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Effects of increasing ultraviolet B radiation on decomposition and soil organic matter dynamics: a synthesis and modelling study

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Abstract The net effect of increasing ultraviolet B radiation levels on ecosystems is unknown. Most of the relevant ecological research has focused on the responses of living plants and algae to ultraviolet B exposure, with little attention directed toward other groups. However, research in such diverse areas of study as the degradation of textiles, pigments, synthetic polymers, paper, cellulose, wood, and museum artifacts show that ultraviolet light is a significant factor in the decay of many organic compounds. In aquatic ecosystems, the photochemical degradation of recalcitrant, dissolved organic compounds is increased by ultraviolet B exposure, and similar reactions could make important contributions to organic matter turnover in terrestrial ecosystems. This hypothesis is supported by observed patterns of decomposition of exposed surface litter in arid and semi-arid environments. Since plant lignins are both photochemically reactive and form a significant component of soil organic matter, ultraviolet B-induced lignin degradation could alter material cycling in terrestrial ecosystems. However, results of a model simulating the potential effects of ultraviolet B-induced lignin degradation suggest that higher rates of litter turnover may have only slight effects on soil organic matter dynamics.

Key words UV-B radiation · Photodegradation · Litter · Decomposition · Stratospheric ozone

Introduction

Concentrations of stratospheric ozone are declining and will apparently continue to decrease over the next century in spite of international efforts to reduce the loss (Crawford 1987; Anderson et al. 1991; Schoeberl and Hartmann 1991). This results in higher levels of biologically effective ultraviolet radiation at the earth's surface (Jerlov 1950; Smith and Baker 1979, 1980, 1989), but the magnitude of impact varies seasonally and geographically, for example, a record 64% thinning of stratospheric ozone over Antarctica was observed during the austral winter in 1991 (Gribbin 1992a, b). Stratospheric ozone depletion has not been as closely examined elsewhere but concentrations in northern temperate latitudes may have declined by 5–10% over the last decade (Kerr 1991; Stolarski et al. 1992; Madronich 1993), and ozone holes similar to those over Antarctica have been predicted to occur in arctic regions (Austin et al. 1992). Although it is difficult to translate these atmospheric measures into biologically meaningful terms, a 1% change in the level of stratospheric ozone may result in a 2% change in the biologically effective dose of ultraviolet light at the earth's surface (Caldwell 1971; Setlow 1974).

Ultraviolet radiation has a number of effects on living organisms (Tevini 1993a), but studies are only beginning to examine impacts at the ecosystem level (Scientific Commitee on Problems of the Environment 1992). It has been determined that ultraviolet B radiation affects marine ecosystems in antarctic waters by inhibiting photosynthesis of phytoplankton (El-Sayed et al. 1990; Cullen et al. 1992; Smith et al. 1992; Häder 1993), but impacts on trophic relationships have not been examined (Scientific Committee on Problems of the Environment 1992). Studies of ultraviolet B radiation in terrestrial ecosystems have focused primarily on plant production. In general, exposure reduces growth, photosynthetic activity, and flowering, although particular effects vary among species, among cultivars of a species, and among local populations of a species (Tevini and Teramura 1989; Ziska et al. 1992; Tevini 1993b). However, little attention has been focused on other ecological processes, aside from competitive interactions between plant species (Fox and Caldwell 1978; Gold and Caldwell 1983; Caldwell et al. 1989).

In terrestrial ecosystems, significant quantities of nutrients are released by the decomposition of dead organic

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matter. Photochemical activity increases the biodegradation of organic materials in aquatic environments that are otherwise resistant to biologically mediated decay (Geller 1986; Kieber et al. 1989; Cotner and Heath 1990). Few comparable experiments have been conducted in terrestrial ecosystems, but photochemical degradation has been proposed as an explanation for the very rapid loss of above-ground litter observed in the Russian steppes (Zlotin 1979) and in the northern Chihuahuan Desert of southern New Mexico, USA (Moorhead and Reynolds 1989). Moreover, photochemical reactions of lignin compounds in wood and paper products have been examined in considerable detail (Kalnins et al. 1966; Leary 1968; Lin and Kringstad 1970; Gierer and Lin 1972; Hon et al. 1980; Hon and Feist 1981; Castellan et al. 1987), and the results suggest that ultraviolet B radiation makes a potentially significant contribution to the degradation of plant litter exposed to sunlight.

Increasing levels of ultraviolet B radiation will undoubtedly have many direct and indirect effects on litter decay and nutrient cycling processes within ecosystems. Changes in the quantity, quality, and location of plant litter will almost certainly affect patterns of decomposition and nutrient mineralization. Moreover, preliminary observations indicate that the composition of fungal communities colonizing decaying plant litter are altered by exposure to ultraviolet B radiation, which appears to retard the decomposition of these materials (Gehrke et al., unpublished). It will be very difficult to evaluate the net effects of increasing ultraviolet B radiation on patterns of decay and nutrient cycling, given the multitude of interacting ecological responses. In this paper we focus on a single aspect of this question, the direct contribution of ultraviolet B radiation to the photochemical degradation of organic compounds. Our specific objectives are (1) to summarize the available information relevant to ascertaining potential impacts of solar radiation on litter decay, (2) to briefly evaluate the mechanisms underlying these effects, and (3) to explore potential impacts of increasing ultraviolet B radiation on the dynamics of surface litter and soil organic matter with a simulation model.

Materials and methods

Evidence for photochemical degradation of terrestrial litter

The importance and the specific function of photochemical reactions in the degradation of litter in terrestrial ecosystems are unclear. However, evidence is accumulating which suggests that photochemical reactions may make a substantial contribution to litter decay under ordinary conditions. In general, degradation of dead organic matter is accomplished by the combined actions of various biotic and abiotic processes (Swift et al. 1979), with climate and litter quality exerting such strong controls that decay is often described solely as a function of these factors. For example, Meentemeyer (1978) developed a model of litter decay for temperate forests whereby litter mass loss was directly related to actual evapotranspiration and inversely proportional to lignin content. However, this approach is inaccurate in more open canopy environments, such as deserts, where actual losses of surface litter far exceed estimates (Whitford et al. 1981; Schaefer et al. 1985).

The degree of exposure has a significant impact on litter disappearance. For example, Zlotin (1979) and Montaña et al. (1988) found that abiotic factors accounted for a much larger fraction of litter losses in open steppe and desert ecosystems than in forests. In particular, Zlotin's work examined litter decay across an oak forest – steppe meadow ecotone in Russia; 72 and 14% of the total litter loss in the meadow and forest, respectively, was attributed to physical processes. Within the northern Chihuahuan Desert, USA, Whitford (1989) found that the activity and functional diversity of detrital food webs were greater in shaded microhabitats than in exposed areas. These patterns led Montaña et al. (1988) to propose that an aridity gradient controlled litter decay, with biotic processes dominating under mesic conditions and abiotic processes dominating in arid circumstances. However, an exposure gradient is also compatible with these data.

A number of specific abiotic mechanisms have been proposed to account for litter losses in arid and semi-arid ecosystems (Vossbrinck et al. 1979; Zlotin 1979; Montaña et al. 1988; Moorhead and Reynolds 1989). However, Pauli (1964) was, perhaps, the first to realize that the degradation of complex organic molecules in litter (such as lignins) can be enhanced by high radiation intensity and speculated that this was one of the reasons why the soil organic matter content is typically low in arid regions. Photochemical reactions seem most likely to affect degradation of surface litter in arid open-canopy ecosystems, such as the Russian steppes (Zlotin 1979) and northern Chihuahuan Desert (Moorhead and Reynolds 1989). The environmental conditions of these ecosystems should permit high rates of photochemical reactions. For example, sunlight intensity is very high at the Chihuahuan site, which has an elevation of 1200–1500 m. Microclimatic conditions at the soil surface are stressful for decomposer organisms because soil temperatures can exceed 60 °C and moisture availability is usually very low and erratic (Whitford and Ettershank 1975). Nevertheless, surface litter loss is rapid while the soil organic C content remains very low.

Although Pauli (1964) suggested that photochemical reactions contribute to litter losses in arid environments, he conducted no experimental tests of this hypothesis and few other subsequent studies have directly examined the effects of radiant energy on litter decay. One exception is an experiment conducted in the northern Chihuahuan Desert, in which nylon netting was used to reduce solar insolation on plots containing litterbags (MacKay et al. 1986). From July through October, 1983, the mass loss of shaded litter (58% ambient sunlight intensity) was lower than controls even though densitites of microarthropods (mostly fungivores and detritivores) were much higher in the shaded litterbags. The hot, dry conditions of late summer and early autumn would probably limit biological activity but not the rates of photochemical reactions. If Pauli's (1964) supposition that polyaromatic compounds, such as lignins, are particularly susceptible to photochemical degradation is correct, then mass loss rates of litter should be related to lignin contents. In fact, Schaefer et al. (1985) found that the mass loss of surface litter in the northern Chihuahuan Desert was directly proportional to the initial lignin content (Fig. 1). These observations contradict the inverse relationship between litter mass loss and lignin content described by Meentemeyer (1978) and others (Melillo et al. 1982) for more mesic ecosystems, and corroborate Pauli's speculation.

Mechanisms underlying photochemical effects on litter degradation

Insights into the mechanisms underlying the likely effects of solar ultraviolet B radiation on litter decay are provided by studies of photochemical reactions in a variety of substrates, including textiles, dyes, pigments, synthetic polymers, paper, cellulose, wood,

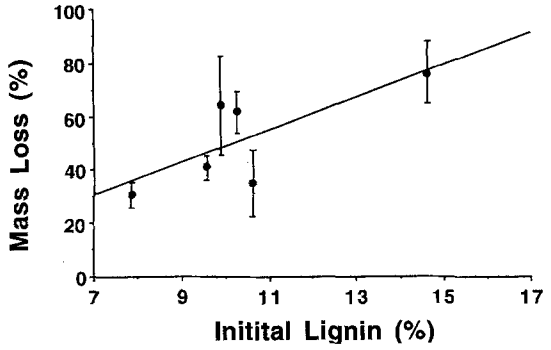

Fig. 1 Effects of initial lignin content on mass loss of surface litter (data from Schaefer et al. 1985). Loss = 6.0740 (lignin) − 12.159; $R^2 = 0.554$

and museum artifacts. Not surprisingly, most of this research focuses on materials that are economically important. For example, an excellent review by Andrady (1993) summarizes the nature and variety of chemical changes in organic polymers (thermoplastics) resulting from exposure to ultraviolet radiation. The key point is that the energy content of near-ultraviolet radiation is within the range of dissociation energies for typical covalent bonds in organic molecules and polymers. When these compounds are exposed to ultraviolet radiation, a number of primary photochemical reactions lead to the formation of ions and radicals. These reaction products can undergo secondary reactions that produce a variety of photodegradation products. Andrady (1993) describes the general process of photodegradation of polyolefins as an example. In brief, light energy drives the photolysis of hydrocarbon bonds and formation of free radicals, which participate in an auto-oxidation cycle that generates photolyzable hydroperoxides, the major inititators in the early stages of photodegradation. Scission and crosslinking within the polymer chain during oxidation modifies the chemical and physical properties of the polymer. Scission generates lower molecular weight compounds, including volatiles, and often increases the solubility of the material. Other effects include loss of tensile strength, extensibility, impact resistance, solvent resistance, and structural integrity.

Although the precise effects of ultraviolet radiation on a particular compound depend on the chemistry and physical state of the material, spectral properties of the radiation, and the chemical nature of the environment (Andrady 1993), three general types of changes occur during photodegradation: (1) discoloration, (2) changes in molecular weight (especially the production of low molecular weight compounds), and (3) alterations in mechanical properties. It is these changes in the physical characteristics of materials that have stimulated detailed studies of photochemical reactions in organic compounds (Epps and Perenich 1983; American Association of Textile Chemists and Colorists 1987; Crews 1987; Wagner 1987; Woeppel 1989). For example, nylon (polyamide fibers) is used in manufacturing cloth, ropes, seat belts, upholstery, and parachutes, but colors fade and the tensile strength of nylon fibers declines rapidly when exposed to sunlight. Ultraviolet radiation is the major cause of photo-oxidation in nylon and a number of commonly used dyes accelerate the process (Schwemmer 1956a, b; Salvin 1968; Dunlap et al. 1969; Wagner 1987). In contrast, other dyes and ultraviolet absorbers (colored and colorless) reduce the effects of ultraviolet exposure (Hayes et al. 1966; Anton 1982). Whether a light-absorbing compound enhances or inhibits photodegradation of a material depends on the absorber's response to light, in that absorbers that produce chemically reactive compounds are more likely to increase photodegradation rates. Other chemical aspects of materials are also important, for example, many textiles can be treated with compounds that quench the reactions propagating photodegradation (Ladisch et al. 1983; Carr and Lewis 1993; Collins and Davidson 1993; Weatherall 1993). Furthermore, fluctuating chemical characteristics of the environment can have a major impact on photodegradation processes, such as the effects of human perspiration on fabric dyes (Mishra and Norton 1993).

Photoreactions of dissolved organic compounds in aquatic systems and of lignin compounds in wood and paper products appear to be similar to the reactions of synthetic organic polymers. In a review of the photochemistry of natural waters, Zafiriou et al. (1984) reported that photolysis often produces radicals from peroxides, disulfides, and phenols, while aldehydes and ketones react by the type I and type II Norrish pathways (Andrady 1993). However, natural systems usually have a complex mix of photoreactive compounds and many potential reactions are not well understood. Moreover, the chemical products of photoreactions interact with each other and other compounds, and biologically mediated reactions co-occur. It is very difficult to extrapolate from the composite results of all these various physical, chemical, and biological reactions taking place. Nevertheless, their end result has been demonstrated. For example, deep sea (> 500 m) residues of oceanic dissolved organic C are primarily composed of biologically refractory compounds, such as humic substances (Mopper et al. 1991). These materials are photochemically degraded in surface waters (photic zone) into biologically labile and/or volatile organic compounds, for example, the biological uptake of pyruvate in sea water is highly correlated with its rate of photochemical production from the breakdown of high molecular weight, dissolved organic C (Kieber et al. 1989). Similarly, the intensity of photolytic conditions proportionally increases photodegradation and subsequent bacterial degradation of macromolecular dissolved organic C (Geller 1986).

Investigations of lignin photochemistry in wood and paper products are also relevant to evaluating litter decay in terrestrial environments. Lewis and Fronmuller (1945) were among the first to study the underlying photochemical reactions responsible for the discoloration of paper, including demethylation of lignin. Although it is difficult to evaluate the precise quality and quantity of light used by Lewis, a 10-h exposure reduced the detectable lignin content of the paper by 13%. Subsequent studies identified the oxidation of α-carbonyl groups as particularly sensitive to ultraviolet radiation (ca. 300 nm), producing free phenoxy radicals that serve as intermediates in the lignin degradation and discoloration process (Leary 1968; Lin and Kringstad 1970; Gierer and Lin 1972; Castellan et al. 1987). Similarly, free radical formation by lignins and polyphenols in wood are readily produced by exposure to solar radiation, fluorescent light, and artificial ultraviolet light (Kalnins et al. 1966; Hon et al. 1980; Hon and Feist 1981), leading to a host of physical and chemical changes that affect structure and appearance (Kalnins 1966).

The effects of light on material degradation are so ubiquitous and significant that they are a major concern among museum scientists. The threat of photodegradation to museum artifacts has resulted in the development of management policies concerning illumination and methods for quantifying the exposure of artifacts to ultraviolet light (Brill 1980; Thompson 1986; Crews 1987; Wagner 1987; Woeppel 1989). For example, the Blue Wool standard has been adopted by the International Organization for Standardization (ISO) and as the British Standard for evaluating the lightfastness of dyed fabrics and paints (Wagner 1987). In this approach, selected materials are compared to specially prepared blue dyeings on wool for signs of fading during continuous exposure to light. The method provides a useful means of evaluating light fastness of materials, although attempts to establish quantitative relationships between light exposure and fading have met with limited success.

In summary, photodegradation of organic compounds generally involves three initial stages: (1) absorption of radiant energy, (2) formation of a free radical, and (3) combination of the free radical with oxygen to form a peroxy radical. Beyond this point, an enormous number of chemical reactions can occur that will change the nature of the substrate. Although mechanisms underlying the ultraviolet-induced photochemical degradation of many compounds have been examined, it is difficult to use this knowledge to evaluate

the overall effects of ultraviolet radiation on the decomposition of terrestrial litter. Pauli (1964) found that exposure to solar radiation (200–800 nm) induces reactions that produce many degradation products from large organic molecules. In secondary reactions, smaller molecules may interact to form new compounds, especially during drying and rewetting cycles common to arid environments. Furthermore, it is likely that photochemical degradation of biologically refractory compounds may stimulate biological activity. The total direct and indirect contributions of photochemical reactions to litter decay may be significant. However, apparently no published studies have tested this hypothesis or quantified exposure–response relationships.

Simulation study

Since plant lignins constitute a major component of recalcitrant soil organic matter (Stott et al. 1983), ultraviolet B-enhanced lignin degradation could have a significant impact on soil organic matter pools, and thus, on soil fertility. In their model of C and nutrient dynamics in prairie ecosystems of the USA (CENTURY; Fig. 2), Parton et al. (1987) discovered that "regional trends in soil organic matter can be predicted using four site-specific variables, temperature, moisture, soil texture, and plant lignin content". The importance of lignin in their study is not surprising because (1) the ratio of lignin to N in litter was used to define the partitioning of plant residues into metabolic and structural pools, (2) the decay rate of the structural pool is a function of lignin content, and (3) the lignins in the structural pool transfer directly to the slowly decomposing soil organic matter pool during decay. Given the importance of lignin in determining fates, rates, and allocations of material with this approach, any change in lignin dynamics could be expected to have an impact on model behavior. In fact, increased photodegradation of lignins might be expected to reduce the calculated soil organic matter content because (1) photoreaction products are more likely to enter the active soil pool as smaller molecular weight compounds where they are readily used by microbiota (Geller 1986), (2) the flow of structural material to the active soil pool is less efficient (higher respiratory C loss) than the flow to the slow pool, and (3) transfer of material from the active pool to the passive pool is less efficient than transfer from the slow pool to the passive pool (Fig. 2). Changes in the relative sizes of soil organic matter pools could alter site fertility because the active, slow, and passive pools have C : N ratios of 8 : 1, 11 : 1 and 11 : 1, respectively.

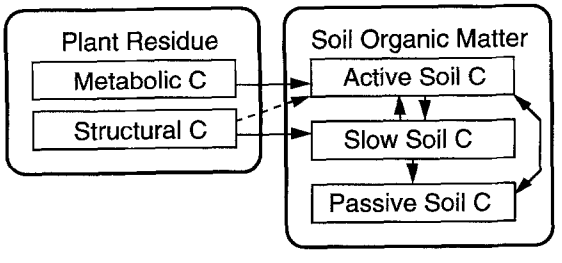

Fig. 2 C flow diagram for CENTURY model (Parton et al. 1987). *Dashed arrow* indicates one modification of model made in the present study to simulate the photodegradation of lignins within the plant litter pool

Modeling rationale

The CENTURY model has been applied very successfully to a wide range of grassland communities and explicitly examines pools of litter and soil organic matter that may respond to ultraviolet B radiation. We used this model to examine the effects of ultraviolet B-induced lignin degradation in two ways. The first was to increase the rate of flow of lignin from the structural litter pool to the slow soil pool to simulate the possible production of reactive organic compounds with increased solubility that would tend to become stabilized within the soil matrix. The second approach consisted of adding a flow of lignin from the structural litter pool to the active soil organic matter pool (Fig. 2), consistent with reports that biota in aquatic systems can more rapidly use photoreaction products than macromolecular precursors (Geller 1986).

Since stratospheric ozone in northern temperate latitudes may have declined by 5–10% over the last decade (Kerr 1991; Stolarski et al. 1992), which may represent a 10–20% increase in the effective dose of ultraviolet light received at the earth's surface (Caldwell 1971; Setlow 1974), the additional loss of lignin from the structural pool was set at 0–25% of the otherwise calculated flow of lignin to the slow soil pool, assuming optimum temperature, moisture, and nutrient conditions. Simulations were conducted for a 20-year period, with an annual litter input of 100 g $C\,m^{-2}$, comprising 20% lignin, 65% holocellulose and 15% metabolics (Fig. 2). These litter characteristics approximate wheat straw, a low-quality litter type.

A relatively fine-textured soil (90% clay+silt fractions) was used for all simulations, but since soil texture affects the stabilization of soil organic matter (Parton et al. 1987), a comparative simulation with coarser textured soil (25% sand) was performed (not shown). The coarser soil resulted in slightly smaller soil organic matter pools, but the relative effects of ultraviolet B radiation remained consistent with simulations using the fine-textured soil.

Simulation results

An increase in the lignin turnover had an immediate and substantial effect on the end-of-year amount of remaining plant residue. A 25% increase in lignin turnover produced end-of-year quantities of lignin and holocellulose in residual litter that were 64 and 32% lower than control values, respectively (Fig. 3a). The precise fate of the lignin, i.e., whether the increased loss of lignin was accomplished via greater flow to the active or to the slow soil pool, had no effect on the amount of litter remaining at the year end. In contrast, the active, slow, and passive soil pools were affected differently by the manner in which ultraviolet-in-

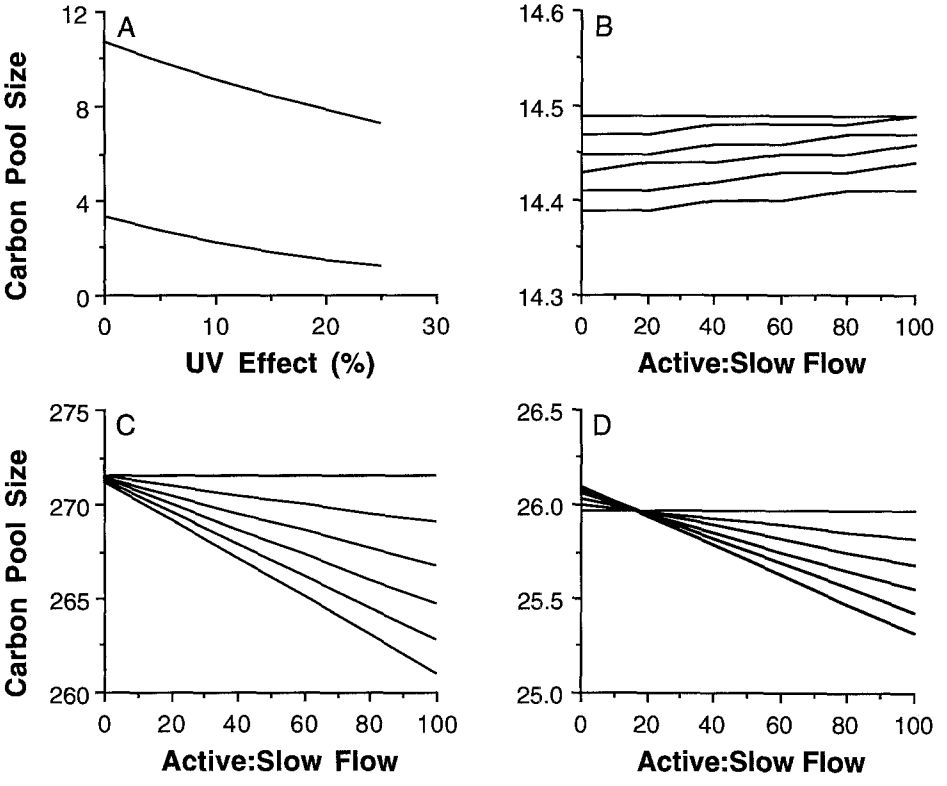

Fig. 3A–D Effects of ultraviolet (*UV*) B-enhanced lignin degradation on C pool sizes (g C m^{-2}) after 20 years of simulation: **A** end-of-year cellulose (top) and lignin (bottom) in residual litter; **B–D** lignin in residual litter; showing active (**B**), slow (**C**), and passive (**D**) soil organic matter. In all cases, from top to bottom, the lines represent 0, 5, 10, 15, 20, and 25% increases in lignin turnover of litter. The abcissa represents the fraction of the ultraviolet B-induced lignin decay routed to the active vs. slow soil soil pool

duced lignin decay was simulated. The size of the active pool was changed very little in any case, decreasing by only 0.6–0.7% with a 25% increase in lignin turnover (Fig. 3b). The slow pool decreased by 0.1–3.9%, with the magnitude of the reduction being inversely proportional to the amount of lignin flow through the active pool (Fig. 3c). The passive pool actually increased by 0.5% when the additional lignin loss was allocated to the slow pool, but decreased by up to 2.5% when the flow was routed to the active pool (Fig. 3d).

Discussion

Given the importance of litter decay as a source of nutrients in terrestrial ecosystems, changes in litter decomposition processes could affect site fertility and nutrient cycling. However, assessing the net effect of any change is difficult because of the complex relationship between litter decay, site fertility, and soil organic matter. For example, McClaugherty and Berg (1987) found that N concentrations in decaying litter increased over time, as the proportion of holocellulose decreased in the remaining litter. Since holocellulose contains very little, if any, chemically bound N, loss of holocellulose primarily represents loss of C from decaying litter. This means that the N content of litter increased as the recalcitrant fraction increased, a pattern also reported by Melillo et al. (1989). An explanation for this phenomenon is that decay processes sequester nutrients in the microbial mass (seldom distinguished from the remaining plant litter) and by the formation of recalcitrant complexes from reactive degradation products.

Plant lignins constitute a major component of recalcitrant soil organic matter (Stott et al. 1983) and are photochemically reactive, and so increasing levels of ultraviolet B radiation may affect nutrient cycles by increasing the turnover of compounds that would otherwise contribute to the formation of nutrient-rich recalcitrant soil organic matter complexes. Although most ecosystems will probably receive increasing levels of ultraviolet B exposure over the next few decades, those in which ultraviolet B impacts on the degradation of litter are likely to be most important are those already receiving high sunlight inputs (arid and semi-arid environments, high elevations), those likely to receive greater additional ultraviolet radiation (high latitudes, high elevations), and those in which large amounts of litter are exposed to direct sunlight for prolonged periods of time (open-canopy ecosystems).

A simulated increase in lignin degradation due to ultraviolet B radiation had a substantial effect on litter turnover but relatively little impact on soil organic matter dynamics. This response seems counterintuitive because decaying materials eventually accumulate in the more recalcitrant pools of the CENTURY model (Fig. 2), that is, our changes to lignin decay modified only the route, not the end point, of lignin C flow. However, C transfers between pools in CENTURY are achieved at a metabolic cost, i.e., some of the C associated with each flow is respired. Routing additional lignin flow directly to the active soil pool increases the total metabolic cost of eventual C transfer to the recalcitrant soil pools, yet turnover of

the active pool is so rapid that the additional input has little effect on the size of the active pool (Fig. 3 b). Alternatively, the slow and passive soil pools have such low turnover rates that little C is lost from these pools during 20-year simulations. For these reasons, the major impact of increased lignin degradation was to increase the overall respiratory loss of C from the system, seen as a reduction in litter pool sizes, rather than to make substantial changes in soil organic matter pool sizes. The amount of respired C increased in proportion to the relative amount of lignin flow that was routed directly to the active soil pool.

Our interpretation of these simulation results may be affected by the importance of the environmental drivers and nutrient limitations on model behavior. We assumed that all conditions were optimum, so that the simulations represent the maximum possible responses to an increased lignin turnover. We believe that these assumptions primarily affect the rate of overall system dynamics rather than the end point, i.e., our 20-year simulations may be equivalent to 100 years of decay under fluctuating field conditions. Furthermore, the generation of photoreaction products is probably not greatly affected by nutrient availabilities even though the activities of soil biota are often influenced by nutrient limitations. Increasing ultraviolet B radiation is unlikely to initiate photochemical reactions in underground soil organic matter pools because ultraviolet light normally does not penetrate the soil more than a few microns. Therefore, increasing ultraviolet B levels could affect short-term litter dynamics and yet have little effect on soil organic matter.

Although this paper focuses on the direct effects of ultraviolet B radiation on litter decay, increasing exposure also will have a number of indirect effects on decomposition. In addition to reducing productivity, ultraviolet B variously affects plant chemistry (Tevini and Teramura 1989; Bornman and Vogelmann 1991), the allocation of biomass (Murali and Teramura 1985; Barnes et al. 1990), and the composition of the plant community (Caldwell et al. 1989). Alterations in litter type and chemistry would likely modify decomposition, and the allocation of above-ground versus below-ground biomass is important because ultraviolet B does not penetrate the soil, i.e., increased production of above-ground litter might enhance net litter turnover via photodegradation. Furthermore, ultraviolet radiation is likely to affect decomposer organisms in exposed litter. Preliminary investigations suggest that exposure to ultraviolet B alters the species composition of fungal communities colonizing leaf litter and slows decomposition of the litter (Gehrke et al., unpublished). Therefore, increasing ultraviolet B exposure may increase the photochemical degradation of exposed litter while decreasing the rate of biologically mediated decay, in addition to changing the amount, chemical composition, and physical location of litter.

It is premature to extrapolate the net effects of increasing levels of ultraviolet B radiation on the structure or behavior of ecosystems, based on the results of studies examining any single aspect of ultraviolet B impact. Experimental studies that integrate the various ecological effects of ultraviolet B exposure are needed, including an expanded examination of decomposition and nutrient cycling processes.

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