a
<i>Abutilon</i> ***	(A)	0.5a	5.8b	1.1a	0.1a	0.0a
<i>Setaria</i> *	(A)	0.1a	3.7b	0.3a	0.0a	0.0a
		September				
		C	FR	SR	FA	SA
<i>Fragaria</i>	(P)	0.4	0.5	0.4	0.6	0.4
<i>Oxalis</i> ***	(P)	0.4a	2.8b	0.1a	0.0a	0.0a
<i>Aster</i> ***	(P)	0.5a	5.4b	0.7a	0.0a	0.1a
<i>Barbarea</i>	(B)	0.0	4.2	0.5	0.0	0.0
<i>Oenothera</i>	(B)	0.0	0.2	0.0	0.0	0.0
<i>Abutilon</i> *	(A)	0.0a	0.7b	0.9b	0.0a	0.0a
<i>Ambrosia</i>	(A)	0.0	0.3	0.2	0.0	0.0
<i>Setaria</i>	(A)	0.0	0.1	0.1	0.0	0.0

relative to the controls was in May when both spring and fall addition plots had significantly lower total plant density.

The fall litter removal significantly increased the density of several different species, primarily annuals and biennials (Table 3). In May, *Ambrosia artemisiifolia*, *Abutilon theophrasti*, *Setaria faberii*, *Oenothera biennis*, and *Oxalis stricta* had significantly higher densities in

Table 4. Species richness in May and September for each treatment. Abbreviations, statistical analysis and significance levels as in Table 1

	C	Removals		Additions	
		FR	SR	FA	SA
Species richness (May)***	12.8a	16.1b	15.3b	9.3c	8.7c
Species richness (Sept)***	9.9a	14.7b	12.9b	9.5a	9.1a

the fall removal than any other treatment. Only *Barbarea vulgaris* had significantly higher densities in both the spring and fall removal relative to the other treatments. Litter additions had no significant effect on the density of any individual species relative to control plots. Litter manipulations did not affect the dominant subcanopy species, *Fragaria virginiana*.

In September, two perennial species, *Oxalis stricta* and *Aster pilosus* had significantly higher densities in the fall removal treatment relative to the other treatments (Table 3). Additionally, *Abutilon theophrasti*, an annual, had significantly higher densities in both the spring and fall removal treatments relative to the other treatments. Overall, the effect of the fall removal treatment on seedling densities was less pronounced by September. *Aster pilosus*, which was important in September, was likely present in the May sample but was too small to be accurately identified.

### Species richness

Litter removals significantly increased species richness over control plots and litter addition plots in both May and September (Table 4). Litter additions significantly decreased species richness relative to controls in May, but not in September.

## Discussion

### Biomass

Short-term litter manipulations did not alter the biomass of any species with the exception of a negative impact on *S. canadensis* in the spring litter addition treatment (Table 1). Because there was more litter added in the spring than in the fall, we cannot determine whether this reduction in biomass was a seasonal effect or due to different amounts of litter added or both. Nonetheless, only litter in very high quantities (> approx. 1500 g/m<sup>2</sup>) appears to affect plant biomass in this *Solidago*-dominated old-field community, at least in the short term. Litter of this magnitude also decreases standing biomass in tall grass prairie communities (e.g., Weaver and Roland 1954; Old 1969; Hulbert 1969). Litter only rarely reaches such high levels, however, in old-fields in this area (Facelli and Carson 1990).

### Plant densities and species richness

Litter removals significantly increased both plant densities and species richness, particularly in the fall litter removal plots (Tables 2 and 3). There are several possible but not mutually exclusive explanations for this response. First, some seeds may have dispersed into the plots after the fall removal and before the spring removal. Thus, we may have removed seeds when we removed the litter in the spring accounting for the differences in the effect of the fall vs the spring removal. We consider this unlikely because adults of the species that had high densities in the litter removal plots were at very low abundance or completely absent in this community (see the biomass of non-*Solidago* spp. Table 1) and old-field soil seed banks usually contain seeds of the species that we found in our plots (Oosting and Humphreys 1940; Livingston and Allesio 1968).

A second, more likely explanation for the increase in both density and species richness is that many of the seeds of the species found in our litter removal plots require germination cues including moisture, temperature, and light fluctuations (e.g., Pickett and Baskin 1973; Baskin and Baskin 1977, 1988; Peterson and Bazzaz 1978; Bazzaz 1979; Goldberg and Werner 1983; Gross 1984; Fenner 1985). Both the fall and spring litter removal would have changed several of these factors (Mackinney 1929; Hopkins 1954; Sydes and Grime 1981b; Goldberg and Werner 1983; Beatty and Sholes 1988), accounting for at least part of the increase in plant density in the removal plots. The fall removal plots, however, with a higher density of seedlings had an entire winter without a thick litter layer thereby exposing seeds to different germination cues than seeds in the spring removal. Also, some seeds in the fall removal treatment may have germinated very early in the growing season before the spring litter removal. The absence of these germination cues may also account for the lower density of seedlings and species richness found in the litter addition plots. This study, however, was not designed to determine whether seeds failed to germinate or germinated and then failed to penetrate the litter layer (see below).

Litter may also act as a physical obstruction barring plants from access to light (Sydes and Grime 1981b). Also, small seeded species may not have enough stored reserves to penetrate a thick litter layer (Fenner 1985; Gross 1984). The greater response of the vegetation to the fall removal suggests that litter is having its main impact outside of the main growing season following senescence of the vegetation in the fall or very early in the growing season prior to major periods of plant growth.

Another factor that may have promoted higher densities in the fall removal treatment was the small amount of litter found in these plots in May (50 g; Table 1) as compared to the almost complete absence of litter in the spring removal treatment (7 g). For some species, small amounts of litter of this magnitude may ameliorate the local microclimate and increase germination and survivorship (Glendenning 1942; Gross 1984;

Willms et al. 1986; Fowler 1986; Hamrick and Lee 1987).

Finally, we cannot exclude the possibility that litter removal also removed allelopathic agents that were inimical to seed germination and survivorship (e.g., Rice 1984 and citations therein).

#### *Litter and plant community organization*

Our data suggest that litter may be an important and overlooked factor promoting low diversity and density in fertile old-fields where productivity is high (e.g., Bazzaz and Mezga 1973; Swieringa and Wilson 1972) and litter accumulation is substantial. Fertilization experiments generally increase productivity and decrease diversity (e.g., Bakelaar and Odum 1978; Tilman 1987; Carson and Barrett 1988). Light preemption by a well developed canopy is usually suggested as the factor causing the decrease in diversity (e.g., Tilman 1987; Carson and Barrett 1988; but see Carson and Pickett 1990 for the interacting role of light and water). Litter accumulation and decomposition are rarely measured and manipulated concomitantly with these enrichment experiments. We suggest that *both* litter accumulation and resource competition (e.g., light preemption by the canopy) may combine to promote low plant diversity in productive communities or following fertilization. Watt (1971, 1972), Wheeler and Giller (1982), and van der Valk (1986) came to similar conclusions concerning the role of litter for grassland, fen, and marsh communities respectively. Indeed, Tilman (1987) found that litter accumulation following fertilization in some old-fields in Minnesota promoted low plant diversity. Thus, competitive exclusion in productive communities may not always be the direct result of resource competition as previously argued (e.g., Tilman 1987; Carson and Barrett 1988), but also a result of litter accumulation (see also Grime 1979).

*Litter and disturbance.* Tilman (1983) found that animal disturbances that reduce the litter layer had their greatest impact in nutrient rich conditions where litter layers are likely to be highest. Thus, the importance of small disturbances in promoting species diversity in some communities (e.g., Armesto and Pickett 1985) may be linked to removal of the litter layer as well as to disrupting the established plant canopy (see also Watt 1971). A disturbance that only affects the canopy but not the litter layer may not provide seeds with the proper germination cues and consequently have little effect on diversity. A disturbance that only alters the litter layer may increase germination but allow only a few seedlings to survive into the fall (as in this study, Tables 2 and 3) partially due to light preemption by the canopy (Gibson 1988; Carson and Pickett 1990). Thus, similar canopy disturbances may have very different results in communities with similar architectures but different quantities of litter.

*Community organization and litter thresholds.* Our study and studies from other communities suggest that there

may be broad thresholds above or below which litter will either increase yield and diversity, have only a minor negative impact, or significantly reduce yield and diversity (see also Grime 1979 p. 164). We recognize that the effect of litter on the community may be influenced by individual species and in turn that many species will respond individually to litter quantity or quality (e.g., Winn 1985; Al-Mufti et al. 1977). Still, litter quantity alone may be a good predictor for community attributes such as diversity and productivity. Specifically, litter below approximately 100–300 g per m<sup>2</sup> has been shown to increase yield and diversity, probably by conserving soil moisture (e.g., Glendenning 1942; Winn 1985; Willms 1986). Litter accumulation between 300 and 900 g per m<sup>2</sup> often has little effect on community production or biomass and variable effects on plant diversity and density (Penfound 1964; Willms 1986; this study). Litter above 900 g per m<sup>2</sup> generally decreases productivity and diversity as well as plant reproduction (Weaver and Rowland 1954; Old 1969; Knapp and Seastedt 1986; this study). Although the thresholds for each threshold category were lower, Sydes and Grime (1981a) came to similar conclusions for the effects of deciduous tree leaf litter on woodland herbs in England. Deciduous tree leaf litter characteristically has a higher surface to volume ratio than herbaceous litter. Therefore, a smaller quantity of tree leaf litter may intercept more light and also act as a more formidable barrier to seedlings than herbaceous litter. These generalizations may not hold up in all communities, nevertheless, they may serve as approximate indicators or testable hypotheses concerning the potential impact of litter on community organization.

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#### References

- Abbot DT, Crossley DA (1982) Wood litter decomposition following clear cutting. *Ecology* 63:35–42
- Al-Mufti MM, Sydes CL, Furness SB, Grime JP, Band SR (1977) A quantitative analysis of shoot phenology and dominance in herbaceous vegetation. *J Ecol* 65:759–791
- Armesto JJ, Pickett STA (1985) Experiments on disturbance in old-field plant communities: impact on species richness and abundance. *Ecology* 66:230–240
- Barrett LI (1931) Influence of forest litter on the germination and early survival of Chestnut Oak, *Quercus montana* (Willd). *Ecology* 12:476–484
- Bakelaar RG, Odum EP (1978) Community and population level responses to fertilization in an old-field ecosystem. *Ecology* 59:660–665
- Baskin JM, Baskin CC (1977) Role of temperature in the germination ecology of three summer annual weeds. *Oecologia* 30:377–382

- Baskin JM, Baskin CC (1988) Germination ecophysiology of herbaceous plant species in a temperate region. *Am J Bot* 75:286-305
- Bazzaz FA (1979) The physiological ecology of plant succession. *Ann Rev Ecol Syst* 10:351-371
- Bazzaz FA, Mezga DM (1973) Primary productivity and microenvironment in an *Ambrosia* dominated old-field. *Am Mid Nat* 90:70-78
- Beatty SW, Sholes ODV (1988) Leaf litter effect on plant species composition of deciduous forest treefall pits. *Can J For Res* 18:553-559
- Carson WP, Barrett GW (1988) Succession in old-field plant communities: effects of contrasting types of nutrient enrichment. *Ecology* 69:984-994
- Carson WP, Pickett STA (1990) Role of resources and disturbance in the organization of an old-field plant community. *Ecology* 71:226-238
- Cheplick GP, Quinn JH (1987) The role of seed depth, litter, and fire in the seedling establishment of amphicarpic peanutgrass (*Amphicarpum purshii*). *Oecologia* 73:459-464
- Dyksterhuis EJ, Schmutz EM (1947) Natural mulches or litter of grasslands: with kinds and amounts on a southern prairie. *Ecology* 28:163-179
- Facelli JM, Carson WP (1990) Heterogeneity of litter accumulation in seral communities. *Bull Torr Bot Club* (in press)
- Facelli JM, Pickett STA (1990) Plant litter: its dynamics and effects on plant community structure. *Botanical Review*
- Fenner M (1985) *Seed Ecology*. Chapman and Hall Ltd. New York, New York, 150 pp
- Fowler NL (1986) Microsite requirements for germination and establishment of three grass species. *Am Mid Nat* 115:131-145
- Fowler NL (1988) What is a safe site? neighbor, litter, germination date, and patch effects. *Ecology* 69:947-961
- Gibson DJ (1988) The maintenance of plant and soil heterogeneity in dune grassland. *J Ecol* 76:497-508
- Gleason HA, Cronquist A (1963) *Manual of vascular plants of northeastern United States and adjacent Canada*. Willard Grant Press, Boston, Mass. USA
- Glendenning GE (1942) Germination and emergence of some native grasses in relation to litter cover and soil moisture. *J Am Soc Agron* 34:797-804
- Goldberg DE, Werner PA (1983) The effect of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia* 60:149-155
- Grime JP (1979) *Plant strategies and vegetation processes*. John Wiley and Son, New York, USA
- Gross KL (1984) Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. *J Ecol* 72:369-387
- Gross KL, Werner PA (1982) Colonizing abilities of biennial plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63:921-931
- Hamrick JL, Lee JM (1987) Effect of soil surface topography and litter cover on the germination, survival, and growth of musk thistle (*Carduus nutans*). *Am J Bot* 74:451-457
- Heady HF (1956) Changes in a central California annual plant community induced by manipulation of natural mulch. *Ecology* 37:798-811
- Hopkins HH (1954) Effects of mulch upon certain factors of the grassland environment. *J Range Mgt* 7:255-258
- Hulbert LC (1969) Fire and litter effects in undisturbed blue stem prairie. *Ecology* 50:874-877
- Jong TJ de, Klinkhamer PGL (1985) The negative effects of litter of parent plants of *Cirsium vulgare* on their offspring: autotoxicity or immobilization. *Oecologia* 65:153-160
- Knapp AK, Seastedt TR (1986) Detritus accumulation limits productivity of tallgrass prairie. *Bioscience* 36:662-668
- Livingston RB, Allesio ML (1968) Buried viable seeds in successional field and forest stands, Harvard Forest, Mass. *Bull Torr Bot Club* 95:58-69
- Mackinney AL (1929) Effects of forest litter on soil temperature and soil freezing in autumn and winter. *Ecology* 10:312-321
- Monk CD, Gabrielson FC (1985) Effects of shade, litter and root competition on old-field vegetation in South Carolina. *Bull Torr Bot Club* 112:383-392
- Odum EP (1960) Organic production and turnover in old field succession. *Ecology* 41:34-49
- Old SM (1969) Microclimate, fire and plant production in an Illinois prairie. *Ecol Monogr* 39:355-384
- Oosting HJ, Humphries ME (1940) Buried viable seeds in a successional series of old-field and forest soils. *Bull Torr Bot Club* 67:253-273
- Penfound WT (1964) Effects of denudation on the productivity of grassland. *Ecology* 45:838-845
- Peterson DL, Bazzaz FA (1978) Life cycle characteristics of *Aster pilosus* in early successional habitats. *Ecology* 59:1005-1013
- Pickett STA, Baskin JM (1973) The role of temperature and light in the germination behavior of *Ambrosia artemisiifolia*. *Bull Torr Bot Club* 100:165-170
- Rice EL (1984) *Allelopathy*, Second Edition, Academic Press, NY USA
- SAS Institute (1985) *SAS Users Guide: Statistics*. Cary, NC, SAS Institute Inc.
- Seastedt TR (1988) Mass, nitrogen, and phosphorus dynamics in foliage and root detritus of tallgrass prairie. *Ecology* 69:59-65
- Snedecor GW, Cochran WG (1989) *Statistical Methods*. Eighth Edition, Iowa State University Press, Ames, Iowa USA
- Sokal JR, Rohlf RR (1981) *Biometry*. Second Edition, WH Freeman, San Francisco, CA, USA
- Swieringa S, Wilson RE (1972) Phenodynamic analyses of two first-year old fields. *Am J Bot* 59:367-372
- Sydes C, Grime JP (1981 a) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland. I. Field investigations. *J Ecol* 69:237-248
- Sydes C, Grime JP (1981 b) Effects of tree leaf litter on herbaceous vegetation in deciduous woodland II. An experimental investigation. *J Ecol* 69:249-262
- Tilman D (1983) Plant succession and gopher disturbances along an experimental gradient. *Oecologia* 60:285-292
- Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecol Monogr* 57:189-214
- Ugolini FC (1964) Soil development on the red beds of New Jersey. *W.L. Hutcheson Mem For Bull* 2:1-34
- Valk AG van der (1986) The impact of litter and annual plants on recruitment from the seed bank of a lacustrine wetland. *Aquat Bot* 24:13-26
- Vitousek P (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119:553-572
- Watt AS (1971) Factors controlling the floristic composition of some plant communities in Breckland. In: Duffey E, Watt AS (eds), *The scientific management of animal and plant communities for conservation*, Blackwell Scientific Publications, Oxford, England, pp 137-152
- Watt AS (1974) Senescence and rejuvenation in ungrazed chalk grassland (grassland B) in Breckland: the significance of litter and of moles. *J Appl Ecol* 23:1157-1171
- Weaver JE, Roland NW (1952) Effects of excessive natural mulch on development, yield, and structure of native grassland. *Bot Gaz* 114:1-19
- Weigert RG, McGinnis JT (1975) Annual production and disappearance of detritus on three South Carolina old-fields. *Ecology* 56:129-140
- Werner PA (1975) The effects of plant litter on germination in teasel, *Dipsacus sylvestris* Huds. *Am Mid Nat* 94:470-476
- Wheeler BD, Giller KE (1982) Species richness of herbaceous fen vegetation in Broadland, Norfolk in the relation to the quantity of above-ground plant material. *J Ecol* 70:179-200
- Willms WD, Smoliak S, Bailey AW (1986) Herbage production following litter removal on Alberta Native grasslands. *J Range Mngt* 39:536-540
- Winn AA (1985) Effects of seed size and microsite on seedling emergence of *Prunella vulgaris* in four habitats. *J Ecol* 73:831-840