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Element interactions in forest ecosystems: succession, allometry and input-output budgets

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Abstract. Element interactions within forests differ from those in other major ecosystems for three major reasons: – a greater allocation of carbon to structural material; – a greater element storage within biomass; and – the diversity of carbon- and nutrient-containing metabolites produced. The most important of these differences is structural material, which can lead to C:element ratios in biomass (as a whole) 100 × greater than those in unicellular organisms. Stand allometry causes the amount of carbon stored and C:element ratios in biomass to change in predictable ways in the course of secondary succession. Such changes affect microbial dynamics and C:element interactions within soils. Bicarbonate, organic acids, nitrate, phosphate, and sulfate are major anions within forest soils: they control leaching of both anions and cations. Biotic interactions of C, N, P, and S during both uptake and mineralization control the potential for production of these anions within forests, and geochemical interactions regulate their mobility and loss.

Introduction

A.C. Redfield (1958) suggested that the predictable stoichiometry of major elements in marine phytoplankton and bacteria could regulate the cycling of all of the biophilic elements in marine ecosystems on both local and global scales. Subsequent work has generally confirmed his overall model, and the biological interactions of C, N, S, and P are widely recognized as controlling much of marine biogeochemistry (Broecker 1974; Peterson & Melillo 1985).

Can the Redfield ratios or similar models be used to describe and to understand the biogeochemistry of terrestrial ecosystems? A number of models of both process-level element fluxes (i.e. nitrogen mineralization) and exchanges of elements with the atmosphere and hydrosphere have been attempted, and several have proved useful. For example, early analyses of decomposition and nutrient mineralization (Romell 1935) implicitly incorporated the carbon versus nitrogen requirements of decomposers through the use of critical C/N ratios for nitrogen mineralization. More recently, the underlying basis of such ratios (stoichiometry and resource-use-efficiency) has been made explicit (McGill et al. 1981; Rosswall 1981), and extended to P and S as well as N (McGill & Cole 1981; Hunt et al. 1983).

On a higher level of organization, the significance of the immobility and lack of a gas phase of phosphorus has been recognized and exploited in models of terrestrial biogeochemistry. Several related models illustrate how P controls the accumulation and transfers of C, N, and S during soil development (Walker & Syers 1976; McGill & Cole 1981; Cole & Heil 1981; Vitousek & Walker 1987), just as it controls element accumulation and cycling in lakes (Schindler 1977).

The development of these conceptual and quantitative models, together with the empirical research that they have inspired, represents a most productive line of research. It seems fair to say that "the stoichiometry of life" (Reiners 1986) is both an important axiom and a practical tool of ecosystem-level ecology, one that is likely to grow more important as we work towards regional and global scales.

Forest ecosystems

How well can models based on biological stoichiometry be applied to forest ecosystems? In an earlier volume devoted to interactions of the biogeochemical cycles (Bolin & Cook 1983), Melillo & Gosz (1983) demonstrated that the ratios of C, N, S, and P accumulation and cycling in forests differ strikingly from the Redfield ratios, and indeed that they differ among forests and among biomes. There are three major causes for these differences – structural material, storage, and the diversity of metabolic pathways. None of these is unique to forests, but all are most fully developed here.

The most important factor altering the stoichiometry of elements in forests is the presence of carbon-containing structural material. The Redfield ratios were developed for unicellular producers and decomposers, and they represent element ratios in protoplasm. Where any element is used to make structural tissues (as with carbon in plants and phosphorus in vertebrates), the Redfield ratios cannot be applied directly (Reiners 1986). Most of the biomass carbon in forests is in structural forms in wood (lignin, cellulose, hemicellulose), and hence ratios of C to other major elements are high. Even leaves can have high (and highly variable) amounts of structural material – in extreme cases the C/N ratio of leaves can be 8–10 times that in phytoplankton.

Second, perennial plants can store substantial quantities of C, N, S, and P in metabolically inactive forms (Chapin et al. 1986a). For example, excess nitrogen can be stored as arginine (with a C/N ratio of 1.5:1), or even as nitrate (Bloom et al. 1985). Energy and nutrient storage are particularly important in slow–growing plants adapted to infertile soils (Chapin 1980), where such storage can buffer variations in nutrient availability and/or allow plants to accumulate pulses of particular nutrients. The inclusion of storage products substantially alters the stoichiometry of major elements in plant tissue.

Finally, the diversity of metabolic pathways in trees can alter the stoichiometry of C, N, S, and P. Trees which contain large quantities of nitrogen–-containing "secondary compounds" such as alkaloids or cyanogens (i.e. many tropical trees) can be expected to be relatively enriched in nitrogen – a mechanism which may account for the extraordinarily high N/P ratios of many tropical forests on oxisols (Vitousek & Sanford 1986). Similarly, trees which accumulate carbon-based compounds like phenolics and terpenes are relatively enriched in carbon (McKey et al. 1978; Bryant et al. 1983; Coley et al. 1985).

Because of these large variations in element ratios within forests (Vitousek 1982, 1984; Melillo & Gosz 1983) and the multiple mechanisms that cause these variations, it could be suggested that studies of element interactions based on stoichiometry simply break down in forests. While it is certainly true that no single ratio can be applied to all forests, or within a single forest type, we believe that there is nonetheless considerable value in using element ratios to examine biogeochemical interactions in forests. Variations in ratios are often interpretable (and testable) in terms of controlling mechanisms. More importantly, variations in element ratios affect other trophic levels, overall patterns of element cycling within ecosystems, and the exchanges of elements across ecosystem boundaries.

Our approach will be to evaluate C, N, S, and P interactions within plant biomass and within the decomposer/mineralizer subsystem. We will then discuss the interactions of C, N, S, and P in the input/output budgets of forest ecosystems.

Plant biomass

One obvious feature of element interactions in forests is that all organisms require relatively large quantities of C, N, S, and P, and any absolute limitations in the supply of one will affect plants and microbes ability to accumulate and use the others. In practice, though, limitations are rarely absolute, and well-adapted plants function normally at resource supply rates and element ratios that seem impossible to investigators familiar with agricultural systems.

A great deal of information on element accumulation, use, and cycling within forests has been collected and evaluated. Compendia of data include Rodin & Bazilevich (1967); Cole & Rapp (1981); Van Cleve et al. (1983); Jordan (1985); and Vogt et al. (1986); some discussions of element ratios and their regulation include the above plus a number of others (Vitousek 1982, 1984; Melillo & Gosz 1983; Pastor et al. 1984). We believe that this information base is substantial for the C, N, and P content of aboveground plant biomass and litter. (The latter is important because N, P, and to a lesser extent C are retranslocated from plant tissue prior to senescence, and so element ratios in litter can differ substantially from those within plants.) The information base and interpretations are much weaker for sulfur, which rarely limits forest productivity, and for root nutrient content and turnover.

We will not attempt to repeat previous syntheses of element ratios in forests. Rather, we will briefly summarize patterns of element interaction within forest biomass, and focus our attention on stand allometry, a less frequently discussed factor which affects element interactions in forests.

Existing information suggests that differences in element ratios are correlated with climate, rates of nutrient supply, and successional stage. The overall trends in C, N, and P ratios are:

- Higher C/N and to a lesser extent C/P ratios occur in leaves and litter in colder climates. This pattern occurs both across and within biomes; it can be observed within the taiga (Van Cleve et al. 1983) and within tropical forests (Fig. 1; Vitousek & Sanford 1986).

- High C/N and/or C/P ratios occur in forests where N and/or P are in short supply (Vitousek 1982, 1984). The widespread use of foliar analysis (cf. Van den Driessche 1974) to identify nutrient-deficient forest stands is based on this association (nutrient concentrations are simply the inverse of dry mass/nutrient ratios). This pattern has been observed for both N and P across and within biomes (Anderson et al. 1983; Van Cleve et al. 1983). For example, old infertile soils support forests with high C/P ratios in both temperate and tropical areas (Melillo & Gosz 1983; Vitousek & Sanford 1986; Walbridge 1986). However, it can be difficult to separate the influence of climate from that of nutrient supply. High C/N ratios in many upper montane tropical forests (Fig. 1) are probably

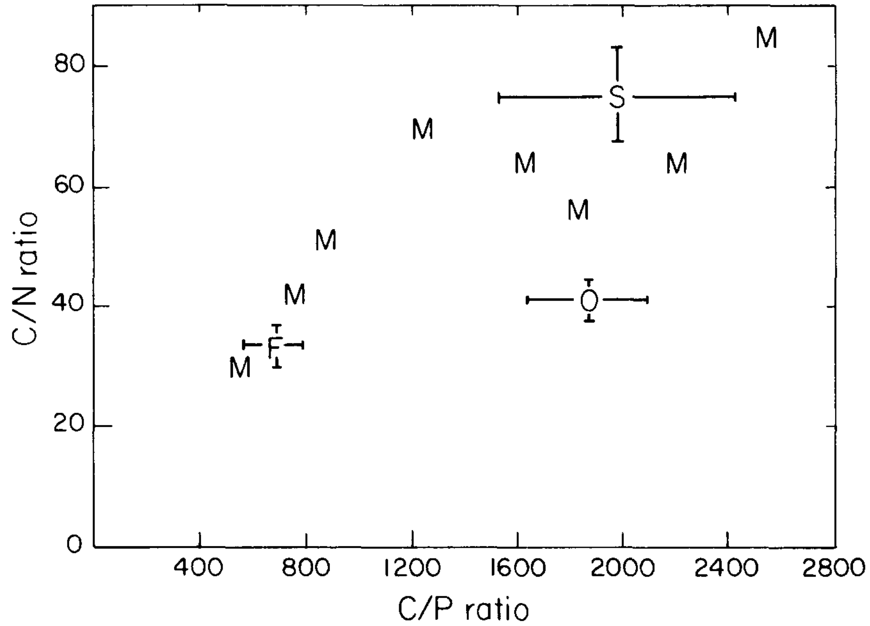

Fig. 1. C:element ratios in the fine litter of tropical forests. "F" represents the mean (± S.E.) of 10 lowland tropical forests on moderately fertile soils; "O" represents 10 lowland tropical forests on oxisols and ultisols; and "S" represents 2 lowland tropical forests on white-sand soils. Each "M" represents a montane tropical forest; those on the lower left are generally lower montane forests while those on the upper right are upper montane forests. Data from Vitousek & Sanford (1986).

proximally caused by low nitrogen availability in montane soils. Ultimately, low N mineralization is probably caused by reduced decomposition in that cooler climate (Grubb 1977; Tanner 1977, 1981). The direct effects of nutrient supply on element ratios can be tested with fertilization. Forest fertilization generally yields decreased C/N and/or C/P ratios in low-nutrient sites; these results are similar to the patterns observed along natural gradients from low to high nutrient availability (Miller et al. 1976; Birk & Vitousek 1986), although species replacement may be necessary before the full effects of fertilization can be observed (Chapin et al. 1986b).

- Low C/N and C/P ratios are generally observed early in secondary succession (Uhl & Jordan 1984; Ewel 1986), while high C/P ratios are found late in primary succession (Vitousek & Sanford 1986). These patterns too may reflect nutrient availability – N mineralization and nitrification generally increase shortly after disturbance (Vitousek and Melillo 1979; Vitousek & Matson 1985), and phosphorus availability declines late in soil development (Walker & Syers 1976).

Obvious differences exist in the gross morphology of the tree species which dominate forest ecosystems in the various major biomes. Although developmental aspects of tree form have been discussed at length (e.g. Halle et al. 1978), not all of the possible implications for nutrient accumulation and use have been examined thoroughly. In this section, we consider some relationships between tree allometry and C, N, P and S accumulation in forest biomass. In particular, we consider: (i) the changes in element accumulation which result from changing allometry during the development and maturation of natural forest stands; (ii) the theoretical influence of differences in tree form across six broadly-defined forest biomes; and (iii) the actual effect of the interaction between variation in allometry and tissue chemistry for three major biomes.

Stand development. Leaf (and probably fine root) biomass usually reaches a maximum early in the development of an even-aged stand or forest plantation, whereas the amount and proportion of biomass in tree boles may continue to increase until mortality of mature individuals occurs. These allometric changes themselves drive changes in element ratios within accumulated biomass.

To illustrate the patterns of change in element ratios in accumulated biomass during stand development, we analyzed an example of forest succession for natural *Picea abies* stands in the USSR (DeAngelis et al. 1981).

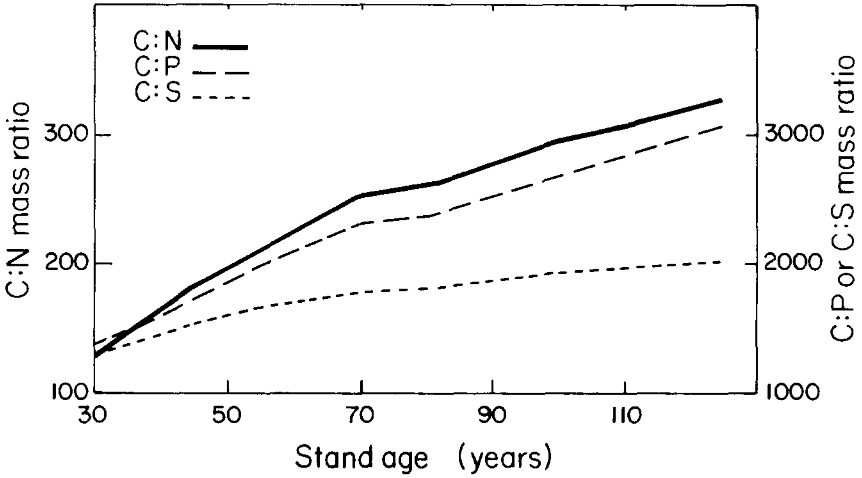

Fig. 2. C:element ratios over the course of stand development in *Picea abies* plantations. A constant tissue chemistry (from Nihlgard 1972) is assumed; variations in element ratios reflect relative differences in the amount of leaves, branches, wood, and roots.

Between the ages of 30 and 126 years, leaf biomass as a percentage of total biomass declined from about 17% to 3%; branch biomass from about 19% to less than 7%; and bole bark from 6% to less than 4%. Bole wood increased from about 44% to nearly 70% of the total biomass, which overall increased from about 30 t/ha to 250 t/ha during this time interval. Changes in the proportion of biomass in coarse roots were rather small. Even if chemical composition remained constant during stand development, carbon to element ratios would increase as the proportion of nutrient-rich tissues declined. The rate of change would be most rapid during the first 30–50 years of development in these rather slow growing *Picea* forests (Fig. 2).

Similar results have been observed in a large variety of studies which have measured both biomass pools and tissue chemistry (often only N and P) in a range of biomes (cf. Laudelot 1962; Switzer & Nelson 1972; Toky & Ramakrishnan 1983a, b; Sprugel 1984; Jaffré 1985; Gholz & Fisher 1985). The accumulation of wood invariably increases C:element ratios during stand development.

Differences among biomes: allometry. Significant differences exist among six broadly-defined forest biomes in the proportions of leaf, branch, bole, and root biomass of mature stands (Table 1; summarized from Turner et al. undated; DeAngelis et al. 1981; Cannell 1982; Medina & Klinge 1982). Because the concentrations of C, N, P, and S differ markedly among these four classes of plant tissue, allometric variations between biomes should result in differences in the element ratios of accumulated biomass. The purely allometric component of this variation can be examined by assuming that the element concentrations in classes of tree tissue are the same in all the forest types. We assume the following tissue concentrations (units are % dry mass), leaves: N = 1.80, P = 0.150, S = 0.137; branches: N = 0.40, P = 0.045, S = 0.053; bole: N = 0.23, P = 0.025, S = 0.035; and roots: N = 0.44, P = 0.066, S = 0.040. These values are the arithmetic mean of tissue chemistry values summarized from Rodin & Bazilevich (1967) and Cole & Rapp (1981). Throughout, we assume that carbon constitutes 52% of the dry mass of organic matter.

Relatively small differences in the element ratios in accumulated biomass can be attributed to variations in allometry among the six forest biomes (Table 1). For example, the largest overall difference in the C/N ratio, that between the northern conifer and temperate deciduous forest biomes, is only about 13%. This result occurs because the largest relative differences in allometry are for the leaf biomass compartment, and leaves comprise only a small proportion of total biomass in mature forests. Nevertheless, ratios of C to mineral elements under these idealized assumptions would be lower

Table 1. Biomass allometry and its theoretical influence on element accumulation in biomass of mature stands in six broadly-defined forest biomes (see text for explanation). Values in parenthesis are standard errors.

Forest biome	No. of[1] stands	t/ha Total biomass	% of total biomass				Mass ratio				
			Leaf	Branch	Bole	Roots	C/N	C/P	N/P	C/S	N/S
Northern/sub-alpine conifer	12	233(19)	4.5(0.3)	10.2(1.3)	62.8(2.1)	22.6(1.7)	143	1246	8.71	1230	8.6
Temperate broad-leaf deciduous	13	286(17)	1.1(0.1)	16.2(1.4)	63.1(3.0)	19.5(2.3)	165	1384	8.40	1300	7.9
Giant[2] Temperate conifer	5	624(62)[2]	2.5(0.5)	10.2(1.6)	66.4(3.9)	20.8(2.9)	158	1345	8.53	1290	8.1
Temperate broad-leaf evergreen	15	315(19)	2.7(0.2)	14.7(1.4)	66.2(2.1)	16.5(2.5)	159	1383	8.73	1280	8.1
Tropical/sub-tropical closed forest	13	494(45)	1.9(0.1)	21.8(2.5)	59.8(3.7)	16.4(2.0)	161	1394	8.65	1280	8.0
Tropical/sub-tropical woodland and savannah	13	107(11)	3.6(0.5)	19.1(3.7)	60.4(2.7)	16.9(2.5)	147	1290	8.80	1210	8.2

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[1] Biomass data summarized from Turner et al. undated; DeAngelis et al. 1981; Cannell 1982; Medina & Klinge 1982.

[2] High biomass, old-growth conifer forest from north-central US, western North America and Japan; not an average value for temperate zone conifer forests.

for the northern conifer and woodland/savannah biomes than the others. This result is more important for C/N than the other ratios because the relative enrichment of N in leaves is greater.

The proportion of nutrient-rich tissue in moist tropical forests could be substantially higher if lianas and epiphytes were included in the calculations. Lianas may account for as much as one-third of leaf biomass in lowland rain forest (Gentry 1983; Putz 1983); they require relatively little support tissue for this large leaf mass. The limited information on nutrient concentrations in foliage, twigs and woody tissues of lianas suggests that they are similar to corresponding tissues in the trees (Greenland & Kowal 1960; Grubb & Edwards 1982; Hase & Folster 1982; Tanner 1985), but the proportion of structural tissues is much lower. The abundance of lianas and epiphytes could be responsible in part for the low wood versus litter production observed in many tropical forests (Jordan & Murphy 1978; Gentry 1983). More generally, understory vegetation has lower average C/element ratios than the overstory (Tanner 1985).

Two additional allometric components which could influence element ratios in accumulated biomass are bark and fine roots. The published information on these components is sparse (compared to the others), although recent summaries (e.g. Vogt et al. 1986) are filling this gap. Trees which have thick bark which protects the cambium from fire certainly support much higher proportions of this tissue than trees is mesic climates; for example, trees of the subtropical/tropical savannahs have 19% of total biomass in aboveground bark, compared with less than 7% for temperate zone hardwoods and conifers. Bark and fine roots are lumped within the bole/branch and root components respectively in Table 1.

Differences among biomes: tissue chemistry. In addition to purely allometric influences, there are systematic variations in tissue element concentrations among forest biomes. Comprehensive data on tissue chemistry (N, P, S) is available for three forest biomes, summarized in Table 2. Information for the coniferous and temperate deciduous biomes is from Rodin & Bazilevich (1967) and Cole & Rapp (1981). For the tropics, information in Rodin and Bazilevich (1967) was supplemented with summary data for foliage from Vitousek & Sanford (1986) and for woody tissues from several additional sources (Greenland & Kowal 1960; Ovington & Olson 1970; Stark 1971; Folster et al. 1976; Grubb & Edwards 1982; Hase & Folster 1982).

Overall, significantly lower N, P, and S concentrations are found in tissues of gymnosperm than angiosperm trees. Differences between tropical and temperate angiosperms are not large, although N is enriched relative to P in all tissues of tropical trees. Bole wood is the most important tissue affecting

Table 2. Element in four classes of tree tissues and in total biomass of three biomes.

Forest biome	Tissue	C/N	C/P	N/P	C/S	N/S
Northern[1] subalpine conifer	Leaf	49	460	9.5	740	15.1
	Branch	137	1300	9.5	1300	9.5
	Bole	433	4730	10.9	5200	12.0
	Root	289	2170	7.5	1490	5.2
	Total biomass	256	2420	9.4	2430	9.5
Temperate[1] broad-leaf deciduous	Leaf	25	310	12.5	330	13.2
	Branch	106	950	8.9	1080	10.2
	Bole	236	2170	9.2	3250	13.8
	Root	107	550	5.1	940	5.2
	Total biomass	155	1180	7.6	1710	11.0
Tropical/sub[2] tropical closed forest	Leaf (fertile)	22	354	16.2	290	13.2
	Leaf (infertile)	33	840	25.8	nd	nd
	Branch	108	1330	12.3	520[3]	4.8[3]
	Bole	159	2050	13.2	740	4.7
	Root	80	650	8.1	210	2.6
	Total biomass	115	1320	11.5	480	4.2

[1] Nutrient concentration data summarized from Rodin & Bazilevich (1967).

[2] Nutrient concentration data summarized from Rodin & Bazilevich (1967); Ovington & Olson (1979); Stark (1971); Grubb & Edwards (1982); Hase & Folster (1982); Vitousek & Sanford (1986).

[3] No data available; estimated by proportion with wood.

nd – no data.

overall biomass/element ratios because it constitutes most of forest biomass (Table 1). The large differences in nutrient concentrations between gymnosperm and angiosperm would probably reflect in part the greater proportion of living parenchyma cells in angiosperm heartwood. There could also be differences in efficiency of nutrient recovery from xylem cells prior to their death; newly-formed cells with living protoplasts contain much higher nutrient concentrations than fiber and xylem elements in the dead wood (Cowling & Merrill 1966).

The interaction between differences in allometry and differences in tissue chemistry among these three major biomes lead to large differences in element ratios in accumulated biomass (Table 2). Differences in allometry are greatly overshadowed by the systematic differences in tissue chemistry, so that the coniferous forests have much higher C to mineral element ratios than temperate and tropical hardwoods.

The foregoing compilations must be interpreted with some caution. First, tissue chemistry data for many of the temperate and northern forests were collected in regions which have been subjected to unnaturally high loading of N and S from atmospheric deposition, so any evolutionary interpretations of the results could be suspect. Second, the methods of tissue analysis used in studies compiled by Rodin & Bazilevich (1967) may not be entirely consistent, particularly for S. Third, measurements of biomass allometry often do not utilize consistent methods or definitions of components such as bole and branch, and their accuracy in estimating leaf biomass is questionable (Marshall & Waring 1986). Finally, it is impossible to assess whether the tissues analyzed in studies summarized by Rodin & Bazilevich (1967) and Cole & Rapp (1981) corresponded with the classes in the biomass allometry studies. In summary, it appears that:

- During the development of even-aged stands of gymnosperm trees, C/N ratios rise more rapidly than C/P ratios in the years immediately following canopy closure (and maximum leaf area index). During the middle and late stages of stand development, both of these ratios increase more rapidly than C/S ratios. This latter result could be due to high S deposition in forests from which data on tissue chemistry were collected. Increases in biomass C:N and C:P ratios over succession are actually observed in a wide range of plantation and natural successional forest ecosystems in a range of biomes.

- Purely allometric differences among six broadly-defined forest biomes are not large enough to cause much variation in requirements for N, P, and S.

- Most of the differences between biomes in nutrient ratios of accumulated biomass can be attributed to systematic differences in tissue chemistry between angiosperms and gymnosperms – the amount of N, P, and S required to maintain organic matter accumulation is much higher for the former than the latter.

Element interactions in the decomposition of litter and soil organic matter

The availability to plants of the nutrient elements N, P, and S is dependent on their conversion from the organic forms in which they occur within plant, microbial and animal tissues to biologically available inorganic forms. The timing of release of mineral nutrients from decomposing organic matter varies with respect to the nutrient in question, the nature of the resource (i.e. type of organic matter), and a variety of other less well defined factors. The mobility of some elements such as K is generally independent of the pattern of decay (e.g. Lousier & Parkinson 1978). In the cases of N, P and S, however, the release pattern often shows some relationship to C dynamics for at least some part of the decomposition process. It may be assumed, therefore, that these dynamics are regulated in part by the same factors and that these are at least partially biological in nature.

The regulation of decomposition may be attributed to three broad sets of factors – the physical environment, resource quality, and the nature of the decomposer community (Swift et al. 1979). The effects of moisture and temperature may be supposed to act in much the same way for N, P and S dynamics as they do for C; it is in the latter two features that the main differences in control may be sought. It is also through these factors that the major element interactions are expressed.

The influence of carbon on element interactions

Release patterns of N, P and S may differ from those of C by either being accelerated or delayed. Classical theory suggests that this is largely determined by the initial C to nutrient (C:Nt) ratio. This has been considered largely in relation to C:N ratios (e.g. Jansson 1958; Berg & Staaf 1981), but the same arguments may apply to the other two elements. In its most fundamental form, this theory is an expression of the law of limiting factors; when N is in short supply (i.e. the C:N is wide), then N will be immobilized in microbial tissue and there will be no net release of mineral-N; when C is limiting (i.e. when C:N is narrow), mineral-N may be released from organic-N as a waste product by deamination or similar processes. The "switch" point between net immobilization and net mineralization is the ratio equivalent to that of the microbial tissue corrected for its energetic efficiency, i.e. that at which the demand for C and N by the decomposer matches the ratio of the two elements in the resource. This theory has long been used to explain the differential fertilization benefit of organic residues. It can also provide a plausible explanation for the time course of nutrient dynamics under a number of situations (e.g. Gosz et al. 1973; MacLean & Wein 1978).

The theory also predicts that different plant tissues release nutrients at different rates, and this prediction is broadly borne out; resources of wide ratio tend to show periods of extended immbolization compared with those of narrow ratio (Swift et al 1979; MacLean & Wein 1978). As a number of authors have pointed out, however, nutrient release patterns cannot always be matched with C:Nt ratios (Park 1976; Aber & Melillo 1980; Berg & Staaf 1981; Heal et al. 1982). A number of other factors may intervene to disrupt the pattern, including:

Elemental interactions. The most obvious of these is the extension of the concept of limiting factors: the limiting effect of one factor may be overridden if another factor becomes limiting during decomposition. If element

A is initially limiting to microbial activity, then it may be possible to show a relationship with the C:A ratio. If at the same time element B is not limiting and has a net release, loss of B could result in it falling below limiting concentration. The C:B ratio would then become the operative index. Analysis of N:P, N:S and P:S ratios to explore such relationships might be rewarding under some circumstances, although it is likely that other, more mobile elements such as K might be more critical in this respect.

Resource quality. Nutrient content is not the only factor which determines the rate of decay of a given resource. A number of other factors have been subsumed under the concept of resource quality, which is defined as those features of the intrinsic character of a resource which affect its rate of decay (Swift et al. 1979). These include the lignin content and the presence of allelopathic compounds, which may interact with nutrients and influence the time course of nutrient release. There is, for example, a mounting body of evidence that the lignin:N ratio is generally a better predictor of rate of decomposition than C:N (Berg & Staaf 1981; Aber & Melillo 1982; Melillo et al. 1982).

The same three factors – climate, soil fertility, and succession – which as control element ratios in biomass also affect the resource quality of organic residue. This convergence is unsurprising – these factors affect nutrient availability (Meentemeyer 1978; Vitousek & Sanford 1986; Vitousek & Matson 1985; Matson & Boone 1984), which in turn controls nutrient concentrations and the kinds of organic compounds in biomass and litter (Gosz 1981; Vitousek 1982; Coley et al. 1985).

Stimulation of release by animal activity. A further factor that may over-ride regulation by nutrient availability to microbes is the influence of grazing by decomposer protozoa or animals. The intervention of these secondary decomposers has been shown to stimulate nutrient release, often in massive amounts (Anderson et al. 1981; Anderson & Ineson 1984; Clarholm 1985). The mechanisms are uncertain in some respects (Seastedt 1984) but Anderson & Ineson (1985) concluded that simple disruption of microbial cells is as important as any other pathway. In this event the relative effect on different elements would simply be proportional to their relative content in the microbial tissue, although the immediate consequences in terms of re-immobilization by microflora (e.g. see Seastedt & Crossley 1983) or uptake by plants might be more complex.

Allometry in the decomposer community. C:Nt theory is predicated on the information that ratios in decomposers are usually narrower than those of the food they consume; that nutrient elements become more concentrated as they move from resource to microbe. Nevertheless, the composition of fungal mycelia may change in response to the availability of an element. For example, Levi & Cowling (1969) demonstrated a direct relationship between the C:N ratio of mycelium and that of the growth in certain wood decay fungi. The primary agents of decomposition in many ecosystems are fungi, which are characterized by polymorphic life histories. The different morphs (mycelium, asexual spores, meiospores produced by sexual reproduction and the variety of survival structures, chlamydospores, sclerotia etc.) may have different elemental compositions. Dowding (1976, 1981) has discussed the processes involving allocation of nutrients within the fungal life cycle and considered their ecological significance. Reproductive structures and spores have higher concentrations of N and P than mycelium, and hence allocations to reproduction may be more marked under conditions of limiting availability of an element. In broad terms it may be supposed that at different stages of the life cycle different elemental interactions prevail. These effects can be quite extreme – Merrill & Cowling (1966) calculated that the amount of N exported from a decomposing trunk in the basidiospores from a single sporophore of *Fomes fomentarius* amounted to the total depletion of N in over 0.2 m3 of wood.

There is also a further concentration of the mineral elements as they move from the primary decomposer to higher trophic levels in the decomposer community (to the invertebrate animals) (Reichle 1971). The changing demand for nutrients also involves differentials among the nutrient elements. For instance, whereas the N:P ratios of ash and birch leaves respectively were 25 and 30, that of mycelium of the basidiomycete *Mycena galopus* growing on them was 13 and that of common detritivores or fungivores was about 6 to 10 (Frankland et al. 1978). This is a relatively unexplored area of potential N, P, S interaction. It suggests that changes in the composition of the decomposer community could result in shifts in the nature of the elemental interactions.

In summary, it may be concluded that interactions between nutrient elements may regulate the functioning of decomposition processes. Unfortunately, few of these possible interactions have been explored in detail.

Succession and allometry

The quality and quantity of resources available to decomposer communities also varies during succession. Slowly-decomposing bolewood becomes a significantly larger fraction of total litterfall in progressively older stands, just as it represents a larger fraction of total forest mass. In contrast, leaf litterfall generally reaches an equilibrium value early in secondary succession (Ewel 1976; Toky & Ramakrishnan 1983a; Sprugel 1984). Wood production should equal woody litterfall in a steady state forest, meaning that in many cases more carbon would return to the soil as woody litter than as leaf litter. In forests which are declining in biomass (cf Sollins et al. 1980; Gosz 1980, Sprugel 1984), this effect could be even larger.

Increased woody litterfall late in secondary succession has several implications for element interactions. First, as discussed above wood has much higher C:element ratios than leaves or other tissues. Second, the carbon quality in wood is low – lower than in leaves on any but the most infertile sites. Finally, the very size of woody litter makes much of the carbon and nutrients it contains inaccessible to decomposers. As a consequence, breakdown of C compounds in wood can lead to substantial immobilization of N and P for protracted periods (Grier 1978; Swift et al. 1979). Lambert et al. (1980) demonstrated that the nutrients in woody litter deposited in "fir waves" in New Hampshire were not released into biologically available forms until the second cycle following treefall ($>$ 60 years later).

Overall, allometry-based changes in litter production during secondary succession generally reduce soil nutrient availability late in succession. They can therefore reinforce the patterns of C versus nutrient interactions discussed above. Where woody residue is kept on-site during and after a disturbance, N and P immobilization on this C-rich substrate can retain nutrients within disturbed sites (Vitousek & Matson 1985).

Interactions in input-output budgets of C, N, S, and P

Biological interactions with C regulate the biological availability and potential mobility of N, P, and S in forest soils. Biological uptake is a major process removing nutrients from soil solution, while release from microorganisms is the major process adding N and to a lesser extent P and S to the soil solution. In addition to these biotic interactions, there are significant geochemical interactions among elements which affect the availability and mobility of C, N, P, and S.

In general, biological processes dominate C and N budgets whereas geochemical processes such as absorption and precipitation play a greater role in S budgets and often dominate P budgets. However, no element is regulated by wholly biological or wholly geochemical processes. For example, caliche ($CaCO_3$) formation can be an important sink for C in semiarid ecosystems (Schlesinger 1985); nitrate adsorption in subsoil reduces leaching losses of nitrogen from some disturbed tropical forests (Matson et al. 1987). Geochemical interactions among C, N, P, and S often come into play only after biological demands for one or more of these elements is satisfied or exceeded, although adsorption of P and S in allophanic soils is certainly competitive with biotic uptake (Uehara & Gillman 1981).

We will examine the geochemical processes and interactions which regulate outputs of C, N, S, and P. All four have major anionic forms (HCO_3^-, organic acids, NO_3^-, $SO_4^=$, and $H_2PO_4^-$), and so (in theory) all could control cation as well as anion outputs (Johnson & Cole 1980). We will review each of these anions individually, and will show where the major geochemical interactions occur.

Carbon. Carbonic and organic acid leaching, while it accounts for only a minor portion of total C export, is an important natural soil leaching agent. Along with base cation uptake by trees, it is the primary cause of natural soil acidification (Johnson et al. 1977). The intensity of carbonic acid leaching is directly regulated by the partial pressure of CO_2 in the soil atmosphere and the equilibrium soil solution pH (Johnson et al. 1977). The partial pressure of CO_2 is in turn regulated by root and soil heterotroph respiration and soil CO_2 diffusivity. Additions of N, S, or P to ecosystems whose productivity is limited by one or more of these elements can cause increases in root and/or heterotroph respiration which will intensify carbonic acid leaching.

Soil solution pH is affected by base saturation, the presence of buffering agents (such as organic acids), and the ionic strength of the soil solution. The relationships between base saturation, ion activities, and pH can be seen in a generalized selectivity coefficient which describes the exchange of cations of H^+ on cation exchange sites (see review by Johnson et al. 1986):

$$Q = \frac{(H^+)^r[C^{r+}]}{(C^{r+})[H^+]^r}, \qquad (1)$$

where Q = selectivity coefficient; () = exchange phase; [] = solution phase; C = cation; and r = valence of cation. Solving for H^+, we have

$$[H^+] = \left[\frac{(H^+)^r[C^{r+}]}{(C^{r+})Q}\right]^{1/r} \qquad (2)$$

This equation shows that we can change soil solution pH by changing exchangeable (H^+) or (C^{r+}) (e.g., by changing base saturation) or by changing solution concentration $[C^{r+}]$. In the short-term, the input of any anion should result in a lower soil solution pH whether the anion is added as a salt or as an acid. This occurs because the concentration of cations $[C^{r+}]$ will be elevated concomitantly with the concentration of the introduced anion in soil solution, which will in turn elevate [H^+] according to Eq. [2]. Thus, increasing concentrations of SO_4^{2-} or NO_3^- will cause a reduction in HCO_3^- leaching. By a similar rationale, increasing concentrations of SO_4^{2-} or NO_3^- will cause the protonation of organic anions, thereby reducing concentrations of the dissociated forms.

Nitrogen. Nitrogen behaves similarly to carbon in that the atmosphere is ultimately the primary source of N and fluxes are dominated by biological processes. Carbon and nitrogen are intimately linked, and the net accumulation of one strongly affects the net accumulation of the other in forests.

Like carbon, nitrogen may leave ecosystems as a gas (via denitrification) or in solution (primarily as NO_3^-). Relatively few studies of N cycling in forests include gaseous components, although many more measurements are now becoming available (cf Goodroad & Keeney 1984; Robertson & Tiedje 1984; Bowden 1986). When dissolved inputs and outputs only are considered, most forest ecosystems accumulate N (inputs > outputs), presumably due to the accumulation of organic matter and nitrogen within successional forests. If organic matter and N accumulate slowly enough that biological demand for N is satisfied or exceeded, NO_3^- leaching usually increases because a) atmospherically-derived N is not taken up rapidly, and b) internally-generated NH_4^+ is nitrified (e.g. Van Breeman et al. 1982; Van Miegroet & Cole 1984).

Nitrate leaching is often stimulated by disturbances including clearcutting (Likens et al. 1978), stem girdling (Edwards & Ross-Todd 1979), insect attack (Swank et al. 1981), and artificial acid irrigation (Abrahamsen 1980). Uptake by trees may play a major role in controlling NO_3^- leaching in many of these cases, but changes in microbial activity are also important. N mineralization and nitrification are usually increased by disturbance, but microbial immobilization by decomposers utilizing high-quality carbon substrates can increase as well (Vitousek & Matson 1984, 1985).

Sulfur. Sulfur and phosphorus differ from carbon and nitrogen in two important respects: a) biological demands for S and P are lower than for C and N, and b) geochemical processes further restrict S and P leaching once biological demands are met. S requirements of forests are only 7% (by weight) of those for N (see Table 2), and thus atmospheric S inputs readily satisfy forest S requirements in all but the most remote areas with low S input. Humphreys et al. (1975) suggested that atmospheric S inputs as low as $1\,kg \cdot ha^{-1} \cdot yr^{-1}$ may be sufficient to supply forest S needs in Australian *Pinus radiata* stands. In polluted regions of the world, atmospheric S inputs (10–$100\,kg \cdot ha^{-1} \cdot yr^{-1}$) greatly exceed forest S requirements (1–$5\,kg \cdot ha^{-1} \cdot yr^{-1}$ for net increment), yet forest ecosystems with high S inputs have net annual accumulations (input > output) of S (Swank et al. 1977; Shriner & Henderson 1978; Meiwes & Khanna 1981; Kelly 1984).

As noted by Haines (1983), the apparent net SO_4^{2-} accumulation in these ecosystems could in theory by due to a number of factors, including tree uptake, incorporation into soil organic matter, soil SO_4^{2-} adsorption or precipitation with Al, organic S leaching, and sulfate reduction followed by volatilization of H_2S, dimethyl sulfide, or other gaseous S compounds. Tree uptake is unlikely to be of sufficient magnitude to account for differences in SO_4^{2-} inputs and outputs. Incorporation of SO_4^{2-} into organic matter may constitute a net SO_4^{2-} sink (e.g. Swank et al. 1984). Measurements of S losses by volatilization and organic S leaching are rare, but available measurements suggest that these fluxes are generally too low to account for SO_4^{2-} input-output imbalances (Adams 1980; Haines 1983).

We believe that several factors point to SO_4^{2-} adsorption (and, in some cases, coprecipitation with Al complexes) as a process often responsible for apparent net SO_4^{2-} accumulation (where it occurs) in forest ecosystems. First, there are good correlations between soil SO_4^{2-} adsorption properties and apparent SO_4^{2-} accumulation in ecosystem (Johnson et al. 1979; Meiwes et al. 1980; Johnson & Todd 1983; Richter et al. 1983). Second, where lysimeter data are available for estimating fluxes through various soil; horizons, net SO_4^{2-} accumulation (i.e. input > output) usually occurs primarily in Fe- and Al-oxide rich subsurface horizons (except in Spodosols, where organic matter blocks adsorption) rather than in organic matter-rich surface horizons (Johnson et al. 1979; 1982; Meiwes et al. 1980; Stednick 1982). Finally, artificially additions of SO_4^{2-} often result in net SO_4^{2-} retention in soils, even where SO_4^{2-} budgets had been in steady-state (Singh et al. 1975; Johnson & Cole 1977; Lee & Weber 1982).

Phosphorus. Unlike C, N, or S, inputs of P via atmospheric deposition are usually negligible, leaving the soil as the only significant natural source of P for leaching and plant or microbial uptake. The immediate source of P for both uptake and leaching is thought to be the "labile P" pool, which is considered to be in equilibrium with soil solution P (Cole et al. 1977; Sharpley et al. 1984; Smeck 1985). This labile P pool is increased by inputs from primary mineral weathering, organic P mineralization, or P fertilization; it is either increased or decreased by secondary P minerals (e.g. calcium, aluminium and iron phosphates as well as adsorbed phosphate), and it is decreased by the formation of occluded phosphates (secondary P minerals incapsulated by Fe and Al oxides), plant uptake, and leaching (Smeck 1985). According to the conceptual models presented by Cole et al.

(1977) & Smeck (1985), any factor which increases or decreases the labile P pool will directly increase or decrease soil solution P. Either biological or geochemical processes may then control P losses by leaching, and it is suggested that biological processes are most important at low P levels and geochemical processes most important at high P levels. Wood et al. (1984) found that P retention was governed primarily by biological processes in litter and surface soils but by adsorption reactions in subsoils at Hubbard Brook, New Hampshire. We suspect the same type of stratification could occur on Walker Branch Watershed, Tennessee (Seagers et al. 1986). Once biological demands are satisfied, geochemical processes in subsoils rapidly come into play to limit P leaching, as has been shown by a number of wastewater and P fertilization studies (e.g. Riekerk 1978; Johnson et al. 1979).

Phosphorus leaching in undisturbed forests is usually very low relative to that of C, N, and S, but leaching is still often the dominant form of P loss from forests not subject to erosion. This slow rate of P leaching, along with removal of P by harvesting, can cause a long-term depletion and redistribution of P during the course of soil development (Walker & Syers 1976). As soils weather and P content declines, the proportion of total P in primary and then secondary mineral forms also decline, and eventually only occluded and organic P forms are present in soils. Since the USDA soil classification system is oriented toward soil development, one might expect a relationship between soil P fractions and soil order (Smeck 1985), and indeed there is some evidence of this. In general the less developed soils (Entisols, Inceptisols) have higher proportions of primary mineral P, while organic and secondary mineral P become important in Ultisols and Oxisols (Smeck 1985). One would expect the phosphate adsorption capacity of soils to increase with the degree of soil weathering also, in that both Fe and Al oxides and acidity increase as soils weather.

Anion adsorption. Anion adsorption (primarily to amorphous iron and aluminium oxide surfaces) is a dominant mechanism for phosphate retention in soils and can be very important to sulfate mobility as well. Both of these anions can enter into "specific" adsorption reactions on hydrous oxide surfaces (Hingston et al. 1967) in which anions enter into a coordination with a metal oxide and displace another anion (usually OH^-). The latter is sometimes called ligand exchange (Hingston et al. 1967).

Specific adsorption of phosphate or sulfate results in an increased negative charge on colloids. This in turn can affect the mobility of other anions, because it results in the displacement of non-specifically adsorbed anions by specifically-adsorbed anions. Increases in net negative charge should also lead to net increases in cation exchange capacity, and Wiklander (1976) & Couto et al (1979) have reported increases in cation exchange capacity following adsorption of phosphate and sulfate.

Phosphate always adsorbs more strongly than sulfate on a given soil, and phosphate will displace adsorbed sulfate as well as nitrate and chloride. Donnan equilibrium equations apparently do not apply, however, since sulfate will not displace phosphate. Thus, fertilization with phosphate will cause the desorption of sulfate and reduce sulfate adsorption capacity, at least in surface horizons.

Conclusions

Biological interactions of C, N, P, and S in forest ecosystems are shaped by the massive accumulation of C in structural organic materials. The amount of structural material produced varies as a function of climate, soil fertility, and successional status, and microbial immobilization of nutrients by decomposers of this structural material can reduce nutrient availability to plants. Additionally, allometric changes in the accumulation and loss of structural material occur during secondary succession; such changes affect element ratios in the biota and C:element interactions during decomposition. Differences in allometry among biomes are less important in controlling element ratios than are systematic differences in tissue chemistry, although the potential significance of lianas and epiphytes in tropical forests appears worthy of further study.

These biological interactions of C, N, P, and S control the potential production of the major anions HCO_3^-, organic acids, NO_3^-, $H_2PO_4^-$, and $SO_4^=$ in forest soils. Geochemical processes then control the mobility and loss of these major anions and hence of cations as well. Losses of these elements vary in predictable ways with climate, soil fertility, and successional status. In the long-term, nutrient availability is controlled by the balance between inputs and outputs. The geochemical processes which control element mobility and loss can therefore feed back to affect biological interactions of C, N, P, and S.

In general, biotic interactions are more important than geochemical interactions in controlling C and N budgets, although geochemical processes such as carbonate deposition may be significant. The relative importance of biological and geochemical interactions affecting P and S varies among forest ecosystems, and even with soil depth within a single forest. We believe that several areas of research on element interactions within forests are likely to prove rewarding. These include experimental studies which separate the effects of climate from those of soil fertility and/or successional stage, observations and experiments on areas affected by massive atmospheric deposition of N and S, detailed studies of the influence of life-forms within both plant and decomposer communities, and studies which link geochemical and ecological approaches and methodologies.

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