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Plant Litter: Its Dynamics and Effects on Plant Community Structure

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I. Abstract

We discuss the dynamics of plant litter, the effects of litter on the chemical and physical environment, the direct and indirect effects of plant litter on plant populations and communities, and different adaptative traits that may be related to litter accumulation. The production of litter depends primarily on the site productivity, but other properties of the environment, as well as chance, may introduce important variation. The existence of time lags between the production of plant organs and their transformation into litter appears as a relevant character of litter dynamics seldom included in models. Herbivory, and other processes that destroy biomass or reduce productivity, may reduce the amount of litter produced. The destruction of litter encompasses a complex of interactions. The main processes, including physical and chemical degradation, consumption by invertebrates and decomposition, are differentially affected by the environment and by the physical and chemical characteristics of the litter itself. The relative importance of those processes varies among systems.

Litter alters the physical and chemical environment directly and indirectly. The decomposition of litter may release both nutrients and phytotoxic substances into the soil. The physical changes produced by litter also alter the activity of decomposers, resulting in an indirect effect on the chemical environment. The accumulated litter intercepts light, shading seeds and seedlings, and reduces the thermal amplitude in the soil. By reducing maximum soil temperatures, and creating a barrier to water vapor diffusion, litter reduces evaporation from the soil. However, litter may also diminish water availability when it retains a large proportion of rainfall. Litter creates a physical barrier for seedling and sprout emergence and to seeds reaching the soil.

The heterogeneity introduced into the abiotic environment by the patchy accumulation of litter may affect community structure. This effect may be both direct (when the litter of one species affects the performance of a second species) or indirect (when litter produced by one species alters the outcome of the interaction between a second and a third species).

Litter tolerance, timing of litterfall to optimize external nutrient recycling, and accumulation of litter to deter competitors (either through physical or chemical effects) have been postulated as strategies associated with litter accumulation. The existing evidence shows that only tolerance to litter accumulation admits adaptative value as the most likely explanation.

Resumen

En ésta revisión bibliográfica analizamos la dinámica de la broza, sus efectos sobre el ambiente físico y químico, y los efectos directos e indirectos de la acumulación de broza sobre la estructura y dinámica de las poblaciones y comunidades vegetales. Finalmente, analizamos distintas adaptaciones de las poblaciones vegetales relacionadas con la acumulación de broza.

La cantidad de broza acumulada en un sitio depende primariamente de su productividad, pero varios otros factores ambientales, así como el azar, pueden introducir importantes variaciones. El lapso entre la formación de un órgano y su muerte y caída, puede ser un factor de gran importancia en la dinámica de la broza. El consumo heterotrófico, así como otros factores físicos que destruyen biomasa o reducen la productividad, también puede afectar su acumulación. La destrucción de la broza constituye un proceso cuasi-sucesional. Los principales subprocesos involucrados—fragmentación física, consumo por invertebrados y descomposición—son controlados por factores ambientales y por las propiedades de la broza misma.

La acumulación de broza puede afectar profundamente el ambiente físico y químico. Los cambios físicos que induce pueden alterar la actividad de los descomponedores, mientras que su descomposición libera nutrientes y compuestos fitotóxicos en el suelo. La broza intercepta luz, sombreando semillas y plántulas, y reduciendo la amplitud térmica del suelo. Al reducir la temperatura del suelo, y al crear una barrera a la difusión del vapor de agua, la broza reduce la evaporación desde el suelo. Sin embargo, puede también disminuir la disponibilidad de agua, si retiene una proporción considerable de la lluvia. Además, la broza constituye un barrera física que puede impedir la llegada al suelo de algunas semillas, así como dificultar la emergencia de plántulas y brotes.

Los patrones de acumulación de broza introducen heterogeneidad temporal y espacial, que puede afectar la estructura y dinámica de la comunidad. Sus efectos pueden ser directos (cuando la presencia de broza afecta el éxito de una población) o indirectos (cuando el efecto de la broza sobre una población altera el resultado de la interacción con una segunda). Adicionalmente, la broza puede afectar las comunidades de invertebrados, lo que puede a su vez repercutir en la comunidad vegetal.

Varios autores han propuesto que la tolerancia a la presencia de broza, la regulación del ciclo de nutrientes mediante distintas estrategias foliares, y la producción de broza como un medio de combatir competidores mediante sus efectos físicos o químicos, son componentes de estrategias adaptativas de distintas poblaciones. La evidencia disponible sugiere que sólo la tolerancia a la broza acepta valor adaptativo como explicación más verosímil.

II. Introduction

The accumulation of litter may affect the environment and the plant community structure and dynamics in many different ways. A practical knowledge of the manifold effects of litter is reflected in many traditional agricultural practices. In central Europe farmers probably started applying litter removed from the forest floor to plowed fields before the Iron Age (Ellenberg, 1988: 24). The use of natural mulching is still a common practice in low-technology agriculture (e.g., Simpsom & Grumbs, 1986a, 1986b) and in modern horticulture and gardening (see e.g., Davies, 1988). Litter may be used to reduce weed infestation (e.g., Davies, 1988; Evans, 1972), to prevent soil freezing (McKinney, 1929), to reduce evaporation (Holland & Coleman, 1987; Weaver & Rowland, 1952), and to prevent soil erosion (Dyksterhuis & Schmutz, 1947; McGinnies, 1987). The addition of litter has successfully improved strip mine reclamation (Day et al., 1986; McGinnies, 1987). Foresters and range managers have always appreciated the importance of litter, and many management schemes address its function in the ecosystem (e.g., Barrett, 1931; Koroleff, 1954; Larson & Whitman, 1942; see Dyksterhuis & Schmutz, 1947 for an early review).

Litter production and decomposition have been widely studied during the last half century, with most studies focusing on the role of litter on the carbon balance (e.g., Golley, 1965; Mellinger & McNaughton, 1975; Odum, 1960; Olson, 1963), and the cycling of nutrients (e.g., Boerner, 1983; Furniss & Ferrar, 1982; Holland & Coleman, 1987). More recently, many researchers have investigated the effects of litter on particular populations (e.g., Cheplick & Quinn, 1987; Hamrick & Lee, 1987; Schlatterer & Tisdale, 1969; Werner, 1975), but only recently have some studies focused on the effects of litter on community structure and dynamics (e.g., Beatty & Sholes, 1988; Carson & Peterson, 1990; Facelli & Pickett, in press; Monk & Gabrielson, 1985; Sydes & Grime, 1981a, 1981b). Few attempts have been made to understand the mechanisms underlying the effects of litter on plant populations and communities.

Here we review the literature on the influence of litter on plant community structure and dynamics. The processes that determine patterns of litter accumulation are analyzed to develop a conceptual model that highlights the complexity of the processes involved, and the heterogeneity of the accumulation of litter in time and space. We analyze how the amount and type of litter may affect the physical and chemical environment, and how these environmental changes alter the plant community organization. Finally, we discuss the possible importance of adaptative traits related to litter accumulation.

For this analysis we define plant litter as the dead plant material of small size lying loose on the ground; we excluded boles and large branches (see Harmon et al., 1986, for a review on the dynamics of large woody debris and coarse litter). In some cases, the dead organs of some herbs, and those of most perennial grasses, remain standing upright for some time. In addition, there are gradations in the position of the dead organs, from standing to lying on the ground, and no clear limit can be set. Depending on the objectives of different studies, some material may or may not be pooled into the litter category. Underground dead plant material certainly affects the soil environment and may be an important factor in community dynamics (see e.g., various chapters in Fitter et al., 1985). However, the dynamics and effects of underground dead material is outside the scope of this review. Species names follow the usage of the original source cited.

III. Patterns of Litter Accumulation

The amount of litter accumulated in a given site is determined by a balance among in situ litter production, deposition of litter from outside the system, litter destruction by physical and biotic agents, and removal of litter. In this section we analyze these four processes, to identify the key factors in the dynamics of litter in different ecosystems.

A. LITTER PRODUCTION

Litter production depends primarily on the productivity of the plant community at a site. In their review of litter accumulation in woodlands Bray and Gorham (1964) found that similar factors determined litter production and primary productivity.

The first determinant was climate, with rainfall and length of the growing season as the main components. Soil fertility, soil water retention, and species composition were important within the same climatic range. Meentemeyer et al. (1982) developed a global model of litter production and found good correlation with climatic factors. Actual evapotranspiration (AET) explained the variation better than latitude or potential evapotranspiration. Soil characteristics related to fertility also added some accuracy to the model. Vitousek (1984) found that the correlation between litterfall and AET was lower when the model was applied only to tropical rain forests, highlighting the importance of different variables at smaller scales.

Herbivores may either increase or decrease the production of litter, though consumption usually reduces the standing biomass and therefore the amount of litter produced. The proportion of biomass consumed varies considerably among systems. It is negligible in young oldfields and mature woodlots, where most of the biomass produced is transformed into litter (Odum, 1960). According to Whittaker and Woodwell (1969) only 9% of the yearly production in an oldfield was consumed by arthropods. Similar values are characteristic for temperate deciduous forest, and even lower (less than 2%) for evergreen forests (Waring & Schlesinger, 1985). In contrast, primary consumers constitute the main pathway of the annual production in grasslands, where large grazers may reduce substantially the rates of litter accumulation (Dix, 1960; Hunt, 1978; Knapp & Seastedt, 1986; Weaver & Rowland, 1952). Herbivores may sometimes increase temporarily the production of litter because of the damage to and subsequent death of unconsumed organs (Choudhury, 1988; Hollinger, 1986; Owen, 1978; Risley & Crossley, 1988). Some herbivores, e.g., grasshoppers, cut more leaves than they consume (Rodell, 1978).

The existence of time lags between the formation of a plant organ and its deposition as litter is one of the factors that appears as largely relevant at the small scale, though it may be unimportant at large temporal and spatial scales. Time lags may depend on the dominant form of life (Golley, 1965). Far less than 50% of the annual production of woodlands becomes litter within a year (Olson, 1963), but in herb-dominated oldfields, most aerial biomass is transformed into litter at the end of the growing season (Golley, 1965). Differences in time lags may be important even within biomes. Standing dead material may be transformed faster into litter in semiarid and moist grasslands than in subhumid ones (Hunt, 1978). Trampling, snow packing, winds, and storms may affect the speed of that transformation. In addition, different organs may have different characteristic time lags. Dead branches usually remain on shrubs and trees for a long time, but most leaves fall as they die (Noy-Meir, 1985; Olson, 1963; Sprugel, 1984). In forest undergoing wave regeneration, fall of leaves as litter may follow immediately the death of the canopy, but the fall of dead branches and bark may be delayed for several years; a pulse of branch mortality may be reflected in the litter production only after ten years (Sprugel, 1984).

B. LITTER DISAPPEARANCE

The mass of litter accumulated may be reduced by physical and chemical degradation, heterotrophic consumption, and decomposition. These processes are tightly interrelated, either as competitive or sequential processes. Decomposition is probably the most important, and certainly the most widely studied, process of litter destruction. Decomposition rates have been calculated for different substrates in many different environments (e.g., Andren & Paustian, 1987; McClaugherty et al., 1985). However, in various of the models of litter dynamics that have been developed (e.g., Andren & Paustian, 1987; Olson, 1963), decomposition submodels have been found to be too simplistic (Furniss & Ferrar, 1982; Spain & Lefevre, 1987) and do not always account for the intrinsic complexity of the litter (McClaugherty & Berg, 1987), nor the role of complex heterotrophic interactions on the substrate quality (Anderson, 1975; Pastor et al., 1987; Scheu, 1987). Decomposition rates vary greatly among ecosystems (Olson, 1963). Faster rates are found in tropical forest (Jenny et al., 1949), and slower rates in subalpine systems (Olson, 1963). Litter decomposition is regulated mainly by temperature and water regimes; soil fertility may be secondarily important (Staaf, 1987). Yearly environmental variations affect decomposition rates within a given system. Escudero et al. (1987) found that the patterns of decomposition in an evergreen oak forest with continuous litter production, was a function of the climate of the season the leaves were shed (see also Madge, 1965). Decomposition was faster in autumn than in summer, because of summer water limitation. In deserts, decomposition is negligible during most of the year because lack of water limits microbial activity on the soil surface. Instead, physical and chemical degradation (Moorhead & Reynolds, 1989), and consumption by termites may predominate (Noy-Meir, 1985).

The microenvironment surrounding the litter affects the decomposition rate (Furniss & Ferrar, 1982), creating patchiness in litter accumulation. Litter incorporated into the soil by tillage is decomposed faster than litter remaining on the soil surface (Stinner et al., 1984). In grasslands, decomposition is faster when trampling by cattle or snow packing enhance the contact of litter with the soil (Dix, 1960; Knapp & Seastedt, 1986). Litter exposed to air is decomposed mostly by fungi because fungi resist water stress better than bacteria, but this may result in slower decomposition because fungi become limited by nitrogen (Holland & Coleman, 1987). In flooded habitats, biochemical decomposition may be limited by low oxygen concentration and low pH (Polunin, 1984). However, Day (1983) found that litter disappeared faster in the wettest sites of a lowland forest; pulses of flooding may hasten decomposition due to enhanced leaching, and the consequent changes in litter quality. In aquatic systems litter is mixed with inorganic debris. The chemical and physical properties of that debris is the main determinant of the decomposition rates of litter (Polunin, 1984).

The chemical composition of the litter is another important variable affecting decomposition rates (Day, 1983; Furniss & Ferrar, 1982). The contents of lignin, nitrogen, hemicellulose, cellulose, and secondary compounds (particularly phenolic acids) are the most conspicuous variables (Berendse et al., 1987; Choudhury, 1988; Golley, 1965; Horner et al., 1988; Meentemeyer, 1978; but see Staaf, 1987). Chemical composition varies with species, season, organs, and even between genotypes (Muller et al., 1987). Differences in the chemical binding between different compounds and the nature of the surface exposed to the decomposers (e.g., thickness of cuticle in leaves) may also be relevant (McClaugherty & Berg, 1987). Short-lived organs usually have less lignin (Berendse et al., 1987; Coley et al., 1985) and secondary chemicals (Choudhury, 1988; Coley et al., 1985; Rhoades & Cates, 1976) and consequently decompose faster. In contrast, long-lived organs usually have more lignin and secondary compounds, and the litter produced lasts longer; older leaves usually contain more lignin and less protein (Feeny, 1970) and also decompose slowly. Events that affect the senescence rates (e.g., freezing, competition, herbivory, etc.), may change the chemical composition of the litter (Polunin, 1984). Adverse growth conditions, such as low soil fertility, may also increase the concentration of tannin and phenolic compounds in leaves (Flanagan & van Cleve, 1983; Muller et al., 1987). Damage by insects may increase the concentration of secondary compounds or alter the properties of the surfaces exposed to the attack by decomposers (Choudhury, 1988; Feeny, 1970; Kaiser, 1983). For example, sycamore (*Platanus occidentalis* L.) leaves attacked by aphids decomposed more slowly than non-attacked leaves, because the fungus growing on the surface of the attacked leaves made them resistant to colonization by decomposers (Choudhury, 1988). These seemingly subtle differences may have important implications for the cycling of nutrients (see, e.g., Berendse et al., 1987). Horner et al. (1988) discussed the importance of secondary, carbon based metabolites, in the decomposition of litter, and their possible impact on nutrient dynamics. To our knowledge, the hypothesis that the induction of secondary compounds by herbivores may influence decomposition rates has not been tested experimentally.

Litter decomposition encompasses interactions among many populations and environmental variables (Gunnarsson et al., 1988; see Kurihara & Kikkawa, 1986 for an analysis of the trophic interactions in communities of decomposers), each one affecting the quality of the litter as a substrate for other decomposers (see, e.g., Choudhury, 1988; Gunnarsson et al. 1988; Horner et al., 1988; Richards, 1987; Seastedt & Crosley, 1983; Weigert et al., 1970). In seagrass litter (*Zostera marina* L.), leaching and volatilization, which are increased by fragmentation, change the substrate quality (Kenworthy et al., 1987), making litter available for invertebrates and decomposers (Harrison & Mann, 1975; Wahebh & Mahasheh, 1985). The size of the particles left by litter consumers determines which organisms are likely to attack the material subsequently (Furniss & Ferrar, 1982; see also Hagvar, 1988; Richards, 1987). In the absence of earthworms or other invertebrates that fragment the litter, microbial decomposition may be very slow, and litter persists longer (see Lee, 1985 for a review on the ecology of litter-dwelling earthworms). Studies conducted on subhumid and arid systems, where earthworms are scarce or absent, suggest that physical fragmentation is needed to make litter available to arthropods and to trigger microbial activity (Montaña et al., 1988; Noy-Meir, 1985). Factors that affect the structure of the arthropod community may strongly influence litter dynamics (Madge, 1965). For example, the structure of arthropod communities in deserts is shaped by long term rain patterns, and the disappearance of litter may depend mostly on such long term patterns rather than on the actual precipitation for a given year (Santos et al., 1984). Accordingly, Elkins et al. (1982) and Whitford et al. (1982) found that litter disappearance is independent of actual annual evapotranspiration (AET) in deserts with high densities of termites. However, Strojan et al. (1987) found that litter persistence was increased by a prolonged drought. It is likely that extreme drought and heat may limit the activity of arthropods on, or close to, the soil surface (Whitford et al., 1982).

Fire is probably the most important abiotic agent of litter destruction, though photodegradation was pointed out by Moorhead and Reynolds (1989) as a main pathway of litter degradation in deserts. Fire is dominant in heathlands (Gimingham, 1972), savannas (Hopkins, 1966), and in some grasslands and forests (Boerner, 1983; Knapp & Seastedt, 1986; Risser et al., 1979). Boerner (1983) found that differences in litter accumulation produced by prescribed burning in the New Jersey Pine Barrens persisted for at least 3 years. The effect of burning the litter of a grassland persisted for two growing seasons (Dix, 1960). Watt (1956) showed that destruction of litter by fire is uneven and may produce a patchy distribution of litter, and suggested that this patchiness may affect the community structure.

C. LITTER MOVEMENT

The deposition of exogenous litter and the removal of the native litter are seldom considered in litter balances. The importance of litter movement depends mainly on the nature of the transporting medium (i.e., water or air) (Polunin, 1984), the geometry and specific weight of the litter (Orndorff & Lang, 1981) and the geometry of the environment (MacMahon & Wagner, 1985; Noy-Meir, 1985; Orndorff & Lang, 1981). Litter movement may be very important in aquatic systems, where the energy transmitted by the fluid is large, and litter floats easily (Kenworthy et al., 1987; Polunin, 1984), and in deserts, due to their open structure and to the lightness of dry litter. In deserts, fragmented or intact material is extensively rearranged by wind, transported from open areas to the surroundings of large shrubs and to depressions (MacMahon & Wagner, 1985; Noy-Meir, 1985; West, 1979). Removal of fragmented litter may be a main cause of litter disappearance from open sites (Montaña et al., 1988; Noy-Meir, 1985). Runoff water can also remove litter from higher points and accumulate it in lower areas during torrential rainfall events (Noy-Meir, 1985; Whitford et al., 1982). The geometry of the shrubs (number, diameter, and density of branches) may control the type and amount of litter retained (MacMahon & Wagner, 1985). Wind and waterflow rearrange litter in deciduous (Orndorff & Lang, 1981; Shure & Gottschalk, 1985; Whitford et al., 1982) and tropical forests (Coelho Neto, 1987). Litter moves mostly down slopes, and fallen logs and branches may retain litter and create a marked patchiness in the distribution of litter (Orndorff & Lang, 1981). Litter of pines tends to be accumulated asymmetrically around tree boles, and markedly so on slopes (Frankland et al., 1963). In different sized deforested gaps (from 0.016 to 10 ha in size), the input of leaf litter transported by wind from the surrounding woodland may be as important as the in situ production (Shure & Phillips, 1987), the amount decreasing with increasing distance from the forest edge. A similar pattern was observed in oldfields bordering woodlots (Facelli & Carson, in press). The amount of tree leaves deposited close to the field-woodland edge may be enough to affect the successional community structure (Facelli & Pickett, in press).

D. TEMPORAL VARIATIONS

The amount of litter at a given site may vary widely because of different rates of litter production and destruction. Accumulated litter may vary more or less regularly on successional and seasonal time scales, but may also vary following transient environmental fluctuations. Both the intensity and timing of these variations may affect the litter dynamics, acting indirectly on community structure.

1. Successional Trends

Olson (1963) predicted a rapid accumulation of litter during succession, and a further steady state or quasi-equilibrium. Because Primary Net Productivity (PNP) is initially higher than consumption and decomposition, there is a net accumulation in early succession. A dynamic equilibrium should be reached as PNP diminishes and decomposition rates increase (Olson, 1963; cf. Odum, 1969). Productivity peaks associated with turnover of dominants (Whittaker, 1970), environmental fluctuations, and the existence of time lags in litter accumulation (Golley, 1965) may cause less definite patterns than those predicted by most models.

Surprisingly, there is scarce empirical information on the patterns of litter accumulation through succession. Most available studies deal with single successional stages—i.e., periods without change in the dominant form of life. Perino and Risser (1972) reported that litter increased steadily along four stages (assumed to correspond to a 40 year span) of secondary succession in a tallgrass prairie. Odum (1960) found that litter increased from nearly 50 g/m^2, in a recently cropped field, to around 350 g/m^2 in a third year oldfield dominated by biennials, and reached ca. 500 g/m^2 when perennial grasses began to dominate. Golley and Gentry (1966) found more dead plant material in a twelfth year oldfield community than in a first year oldfield, and Golley (1965) reported a sixfold increase during 11 years of broomsedge dominance. In contrast, Wiegert and Evans (1964) found no change in the amount of litter in a herb-dominated oldfield during an eleven year period. Mellinger and McNaughton (1975) did not find any evidence of litter accumulation when studying oldfields in Central New York ranging from 4 to 36 years. Facelli and Carson (in press) found only slight differences among four oldfields (aged 5, 15, 23 and 29 years) in the New Jersey Piedmont, but the four oldfields had far less total litter than a 47 years old woodlot and an old-growth forest. These results combined suggest a rapid accumulation of litter during very early stages, a temporary equilibrium during mid stages, and a second phase of accumulation when trees displaces the dominant herbs.

2. *Seasonal Variations*

Litter production exhibits definite seasonal patterns, which vary with latitude and vegetation type (Bray & Gorham, 1964). In equatorial rain forests litter production is even throughout the year, while in temperate evergreen forests there are peaks related to leaf production and leaf life span. In xerophytic woodlands the peak of litter production may be either at the beginning or near the end of the dry period, depending on the foliar strategies of the dominant populations (Hopkins, 1966; Madge, 1965).

Environmental factors not directly related to phenology also affect the seasonal patterns. In two riverine forests of Belgium, woody litter increased during the winter due to the strong winds (Hermy, 1987). Christensen (1975) also found that the fall of branches was determined by seasonal strong winds, and that previous climatic conditions (like water shortage during the summer) may predispose trees to higher litterfall. In bracken communities, fronds are transformed into litter by physical agents, such as winds, snowfalls, and rains at the beginning of the winter (Watt, 1956). Maximum litter accumulation in oldfields often occurs after the first killing frosts (Odum, 1960).

Litter production in desert ecosystems is mainly an episodic process (West, 1979) because drought and hot winds produce pulses of leaf mortality. In species that evade drought by becoming dormant, the beginning of the dry season produces a pulse of leaf death, but leaves persist in species that tolerate desiccation. Rainfall events that promote the formation of new leaves often cause the abscission of the older ones (West, 1979). Since leaf production in deserts is closely linked to rainfall, litterfall variations among years may be large (Strojan et al., 1987). In addition, storms, snow and wind can also produce pulses of litter accumulation by damaging branches and twigs (West, 1979).

The seasonal peaks of litter accumulation may change with the successional age of the site (Perino & Risser, 1972). Odum (1960) found that seasonal differences were more conspicuous in young oldfields than in older ones (see also Mellinger & McNaughton, 1975). Facelli and Carson (in press) found that the difference between the litter accumulated in spring and fall diminished linearly with the age of the site. Stinner et al. (1984) found more gradual litter deposition in an oldfield and in a non tillage agroecosystem than in a field after conventional tillage.

3. *Fluctuations*

Large, less predictable variations in accumulated litter are superimposed on successional and seasonal patterns (Bray & Gorham, 1964). Events such as fire, wind storms, dry and hot winds, ice storms, and cool waves may produce important pulses, depending on the phenologic condition of the community and the community composition (Bruederle & Stearns, 1985). Bray and Gorham (1964) reported that species with shallow root systems shed more leaves during a drought than species with deeper roots. In aquatic communities, storms, episodic insect attacks, and icing may be the main determinants of litter accumulation (Polunin, 1984). Herbivores that sever leaves (e.g., grasshoppers, Rodell, 1978), or promote leaf abscission (Choudhury, 1988; Risley & Crossley, 1988) may also produce pulses of litter accumulation. It has been proposed that plants can reduce nutrient losses to herbivores by reabsorbing nutrients, and shedding the leaves soon after the beginning of the attack (Owen & Wiegert, 1976; but see Stiling & Simberloff, 1989). Fires may produce changes in litter composition. In heathlands and savannas, fire consumes the litter of grasses, and accelerates the transition of organs of woody species to litter (Gimingham, 1972). Depending on the disturbance agent and time of the year, litter produced by infrequent events may have properties different from the litter produced during the normal season of peak litter production (Polunin, 1984).

E. A MODEL OF LITTER DYNAMICS

The variables of a global model may not be accurate predictors of litter accumulation in a specific point at a specific time [see as an example the criticism by West (1985) of the global model by Meentemeyer et al., 1982]. The development of models for small temporal and spatial scales requires a more detailed understanding of all major processes determining litter accumulation at those particualar scales (cf. Pickett et al., 1987). Differential litter production and destruction (Olson, 1963), and episodic deposition or removal (Orndorff & Lang, 1981; West, 1979) may introduce large variability in the amount and composition of the litter mat within small distances (Watt, 1956, 1970). This heterogeneity may be partially related to the heterogeneity of the habitat (Watt, 1970) (e.g., more productive patches, patches with faster decomposition, or topographic features that favor litter removal of deposition) or to the occurrence of events that are random and patchy by nature (e.g., branch fall, burrowing, etc.) (Facelli & Carson, in press).

We propose a conceptual model of litter dynamics (Fig. 1) to analyze the dynamics of litter at the site scale. We consider the death of plant organs produced in situ the main input of litter (Fig.1). This input depends primarily on the complex pattern of interactions affecting the acquisition of carbon by the plant community. Of all the biomass fixed by the plants (Gross Primary Production, GPP) a portion is lost by respiration, a portion is allocated to roots, and the rest (Net Aerial Production, NAP) is allocated to different organs (Fig. 1). The partition of biomass among different organs is determined primarily by the spectrum of life forms in the community (LFS).

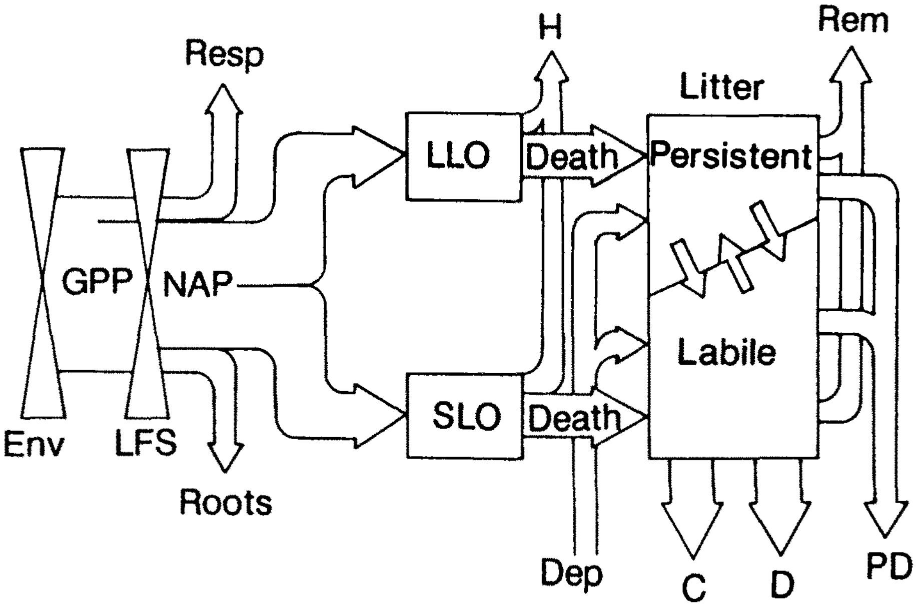

Fig. 1. Conceptual model of litter dynamics, showing the complexity of the processes determining litter accumulation and disappearance. The local environment (Env) determines the Gross Primary Production (GPP); a proportion of the production is respired (Resp) and a proportion is invested into subterranean organs (Roots). The remaining biomass (Net Aerial Production, NAP) is allocated either to long-lived organs (LLO) or to short lived organs (SLO). The allocation to underground biomass, and the partition between different types of aerial organs are regulated by the spectrum of life forms in the community (LFS). Before death, a proportion of biomass is consumed by herbivores (H). The fall of dead organs of different origin produces two different types of litter: persistent and labile litter. Litter accumulates also by deposition of litter produced outside the system (Dep). The arrows between the two types of litter represent the transformations of litter by leaching, arthropods and microorganisms, which hasten (or sometimes slow) decomposition (D) and consumption by invertebrates (C). Litter can also be destroyed by physical processes (PD) or removed by wind or water (Rem). Time lags (not explicitly shown) account for different dynamics, and responses to environmental variables (see text for further explanations).

In herbaceous communities almost all the aerial biomass is allocated to short-lived organs, whereas in forests a large proportion is allocated to long-lived organs (e.g., boles and branches) (Fig.1). Obviously, there is a continuum of life span for plant organs in nature; we consider only two extreme categories in the model for simplicity's sake. Differences in partitioning may affect the kind of litter produced, and the time lag between the acquisition of carbon and mineral nutrients, and the production of litter. Long-lived organs are usually more protected against herbivory than short-lived organs (Berendse et al., 1987; Coley et al., 1985; Rhoades & Cates, 1976). The proportion of biomass taken by herbivores from long- and short-lived organs may be different, which may affect the proportion of biomass that becomes litter (Fig. 1). Depending on the contents of structural and secondary compounds in the tissues, two different kinds of litter are produced: short-lived organs are transformed into easily decomposable litter, while litter from long-lived organs is more resistent to decomposition (Horner et al., 1988) (Fig. 1). Again, for simplification we only include in the scheme the two extremes from the natural continuum ranging from very labile (e.g., petals) to highly persistent litter (e.g., wood). Deposition, removal, and physical destruction may affect either type of litter; consumption and decomposition act mostly on labile litter (Fig. 1). Leaching and biological activity may transform one type of litter into another, either facilitating (e.g., by leaching of secondary compounds) or interfering with decomposers' and consumers' activity (e.g., when fungal activity accumulates antibiotics that deter other decomposers) (Fig. 1). The relative importance of each of these processes in determining the balance of litter at a given site may vary with the ecosystem considered (see previous discussion on litter accumulation).

IV. Effects of Litter on the Environment

Ultimately, all the effects of litter on living organisms are due, directly or indirectly, to effects of litter on the abiotic environment. In this section we discuss the different effects of litter on the environment, and how these changes relate to the physical and chemical properties of the accumulated litter.

A. THE CHEMICAL ENVIRONMENT

During the life and senescence of plant organs different organic and inorganic substances are accumulated. After the death of the organ, or sometimes during its senescence, these compounds are either released by leaching, or are attacked by decomposers and their products released into the soil. The chemical properties of the leachates (e.g., toxicity, mineral contents, solubility, etc.) will depend on the nature of the substances accumulated in the organ before its fall, and on the biochemical transformations produced by decomposers. Here we discuss the changes that these leachates produce on the chemical environment, and the potential effects on the plant community structure.

1. Availability of Mineral Nutrients

Nutrients allocated into aerial organs of plants are either retranslocated to other organs, consumed by herbivores or pathogens, or lost by the plant with the litter. The accumulation of organic matter on the top soil constitutes one of the main factors of soil development. At a nearly geological scale, differences in litter dynamics may cause the formation of different A_0 horizons (Prusienkiewicz & Bigos, 1978). The environmental conditions and physicochemical characters of the litter regulate the rate of nutrient release from the organic matter. The length of residence of nutrients in the litter varies greatly with the type of litter (see section III.E) and may greatly affect the nutrient dynamics. The relationship of decomposition patterns and the phenology of the plants in determining patterns of nutrient availability have been discussed by Escudero and del Arco (1987), and Flanagan and van Cleve (1983). More recently, the effects of previous herbivory and secondary compounds as factors affecting nutrient cycling have been stressed (Choudhury, 1988; Horner et al., 1988).

Litter also exerts important indirect effects on nutrient availability through changes in environmental variables that regulate mineralization. The elimination of litter in grasslands usually promotes the decomposition of organic matter due to increased soil temperatures, thereby increasing nutrient availability for the plants (Knapp & Seastedt, 1986). Accumulated litter in grasslands may also reduce losses of ammonia (Dyksterhuis & Schmutz, 1947; Pastor et al., 1987), decrease wet nitrogen deposition, and alter the chemical composition of rainfall reaching the soil (Knapp & Seastedt, 1986). In unplowed agricultural fields, litter retains mineral nutrients and reduces leaching (Pastor et al., 1987; Stinner et al., 1984), by the temporary immobilization of limiting nutrients by decomposers (Pastor et al., 1987; Rice, 1979).

The redistribution of litter by wind and water can rearrange the patterns of nutrient availability in the landscape (Orndorff & Lang, 1981). Shure and Gottschalk (1985) suggested that litter redistribution in floodplains is an important nutrient vector in the ecosystem. Patchy accumulation of litter can create a patchy distribution of nutrients. In the tundra, nutrient availability is higher beneath the tussocks of *Eriophorum vaginatum* L. because of litter accumulation and increased decomposition (Chapin et al., 1979). Kellman (1979) found higher concentrations of exchangeable nutrients beneath the canopies of trees in a Belize savanna. Litter accumulation, rather than weathering of mineral soil by the roots, seemed responsible for this phenomenon. Chronic litter collection by European farmers may have reduced the productivity of some forests because of the amount of nutrient exported (Bray & Gorham, 1964; Ellenberg, 1988: 24). Changes in patterns of nutrient availability due to litter redistribution are also evident in desert ecosystems (West, 1979, 1985). Litter accumulation beneath shrubs creates patches with increased nutrient availability (Strojan et al., 1987) that persist for some time after the death of the shrub (Noy-Meir, 1985). Litter accumulation may also produce high concentrations of toxic minerals. For example, litter of *Carya* is reported to have high concentrations of heavy metals (Cotrufo, 1977) that could be accumulated on the soil surface and hinder tree seedling establishment (McCarthy & Wistendahl, 1988). Accumulation of litter by halophyte shrubs that store salt in leaves may create patches with higher salt concentrations in deserts (West, 1979). Litter may also alter soil pH, which can affect nutrient availability. Addition of litter of aquatic macrophytes reduced soil pH in experimental pots (Szczeponska, 1977). Microbial decomposition, which is dominant in the absence of earthworms or other soil invertebrates, also reduces soil pH (Lee, 1985). The patchy accumulation of litter of *Calluna* spp. in heathlands lowers the soil pH, increasing the environmental heterogeneity of this factor.

2. *Production of Phytotoxins*

There are abundant references to phytotoxic effects produced by leaching or decomposition of litter (usually included as allelopathy; see review by Rice, 1979). Though the evidence on the negative effect of litter leachates on germination and growth is extensive (e.g., Abdul-Wahab & Rice, 1967; Carter & Grace, 1986; Rice, 1979; van der Valk, 1986; Welbank, 1963), the exact mechanisms are poorly understood. Most of the evidence is based on laboratory or greenhouse experiments in which addition of litter (or litter leachates) reduces the germination and/or the growth of seedlings of different populations (see review by Rice, 1979). The effect of litter leachates on the community structure has seldom been tested in the field, and its influence on the organization of natural communities remains unassessed. Some field studies showed inconclusive (e.g., Carter & Grace, 1986; Collins & Quinn, 1982; DeJong & Klinkhamer, 1985) or negative results (Rice & Parenti, 1978; West, 1979), and the relevance of the phytotoxic effects of litter have been questioned (e.g., DeJong & Klinkhamer, 1985; Stowe, 1979).

The effect of the addition of artificial (plastic or paper) litter on germination and establishment may be less severe than that of natural litter (Schlatterer & Tisdale, 1969; Sydes & Grime, 1981b; Werner, 1975), which suggests a biochemical effect of litter. However, nutrient immobilization, depletion of O_2 in the soil or toxicity of CO_2 produced by decomposers, as well as phytotoxicity may be involved (DeJong & Klinkhamer; 1985, Rice, 1979; Schlatterer & Tisdale, 1969). Carter and Grace (1986) found that at least part of the effect of leachates of *Justicia americana* L. on germination and growth of seedlings of *Polygonum lapathifolium* L. was due to the osmotic effects of the leachates. Indirect effects, e.g., through diminished nitrification (Mooney & Parson, 1973) can also account for the effects found in some studies. Even if phytotoxic effects where demonstrated beyond doubt in the laboratory or greenhouse, it is still possible that other factors, including other effects of litter may override the phytotoxicity in the field. In deserts, for example, litter may promote germination in spite of high contents of phenolic acids (West, 1979) because the improvement of water conditions outweighs the effect of the phytotoxic compounds.

Many of the experiments on litter phytotoxicity were performed with fresh litter or even with live clipped organs, which is unrealistic. Bokhari (1978) found that extracts of fresh leaf litter reduced the germination of grasses more than did old leaf litter (see also Sydes & Grime, 1981b). Leachates are lost very rapidly after organ senescence (Sydes & Grime, 1981b), and substantial changes in litter chemistry happen during the winter. The time elapsed between litter deposition at the end of the growing season and the reinitiation of growth in the following spring, may allow for the disappearance of any phytotoxic compound (Szczeponska, 1977). Sydes and Grime (1981b) found that the initial negative effects produced by litter leachates on seedling size disappeared long before the herbs reached the reproductive stage. In addition, the types of litter that produced more phytotoxicity were those that decomposed faster, and therefore the effect presumably should disappear rather rapidly (Sydes & Grime, 1981b). Szczeponska (1977) reported that litter addition initially reduced the growth of both *Phragmites communis* Trin. and *Typha latifolia* L., but growth rates became similar after three weeks. However, the differences in biomass persisted (see also Carter & Grace, 1986). It is evident that further studies must be conducted in a more realistic way (see e.g., Carter & Grace, 1986; Harper, 1977). Litter should be picked from the field just before the time of germination of the target population in the field. Experiments should be continued until the end of the life cycle, if possible, and the reproductive output assessed. Moreover, experiments should be designed and controlled to ensure that other effects are not confounded with toxicity.

B. The Physical Environment

The presence of litter alters the microenvironmental conditions of the top soil. Litter intercepts incident light and rain, and changes the surface structure, affecting the transfer of heat and water (and probably gasses) between the soil and the atmosphere. Such effects can act on plant community structure directly (through their effect on germination and establishment of plants) of indirectly (through changes in the resource availability and through the effect on other biotic components). In this section we consider the magnitude of these changes and their potential impact on plant community structure.

1. *Light Environment*

The importance of light interception by litter in open systems such as oldfields and grasslands is obvious, but it also may be important in systems with seasonally closed canopies such as deciduous forests (Ellenberg, 1988: 55). Weaver and Rowland (1952) showed that the total radiation below a dense mat of grass litter was 1 to 5% of that above the litter (see also Knapp & Seastedt, 1986). Shading by litter follows the light extinction law of Beer-Lambert, with an exponential reduction of the light intercepted as the amount of litter increases; different types of litter have different extinction coefficients (Facelli & Pickett, in press). Sydes and Grime (1981b) observed that the effect of litter was a function of the weight/surface ratio, suggesting that light interception by litter may exert an important effect on the plant community. The different effects of the litter of broadleaved trees and conifers on the ground vegetation may be partly due to their different shading properties (Ellenberg, 1988; cf. Facelli & Pickett, in press). Oddly, there is scarce information available on changes in light quality induced by litter; most authors assume that litter is a neutral filter, but this assumption has seldom been tested. Vázques-Yanes et al. (1990) showed that litter of tropical trees changed the spectral composition of light, especially when moist. Changes in the light spectrum may have important ecological significance, since light quality affects germination (Fenner, 1985; Vázquez-Yanes et al., 1990), seedling development (Ballaré et al., 1988), and tillering (Deregibus et al., 1985).

Litter may prevent the germination of plants that respond positively to light (Grime, 1979; Sydes & Grime, 1981b; Vázquez-Yanes et al., 1990). Spence (1982) attributed the negative effect of litter on the germination of reed (*Phragmites* sp.) to the interception of red radiation by litter. Seedling establishment may also be negatively affected through light deprivation by litter. Hamrick and Lee (1987) found higher mortality of seedlings of *Carduus nutans* L. that germinated under a thick layer of litter. They observed that these plants had larger hypocotyls than those growing with less or no litter, and suggested that mortality was due to the energy spent in penetrating the litter mat. Even the establishment of species with very large seeds may be hindered by litter. Barrett (1931) found that a dense litter mat diminished the germination of oak, and that a large proportion of the seedlings growing under litter were etiolated, or were so elongated that they were more prone to mechanical damage. Tao et al. (1987) also found that shading by litter inhibited the growth of tree seedlings, and Herman and Chilcote (1965) reported increased damping off of Douglas fir seedlings shaded by litter (see also Koroleff, 1954).

Sprouting of perennial herbs may also be negatively affected as a result of light deprivation by litter. The shading produced by the accumulation of litter in *Phragmites* communities reduced shoot density (Haslam, 1971). Grass shoots growing under dense litter must spend significant energy to reach the light, and the resulting tillers have morphological and physiological characters that lessen their capacity to fix carbon (Knapp & Seastedt, 1986). Willms (1988) reported that litter accumulation within the crown of *Festuca scabrella* Trin. reduced productivity, and that litter removal increased the photosynthetically active radiation (PAR) at the base of the tillers, which resulted in a significant increase of productivity in a Tall Fescue prairie.

2. *Soil Temperature*

Litter modifies soil temperature by intercepting solar radiation, and by insulating the soil from air temperature (Evans & Young, 1970; McKinney, 1929). McKinney (1929) reported that litter delayed the freezing of forest soils, and that freezing was more shallow. He also noticed increased time lags in the soil temperature profile when litter was present. Weaver and Rowland (1952) found that the soil temperature in a "mulched" grassland was 8°C lower than that in an unmulched one, and that the temperature of the air was higher than that of the soil surface under the litter. Hulbert (1969) found that both burning and hand litter removal increased the soil temperatures in a grassland by 5°C during the entire growing season. Unburied crop residues may produce similar effects on the soil temperature (Holland & Coleman, 1987).

Changes in soil temperature produced by litter may directly affect plant growth, but may also enhance the rates of mineralization, and therefore nutrient availability (e.g., Chapin et al., 1979; Knapp & Seastedt, 1986). Early sprouting of grasses after litter removal may be more a result of increased soil temperature, than of changes in nutrient availability produced by fire (Penfound, 1964). In grasslands with dense litter accumulation, plants grow more slowly and flower more sparsely due to lower soil temperatures during spring (Weaver & Rowland, 1952; Rice & Parenti, 1978). However, Knapp and Seastedt (1986) reported that both soil and air temperature within the canopy were higher in undisturbed grasslands stands, because litter reduced convective cooling. They attributed low productivity of ungrazed prairies to warmer soil temperatures in spring, which worsen water conditions. Chapin et al. (1979) showed that the accumulation of dead materials in the crown of the tundra sedge *Eriophorum vaginatum* provided insulation that allowed for an extended growing season and faster nutrient cycling, thus improving productivity.

Watt (1956, 1970) stressed the protective effect of litter against cold in bracken communities. He reported that denuded plots had higher maximum and lower minimum temperatures, and that the removal of litter increased the impact of killing frosts, because litter protected the fern apices from freezing damage during winter. In bare areas the soil reaches higher temperatures early in the spring, promoting the early emergence of sprouts that may then be exposed to late frosts (Watts, 1970). Haslam (1971) reported that the absence of litter in some *Phragmites communis* stands increased bud mortality in winter. This resulted in the release from apical dominance and a larger number of shoots developed in the next spring. Litter may also protect seedlings from frost killing in early spring, as shown by Heady (1956) in a California annual grassland. Protection by litter was also reported for an early successional community, where tree establishment was negligible before litter accumulation provided protection against frost heaving (McCarthy & Facelli, 1990; Pickett et al., 1987; Small et al., 1971). Differences between plant communities found in pits and mounds in temperate forests may be partly explained by differences in soil temperature resulting from differential litter accumulation in the two microhabitats (Beatty & Sholes, 1988). The reduction of the soil thermal amplitude produced by litter may impair the germination of seeds whose dormancy is broken by alternating temperatures (Fenner, 1985; Grime, 1979; Thompson et al., 1977). The local extinction of many weedy species from oldfields and ungrazed grasslands may well be due to this mechanism (Facelli et al., 1987; Facelli & Pickett, in press).

3. *Water Dynamics*

The presence of litter affects the exchange of water between the soil and the atmosphere. This effect has been amply observed in grasslands and deserts (Fowler, 1986; Weaver & Rowland, 1954; West, 1979) where litter increases water availability. In comparison, the effect of litter on water dynamics in oldfields and forests has received scarce attention. Litter accumulation in ungrazed grasslands increases infiltration, reduces evaporation from the soil (Larson & Whitman, 1942), and decreases run-off (Dyksterhuis & Schmutz, 1947). Litter also reduces the impact of rain drops on the soil, preventing disaggregation which would lead to diminished infiltration (Dyksterhuis & Schmutz, 1947). These authors also observed that the main effect of litter was determined by its physical structure, rather than by enhanced organic matter content in the soil (but see Walsh & Voight, 1977). Litter may also induce changes in pH that can affect soil physical structure, and therefore water percolation (Walsh & Voight, 1977).

It was shown that both in grasslands and in crop fields, litter on the soil surface increased water availability due to reduced evaporation (Dyksterhuis & Schmutz, 1947; Weaver & Rowland, 1954; Holland & Coleman, 1987). Litter affects water evaporation directly by increasing the resistance to water vapor diffusion from the soil surface, and indirectly, by reducing the soil temperature. Weaver and Rowland (1952) measured water content in previously irrigated grassland plots with and without litter. In full sunlight and wind, the losses in the first and second day were 74% and 64% higher in the plots without litter; slightly smaller differences were found in plots protected from direct sunlight and wind. Hulbert (1969) attributed higher water contents in unburned grassland plots to the effect of litter on evaporation rather than to increased infiltration.

Under some circumstances, water retention by litter may reduce the water available to the plants (Knapp & Seastedt, 1986; Walsh & Voight, 1977). Weaver and Rowland (1952) found that as much as one third of a daily rain may be retained by the litter, and evaporates directly without becoming available to the plants. Tao et al. (1987) found that plots without litter in pine forests of Korea had higher moisture contents than those with the litter cover intact. The net effect of the litter on the water balance may depend on the water retention potential of the litter and on the rainfall pattern. When most of the rain falls in small rainfall events, the proportion of water retained by the litter will be larger than that retained if the same amount falls in a few large events (Walsh & Voight, 1977; cf. Sala & Lauenroth, 1983).Walsh and Voight (1977) studied experimentally the hydrological properties of two kinds of litter, leaves of *Fagus sylvatica* L. and needles of *Pinus sylvestris* L.. Applying simulated rains to both kinds of litter, they found that the proportion retrained in the litter was negligible during heavy rains, but up to 25% in light rains. They observed differences in the hydrological properties and in the pattern of water movement through litter mats formed by both kinds of litter. They reported that in some cases litter may increase the run-off because of flow over or within the litter mat. The condition of the litter prior to the rain event affects its hydrological properties: dry litter may be hydrophobic and retain less water, increasing the overflow (Walsh & Voight, 1977). Coelho Neto (1987) found that the run-off in a secondary tropical forest with heavy litter accumulation was in general low, but highly variable, and that the overflow of water from patches with a heavy, compacted cover of litter was absorbed by less densely covered patches. This pattern could produce patchiness in the soil water availability.

Changes in water availability mediated by litter may have obvious effects on different plant populations. For example, Fowler (1986) found that a light cover of litter increased the establishment of grass seedlings, due to reduced water deficit (but see Fowler, 1988). Similarly, the presence of litter in experimental flats increased the emergence of seedlings of the grass *Amphicarpum purshii* Kunth., when seeds were shallowly buried (Cheplick & Quinn, 1987), because litter reduced desiccation of the soil surface. In an experimental study on the interaction of two successional species, Collins and Quinn (1982) found that litter of a shrub (*Myrica pennsylvanica* Loisel.)

increased the survivorship of the competing grass (*Andropogon virginicus* L.) during two drought episodes. The accumulation of litter around and beneath shrubs in deserts increases water availability and may increase seedling survivorship (Evans & Young, 1970; West, 1979). Litter removal decreased productivity in a mixed grassland, where water may be the main limiting factor (Willms et al., 1986).

4. *Litter as a Mechanical Barrier*

The litter mat constitutes a physical barrier for seeds, seedlings, and shoots because it may impede or retard seeds reaching the soil, and inhibit the emergence of seedlings or sprouts. The mechanical impedance exerted by litter may control the ground layer vegetation in deciduous forests (Ellenberg, 1988; Grime, 1979; Persson et al., 1987; Sydes & Grime, 1981a) and other systems with dense litter mats.

Hamrick and Lee (1987) found that seeds of musk thistle (*Carduus nutans*) were retained by a thick layer of litter which prevented them from reaching the soil. In contrast, Werner (1975) found that the seeds of *Dipsacus sylvestris* Huds. reached the soil soon after dispersal, and none was retained in the litter layer. Tao et al. (1987) reported that seeds of subdominant species in a Korean pine woodland had differential abilities to penetrate the litter mat. Seeds retained in the litter may either have delayed or unsuccessful germination. The germination of seeds of *Aristida longiseta* Steud. seeded over a dense layer of litter was delayed for a month (Fowler, 1986), because they moved slowly from the top of the litter layer to the soil surface. Most *A. longiseta* seedlings that germinated within the litter layer died because their roots were unable to reach the soil (Fowler, 1986). Similarly, the roots of seedlings of *Quercus douglasii* Hook & Arn. often fail to reach the soil, when germinating on top of the thick litter layer produced by introduced grasses in California annual grasslands (Borchet et al., 1989). Variable germination timing of *Bromus tectorum* L. may be due to variability in the movement of seeds through the litter mat (Mack, 1984; Mack & Pyke, 1984). The shape of the seeds and the structure of the litter mat may be the main factors affecting this process. We know of no experiment studying how the size and shape of the propagules or the structure of the litter mat affect the ability of the seed to reach the soil.

Seedlings and sprouts emerging from beneath a litter mat have to devote energy and time to penetrate it. Seedlings produced by small seeds may be unable to emerge, because of energy shortage. Even seedlings originating from large seeds can be confined within the shady and wet environment of the litter mat (Sydes & Grime, 1981a), increasing the risk of fungal infection (Herman & Chilcote, 1965) or herbivore attack (Facelli, unpublished data).

Seedling geometry may be an important determinant of the ability of a seedling to penetrate the litter mat. The position and size of the cotyledons during emergence may affect the resistance of the litter to the growth of the seedling. Though sprouts usually have more energy available, there is some evidence that thick layers of litter can impair their performance (Knapp & Seastedt, 1986). Galuten (1977) found that a thin layer of litter of *Myrica pennsylvanica* had no impedance effect on shoots of *Andropogon virginicus,* but Collins and Quinn (1982) suggested that denser layers could affect sprouting. Grime (1979) analyzed the importance of the geometry of the sprouts of perennial forest herbs in relation to litter tolerance (see also Persson et al., 1987). Litter mats with different physical structure may exert different impedance. The main determinants of impedance may be shape and size of the litter components, and compactness of the mat. Matted litter, i.e., leaf litter held together by fungal hyphae, exerts stronger impedance than loose litter. Mechanical impedance by leaf litter could limit that distribution of some herbs in forest habitats (Marks, 1983; Winn, 1985). Uetz (1974) suggested a method to measure aspects of litter geometry that could be applied to the study of the physical impedance exerted by different litter mats.

V. Effects of Litter on Plant Community Structure and Dynamics

The changes induced by litter in the physical and chemical environment may affect the performance of different populations (e.g., Cheplick & Quinn, 1987; Collins & Quinn, 1982; Hamrick & Lee, 1987; Schlatterer & Tisdale, 1969; Werner, 1975). In addition, those direct effects of litter may alter the outcome of interactions between populations with differential sensitivity to litter accumulation, affecting plant community structure. The paramount importance of litter accumulation patterns, and of the properties of accumulated litter in the dynamics of fire-prone communities has been reviewed elsewhere (Christensen, 1985; Kozlowski & Ahlgren, 1974).

Germination and establishment are two key factors in plant community organization (Grubb, 1977) that seem to be particularly sensitive to the presence of litter. Litter may enhance the establishment of some species by improving water conditions (e.g., Fowler, 1986; West, 1979) or by reducing competition (Facelli & Pickett, in press). Establishment of many species is negatively affected by litter because of shading, mechanical impedance, reduced thermal amplitude in the soil or biochemical effects. Establishment of *Prunella vulgaris* L. was enhanced by herb litter in oldfields, but leaf litter reduced the establishment in forest habitats (Winn, 1985, see also Marks, 1983). Watt (1974) observed that most annuals were excluded from a chalk grassland when absence of grazing resulted in the accumulation of a dense litter layer. Collins and Good (1987) found that most tree seedlings in the New Jersey Pine Barrens occurred in patches with less litter. They concluded that litter was an important component of the regeneration niche of various species in the system. The distribution of tree species in southeastern Pennsylvania may be affected by the ability of their seedlings to tolerate the accumulation of litter (Keever, 1973). In the Highlands grasslands of Victoria, Australia, shrubs only establish in patches where grass litter is removed by various disturbance agents (Williams & Ashton, 1987). Similarly, Hamrick and Lee (1987) suggested that the absence of musk thistle (*Carduus nutans*) in well managed pastures may be attributed to the accumulation of grass litter. In contrast, the establishment of some weeds of arid rangelands (e.g., *Bromus tectorum, Taeniatherum aspersum* Nevski, *Salsola kali* L.) is enhanced by litter accumulation because of improved water availability (Evans, 1972; Evans & Young, 1970). Goldberg and Werner (1983) showed that elimination of litter enhanced the establishment of seedlings of two species of *Solidago,* and that the two species responded differentially to the size of the opening. Fowler (1986, 1988) discussed the role of litter in the formation of safe sites for different grasses.

Sydes and Grime (1981a) found a consistent correlation between shoot biomass and persistent litter in forest floor communities, and suggested that litter was the main factor controlling the structure of these communities (see also Ellenberg, 1988; Hermy, 1987). Persson et al. (1987) attributed changes in the ground forest layer over 50 years to changes in litter composition (i.e., from predominantly *Quercus* and *Corylus* litter to litter of *Ulmus* and *Fagus*). Litter accumulation in grasslands may affect productivity, diversity, and species composition (Knapp & Seastedt, 1986). Fowler (1986) found that litter reduced competition and increased growth rates because of reduced plant density. In the California annual grassland, litter removal decreased productivity (Heady, 1956) probably because of worsened water conditions. Shading produced by litter may reduce the total basal area in ungrazed grasslands (Weaver & Rowland, 1952), and the density of forbs and annual species. Heady (1956) and Monk and Gabrielson (1985) reported that annuals and perennial forbs are more affected by litter than perennial grasses (see also Facelli & Pickett, in press).

Litter accumulation may reduce species richness in grasslands (Facelli et al., 1988; Penfound, 1964; Watt, 1974), oldfields (Facelli et al., 1987; Carson & Peterson, 1990), lacustrine wetlands (van der Valk, 1986), salt marshes (Haslam, 1971), and in pit-and-mound complexes in temperate forest (Beatty & Sholes, 1988). Litter removal usually increases species diversity and the number of flowering species in grasslands (Penfound, 1964; Weaver & Rowland, 1952). Haslam (1971) reported that litter accumulation in *Phragmites* communities maintained the dominance of the reed and prevented the invasion by other species. However, Sydes and Grime (1981b) found that litter reduced dominance and increased diversity in the ground herb community of forests, because litter released dicots from competition by dominant grasses. Litter may promote coexistence at the between-patch level due to the temporal and spatial variability in the litter mat, and to the changes in different environmental factors litter produces (Fowler, 1988). In bracken communities fire and rabbit activities create patchiness in the litter layer that introduced patchiness into the community structure (Watt, 1956, 1970). Patterns of litter accumulation may strongly affect community dynamics. The persistence of litter after the introduction of large grazers probably contributed to the community inertia in a Swedish salt marsh (Bakker, 1985) and in a subhumid Pampa grassland (Facelli, 1988) because litter maintained high water availability and slowed salinization. In a five year successional study in the Argentine Pampa, the reduction of species diversity and the local extinction of ruderal species was seemingly related to the ability of *Lolium multiflorum* Lam. to accumulate a dense layer of litter (Facelli et al., 1987, 1988; see also Evans & Young, 1970). The removal of litter from pits produced by treefalls in a temperate forest made the plant community converge to a composition similar to that growing on the adjacent mounds (Beatty & Sholes, 1988). Kellman (1979) postulated that microenvironmental changes produced by litter accumulation beneath savanna trees may eventually allow the colonization by trees from the rain forest, leading to secular vegetation changes. The impact of litter on oldfield communities may be also important. Monk and Gabrielson (1985) showed experimentally that litter played an important role in community dynamics, though less important than root competition and shading. Szczeponska (1977) suggested that successional changes in river banks were promoted by the accumualtion of litter of macrophytes. Contrastingly, Ellenberg (1988: 642) observed that heavy accumulation of litter in moist meadows of Central Europe arrested succession by preventing the establishment of woody seedlings. Carson and Peterson (1990) showed that litter had a strong, though temporary, effect on plant density and species richness in a *Solidago* dominated oldfield. Detailed studies of a simple seral community (Facelli & Pickett, in press) showed that litter may have very complex effects due to the integration of different individualistic responses. Those responses, in turn, were determined by the direct effects of litter, and by the changes in patterns and strength of their interactions.

The accumulation of litter may also affect the plant community through its effects on the activity of herbivores. The regrowth after the destruction of litter in grasslands attracts herbivores, which was shown to increase differences in the community composition in plots with and without litter (Andrzejewska & Gyllenberg, 1980). In lightly grazed grasslands, the accumulation of litter in initially ungrazed patches may prevent further cattle activity in these patches (Ring et al., 1985; J. M. Facelli, pers. obs.). Grisez (1960) showed the deer browsing was reduced when the saplings were surrounded by dead tree branches (slash). Seed predation by vertebrates may be reduced by litter accumulation because seeds may be more difficult to locate. Shaw (1968) observed that dense litter protected acorns of sessile oak from vertebrate predators, and Sydes and Grime (1981b) observed that litter may protect seeds of herbs from rodents. Wiens (1973) found a strong correlation between the amount of litter and patch selection by grassland sparrows, though it is not clear whether litter played a direct role in the patch selection (see also Terborgh & Robinson, 1986). The acoustic properties of the environment are altered by litter, affecting the sonic communication among birds (van der Heidjen et al., 1983) and probably among other vertebrates and invertebrates that use acoustic communication.

In addition to acting as a substrate for the components of the detritus food web, litter also affects the physical environment in which those organisms live (Dyksterhuis & Schmutz, 1947; Gill, 1969; Richards, 1987; Stanton, 1979; Warren & Zimmerman, 1987). It has been shown that the patterns of litter deposition and the physicochemical properties of litter may determine the structure of the detritivorous community (Gill, 1969; Choudhury, 1988; Olson, 1963; Polunin, 1984; Sydes & Grime, 1981b). For example, fewer earthworms, and more mites and collembolans, are found in grasslands areas with high litter accumulation (Knapp & Seastedt, 1986; Stinner et al., 1984). Earthworms process most of the N contained in the litter in wet and mesic environments (Lee, 1985; Scheu, 1987), and their activities are supposed to be the principal mechanism forming and differentiating O and A_0 horizons in forest soils (Lee, 1985; see also Prusienkiewicz & Bigos, 1978). The addition of earthworms to reclaimed lands decreased the amount of accumulated litter, and increased the productivity of the herb communities (Lee, 1985, and references therein). Other indirect effects of litter may be mediated by its effect on pathogens. The addition of litter increased the number of soil microarthropods in a Michigan oldfield (Gill, 1969). This effect was more likely due to environmental changes than to increased food availability, since the replacement of the natural litter by synthetic (Dacron) litter did not alter the mite density (Gill, 1969). The shady and wet environment created by litter can benefit plant pathogens, increasing seedling mortality (Goldberg & Werner, 1983; Herman & Chilcote, 1965; Sydes & Grime, 1981b). Scarce effort was devoted to studying how different effects of the litter on organisms living in the litter mat affect the plant community structure. Riechert and Bishop (1990) showed that organic mulching increased spider density, which in turn reduced the density of pest insects and leaf damage in horticultural species.

VI. Adaptative Traits Related to Litter Accumulation

Litter can exert an important effect on the success of individual plants, either affecting the probability of germination and establishment, or regulating the outcome of the interactions with the physical and biological environment, and, ultimately, the reproductive output. The widespread presence of litter may therefore affect the evolution of plant strategies (Grime, 1979). There are three aspects of litter dynamics that have been related to adaptative traits: tolerance to the accumulation of dense litter mats (e.g., Grime, 1979; Sydes & Grime, 1981a, 1981b); the timing of leaf abscission as a way to regulate the cycling of nutrients (e.g., Monk, 1966; Otto & Nilsson, 1981); and the accumulation of litter to outcompete other plants by worsening their physical or chemical environment (Grime, 1979; Mutch, 1970; Rice, 1979; Sydes & Grime, 1981a, 1981b).

Adaptations to tolerate litter accumulation exist in many populations, and considerable differences in tolerance to litter accumulation have been found. Monk and Gabrielson (1985) found that pioneer species were more affected by litter than late successional species, and Gross and Werner (1982) reported that the position of biennial species in a sere was correlated with their tolerance to litter accumulation. Seed size and shape, and seedling or shoot morphology and phenology may determine the ability of a plant to tolerate litter. Seedlings originating from small seeds may be unable to penetrate the litter mat or tolerate the shading, but those germinating from larger seeds (a character often found in late successional species) may successfully cope with dense litter mats (Grime, 1979; Keever, 1973; Tao et al., 1987). However, the movement of large seeds through the litter may be impeded or delayed and the seeds may remain in an unsuitable germination site; such delay may also enhance seed predation risk (Grime, 1979; Shaw, 1968). The size and shape of seedlings or sprouts may determine the establishment success under dense litter layers. In forest floor geophytes and hemicryptophytes, the shape of the shoots seems to be adapted to penetrate litter (Grime, 1979). Sydes and Grime (1981b; see also Grime, 1979) suggested that the community structure in the ground layer of temperate deciduous forests is determined by the shoot morphology of the herbs and their ability to penetrate the thick layers of litter found early in the spring. Sprouting or germination timing may be another adaptation to litter tolerance. In habitats with a marked seasonal variation in accumulated litter, germination or sprouting when litter mass is low may be advantageous (Al-Mufti et al., 1977; Grime, 1979). The persistence of some rosette-forming dicots in grass-dominated successional communities in the Argentine Pampa (D'Angela et al., 1986; Facelli et al., 1988) is probably due to the ability of these species (*Carduus acanthoides* L., *Hirschfeldia incana* (L.), Lagreze-Fossat) to place their leaves above the litter layer. These species displace the litter through a change in the position of the leaves, which opens a cup-shaped patch where more leaves can subsequently grow (J. M. Facelli, pers. obs.).

A second hypothesis relating litter dynamics to plant strategies postulates that the timing and chemistry of leaf shedding is a way to regulate the seasonal patterns of decomposition and nutrient uptake (Monk, 1966; Otto & Nilsson, 1981; Trèmoliere et al., 1988). The timing of leaf abscission should be tuned to the decomposer activities and to the reinitiation of the plant growth, in a way that allows plants to absorb most of the nutrients lost with the dead leaves. However, as observed by Berendse et al. (1987), nutrients released into the soil are available to any plant, and plants have to compete to take up these nutrients, preventing the evolution of such strategy. Escudero and del Arco (1987) concluded that none of the leaf strategies found in the nutrient limited forest they studied had any effect on making nutrient availability more gradual or coincident to plant demands, as the hypothesis predicts. Leaf dynamics were related to environmental changes in temperature and water availability, and internal cycling of nutrients or leaf longevity seemed to be the most important adaptations to nutrient shortage (see also Flanagan & van Cleve, 1983; Killingbeck & Costigan, 1988; Shaver, 1983; Vitousek, 1984).

The third hypothesis states that litter can be used by the plant to outcompete its neighbors. The three-strategies model of Grime (1979) includes explicitly the ability to accumulate litter as a strategic trait of competitors, and tolerance to litter as a character of stress tolerants. Specifically, he proposed that the dominance of some species in productive habitats was due to their ability to accumulate litter, and a precise timing between the litter cycle and the life cycle of the population (see also Facelli et al., 1987). Advocates of allelopathy assume that the accumulation of toxic compounds (or their precursors) prior to leaf abscission allows some plants to contaminate the chemical environment of their competitors (see Rice, 1979, and citations therein). It was also claimed that some fire-resistant plants accumulate litter of high flammability increasing the risk and intensity of wildfires, which in turn enables them to avoid competitive suppression by more competitive species that do not tolerate hot fires (Mutch, 1970; Peterson, 1984; Stone & Vasey, 1968; Williamson & Black, 1981). This "fire facilitation hypothesis" has been criticized by Christensen (1985), and Sousa and Connell (1985). The hypothesis relies mostly on the correlation between tolerance to high fire temperature and flammability of the litter produced. The explanation that because these species produce highly flammable litter, they developed fire resistance seems more parsimonious than accepting that the production of conditions that favor high temperature fires is a mechanism devised to deter competitors.

Similarly, alternative and parsimonious explanations for the other patterns of litter production observed must be considered as a null hypothesis for the adaptative explanation (Berendse et al., 1987; Grime, 1979). The most parsimonious explanation is probably that those patterns are the consequence of selection on other characters more directly related to fitness, as, e.g., foliar tactics. Some species may accumulate large amounts of litter just because they have a large productivity and a certain foliar strategy related to resource capture and management (see, e.g., Coley, 1988). In other cases, the accumulation of a large amount of litter may result from reduced rates of decomposition, because of physical and chemical properties of the leaves. The accumulation of secondary chemicals in leaves may respond primarily to selection for antiherbivore protection (Coley, 1988; Coley et al., 1985; Feeny, 1970) or may merely reflect physiological responses to stress (Muller et al., 1987; del Moral, 1972; Siegler & Price, 1976). The presence of those chemicals can affect litter decomposition and produce phytotoxic compounds as byproducts (Flanagan & van Cleve, 1983).

VII. Conclusions

Litter is an important factor affecting community organization and dynamics far beyond its commonly recognized role as a transitory bank of nutrients. Litter can alter the physical and chemical environment, and therefore the demography of various populations. The response of different populations to these environmental changes, together with the effect of the changes in the performance of other populations, may play an important role in shaping the community structure.

The manifold effects of litter on different environmental variables, and the different responses of various populations to its presence precludes a general prediction of the effect of accumulated litter on community structure. Many of the studies reviewed (e.g., Evans, 1972; Fowler, 1986; West, 1979; Willms, 1988; Willms et al., 1986; Winn, 1985) are good examples of how different effects of litter may interact to yield different results in different systems. A general predictive model for the effect of litter should consider the importance of the type (e.g., consider the physical and chemical properties of the litter) as well as the amount of litter present to account for the effects of the litter in the main environmental factors (Facelli & Pickett, in press; Winn, 1985; but see Carson & Peterson, in press). In addition, the model must ponder the relative importance of each of these factors in the system, and finally integrate the individual responses of the populations and their interactions, to account for the indirect effects within the community.

The interactions mediated by litter may be multiple, and cannot be placed easily in the standard interaction tables found in most ecology textbooks. For example, dead leaves produced by a population modify the physical and chemical environment, interfering with—or sometimes facilitating—the germination of the seeds in the surroundings. The fate of seedlings in a patch will be affected directly by litter, and also by the interaction with surrounding plants, pathogens and herbivores that, in turn, may be affected by the amount and physicochemical properties of the litter mat. The temporal extent of these interactions is another factor adding to their complexity. Past events affecting litter production and decomposition, such as productive years, catastrophic deaths, floods, insect outbreaks, etc., affect the amount of litter present at a certain site. This kind of indirect interaction, in which time lags are prominent, is rarely considered by ecologists (but see Bergelson, in press). The patchy nature of litter accumulation (Facelli & Carson, in press), either because of patchy litter production, deposition, destruction or removal, may also affect the spatial structure of the community. The temporal variability of the litter, and the importance of time lags on the processes involved, make litter a potential historic factor, by which previous events can influence the present community structure.

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