

## NUTRIENT CYCLING AND NUTRIENT USE EFFICIENCY

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It seems logical to expect that plants from nutrient-poor habitats would be able to produce more organic matter per unit of mineral nutrient taken up than could plants from nutrient-rich habitats, and both morphological and physiological mechanisms that could cause such a pattern have been proposed (Loveless 1962; Monk 1966; Small 1972; Schlesinger and Chabot 1977; Turner 1977). However, Chapin (1980) reviewed substantial evidence suggesting that plants from infertile habitats consistently have higher nutrient concentrations than plants from fertile habitats grown under the same controlled low-nutrient conditions. He suggested that this pattern could be caused by selection for slow growth, internal nutrient storage, and slow turnover of plant parts in infertile habitats. He further suggested that the efficiency of plant nutrient use (in grams in organic matter produced per unit of nutrient taken up) is simply the inverse of nutrient concentration in plant tissue, and that consequently plants from nutrient-poor habitats appear to be less efficient than plants from nutrient-rich habitats.

Chapin's argument was developed for short-lived plants. In long-lived perennial plants, however, the efficiency of nutrient use is not simply the inverse of plant nutrient concentration. The withdrawal of nutrients from senescing leaves and other plant parts prior to abscission allows a plant to use the same unit of nutrient to build several leaves or other plant parts successively (Clark 1977; Turner 1977). Thus, the efficiency with which an old perennial (or stand of perennials) uses nutrients should be defined as the grams of organic matter lost from plants or permanently stored within plants per unit of nutrient lost or permanently stored. The nutrient use efficiency for a forest is therefore the inverse of nutrient concentration in the aboveground litterfall, root turnover, and the organic matter increment of the vegetation (which in an older forest is mostly wood).

Ecosystem-level studies provide a wealth of information on the amounts and nutrient contents of plant parts shed or lost above ground in a very wide range of sites. The "fine litter fraction" (leaves, twigs, small branches, and reproductive parts) is routinely collected in such studies, and the material collected is routinely analyzed for a suite of plant nutrients (most often including nitrogen, phosphorus, calcium, magnesium, and potassium). When combined with the less commonly performed measurements of throughfall (material leached out of the plant canopy

by rainfall), such measurements yield both the amount of dry weight or organic matter and the amount of each nutrient lost to the trees annually (above ground). In general, organic matter, nitrogen, phosphorus, and calcium move largely in litterfall, potassium moves largely in throughfall, and magnesium is intermediate and rather variable among sites (Cole and Rapp 1980). Consequently, the efficiency of nitrogen, phosphorus, and calcium use for aboveground litter production in a wide range of sites can be calculated from extant data.

Where litter is collected and separated by species, the relative efficiency of different species occupying a site can also be assessed. I will use only aggregated information for entire sites or stands here, however. The nutrient use efficiency of litter production in a stand, forest, community, or site is a collective property (*sensu* Salt 1979) of the individuals of the various species that occur in the site.

Information on litterfall dry mass and/or organic matter content (which generally differ by less than 10%) and nutrient content is available for literally hundreds of sites. Less information on the nutrient content of wood increment is available, and very little is known of the amount of nutrients involved in fine root turnover. I will briefly and somewhat speculatively examine the nutrient use efficiency for production of wood and roots, largely as a means of assessing whether the patterns observed for litter production are offset by contrasting patterns of nutrient use for wood production or root turnover.

I confined my analysis to forests that were at least 20 yr old, since there is a substantial net increment in leaf and twig mass as well as wood early in succession. Further, wetland sites were excluded because nitrogen cycling in particular can follow rather different pathways in flooded soils.

#### SOURCES OF INFORMATION

Several compendia of information on organic matter and nutrient cycling were used as the major sources of data on temperate and boreal forest ecosystems. The excellent summary of International Biological Program results by Cole and Rapp (1980), modified using the results for individual sites from Gosz et al. (1972), Turner et al. (1976), and Sollins et al. (1980) to incorporate only the fine litter fraction, provided information on 30 sites. Information on nitrogen cycling in an additional 17 sites was drawn from Vitousek et al. (in press). Gray and Schlesinger (1981) summarized results from four Mediterranean shrub ecosystems (1 site modified with data from Schlesinger, personal communication) and three temperate forests. Results from two additional Mediterranean systems were drawn from Gray (in press). Information on additional sites (including several with nitrogen-fixing dominants) came from Zavitkovski and Newton (1968), Tarrant et al. (1969), Reiners and Reiners (1970), Wells et al. (1972), Miller et al. (1976), Lang and Forman (1978), Luken (1979), Bartuska (1981), and Binkley (personal communication). In all, 69 temperate or boreal sites were included in my data set. This in no way represents an exhaustive review of litterfall studies in temperate or boreal forests; Rodin and Bazilevic (1967) summarized results for nitrogen and the sum of other minerals from more than a hundred earlier studies (many of which met my criteria), and subsequent studies have added many more.

No extensive compendium of results from tropical studies was located, though the summaries by Franken et al. (1979) and Brassell et al. (1980) were quite useful. Information on a surprisingly large number of evergreen tropical sites (33, including 4 forest plantations) was eventually obtained, and this information and its sources are summarized in table 1. Considerable further information for leaf litter alone (Webb et al. 1969; Cornforth 1970) and for younger stands (Maheut and Dommergues 1960; Egunjobi 1974; Ewel 1976) is also available.

#### ANALYSIS OF RESULTS

The interpretation of the patterns of nutrient use efficiency in litter production was aided by an explicit statement of two extreme alternative hypotheses. It could be suggested that the efficiency of nutrient use is unchanged at any level of nutrient circulation. If this hypothesis were correct, then the nutrient concentrations of litterfall would be constant and a plot of the amount of a nutrient in litterfall versus the litterfall dry mass would not deviate systematically from a straight line passing through the origin. Biologically, this result would suggest either that nutrient uptake directly and linearly controls litter production or that both are very strongly controlled by the same physical factor(s). Alternatively, it could be suggested that nutrient circulation is unrelated to litterfall mass; that other factors control the amount of litterfall independently of nutrient circulation. If this were correct, then nutrient concentrations of litterfall would vary randomly and a plot of litterfall nutrients versus litterfall mass would yield a random scatter which would not deviate significantly from a horizontal line.

The amount of nitrogen, phosphorus, and calcium in litterfall is plotted against the litterfall dry mass in figures 1–3. (Litterfall organic matter mass, which is slightly less, was used for the studies drawn from Cole and Rapp [1980].) Line A in each figure is the expected value for litterfall dry mass if nutrient use efficiency does not vary with the amount of nutrient circulated. Its slope is defined as the mean dry mass of litterfall divided by the mean amount of the nutrient in litterfall. Line B is the expected value for litterfall dry mass if litterfall mass is uncorrelated with nutrient return in litterfall; it is defined as the mean dry mass of litterfall.

The results for nitrogen (fig. 1) deviate significantly from the patterns predicted by both hypotheses. Line B (the mean) accounts for 78.9% of the total sum of squares for litterfall dry mass. Line A accounts for 89.9% of the variation (a highly significant improvement), and a third-order polynomial forced through the origin accounts for 95.5% (a further highly significant improvement). ( $r^2$  as conventionally defined cannot be used as a measure of goodness-of-fit here, since both line A and the polynomial are forced through the origin and could in theory account for less of the variation than does the mean.) The best-fit polynomial lies between lines A and B, but closer to line A. Similar results can be obtained by combining the information in several figures in Rodin and Bazilevic (1967).

The results for phosphorus (fig. 2) and calcium (fig. 3) are more variable among sites, and the tropical forests differ substantially from the other biomes in having a generally greater litterfall mass per kg of P or Ca. The mean (line B) accounts for 80.9% of the variation in litterfall dry mass for P and 81.0% for Ca. (The amount of

TABLE 1  
LITTERFALL DRY WEIGHT AND NUTRIENT CONTENT IN LOWLAND AND MONTANE EVERGREEN TROPICAL FOREST ECOSYSTEMS

LOCATION	DRY WEIGHT				SOURCE
	kg·ha <sup>-1</sup> ·yr <sup>-1</sup>	N	P	Ca	
Africa					
Zaire	12,400	224	7.0	105	Laudelot & Meyer 1954
	12,300	223	9.0	91	Laudelot & Meyer 1954
	15,300	154	9.0	84	Laudelot & Meyer 1954
Ghana	10,680	202	7.4	209	Nye 1961
Ivory Coast	11,900	170	8.0	61	Bernhard-Reversat 1975
	9,200	158	14.0	85	Bernhard-Reversat 1975
	8,300	156	8.5	65	Bernhard-Reversat 1975
	9,620	123	4.0	105	Bernhard-Reversat 1975
	8,640	108	4.0	120	Bernhard-Reversat 1975
	8,800	142	8.0	104	Lundgren 1978
Tanzania					
South America					
Brazil	7,300	106	2.1	18	Klinge & Rodrigues 1968
	12,000	141	4.2	90	Folster & de las Salas 1976
Colombia	8,700	103	3.4	124	Folster & de las Salas 1976
	9,500	109	2.4	53	Folster & de las Salas 1976

Brazil .....	9,900	156	4.1	33	Klinge 1977
	9,000	96	3.4	62	Klinge 1977
	6,370	74	1.4	20	Franken 1979
Venezuela .....	5,950	24			Herrera & Jordan 1981
	5,650	42	2.4	29	R. Herrera, personal communication
Central America/Caribbean					
Panama .....	11,350		9.4	256	Golley et al. 1975
	10,480		2.7	106	Golley et al. 1975
Guatemala .....	9,000	169	5.8	88	Ewel 1976
Jamaica .....	6,590	39	1.3	34	Tanner 1977
	5,510	49	1.5	50	Tanner 1977
	5,510	34	2.1	53	Tanner 1977
	6,500	58	2.4	55	Tanner 1977
Asia/Australia					
Yunan, China .....	11,600	169	11.0	108	Zonn & Li 1962
					(in Bazilevic & Rodin 1966)
Malaysia .....	10,600	100	2.8	65	Lim 1974 and Soepadimo & Kira 1977
					(in Lundgren 1978)
Australia .....	9,000	134	12.0	226	Brassell et al. 1980
	10,450	124	10.2	159	Brassell et al. 1980
	8,900	82	10.0	177	Brassell et al. 1980
	12,200	108	10.9	200	Brassell et al. 1980
New Guinea .....	7,550	90	5.0	95	P. J. Edwards, MS

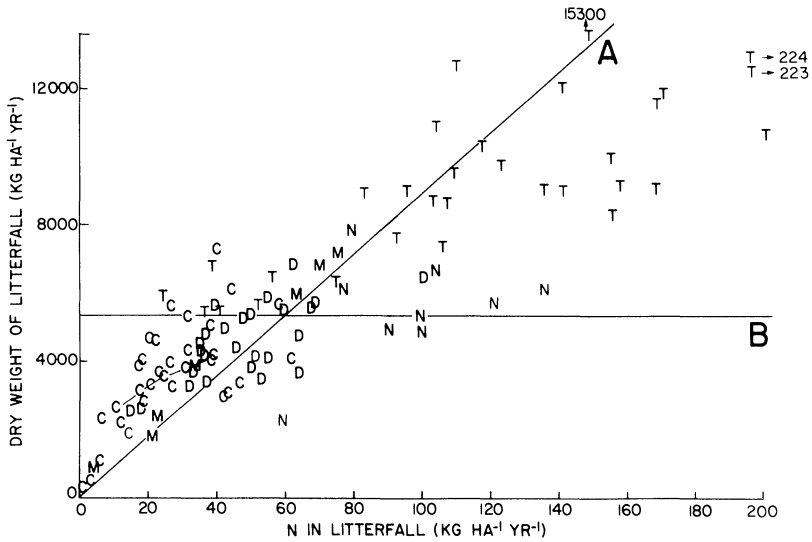


FIG. 1.—The relationship between the amount of nitrogen in fine litterfall and the dry mass of that litterfall. Each symbol represents at least one full year of collection (and usually the mean of 2–6 yr) in a stand. Coniferous forests are represented by C, temperate deciduous forests by D, evergreen tropical forests by T, Mediterranean-type ecosystems by M, and temperate zone sites dominated by symbiotic nitrogen fixers by N. Lines A and B represent the expected value of the relationship given two alternative hypotheses (see text for explanation). The five coniferous forests connected by short line segments represent the results of a long-term fertilization study by Miller et al. (1976).

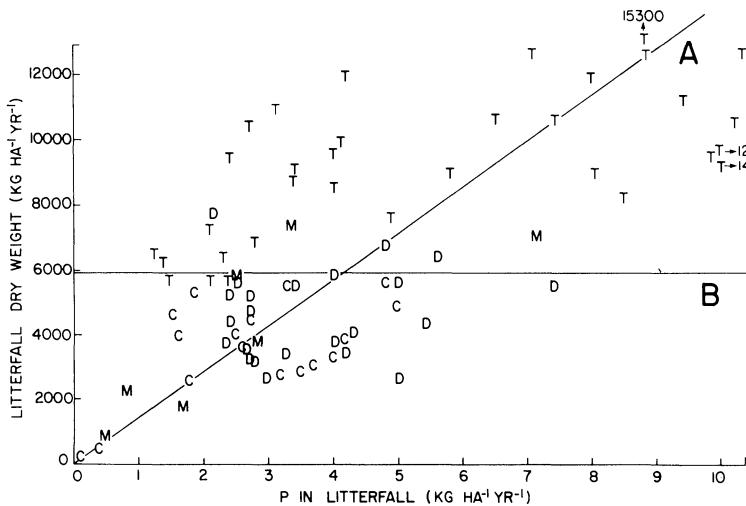


FIG. 2.—The relationship between the amount of phosphorus in litterfall and the dry mass of the litterfall. See fig. 1 for an explanation of the symbols and lines.

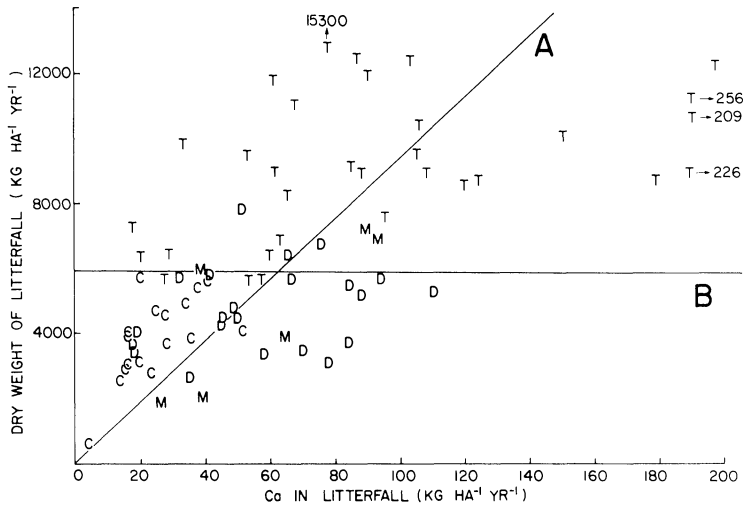


FIG. 3.—The relationship between the amount of calcium in litterfall and the dry mass of the litterfall. See fig. 1 for an explanation of the symbols and lines.

variation in litterfall dry mass accounted for by the means differs slightly for the three elements because several studies only reported results for one or two of the elements.) Line A accounts for 81.5% and 77.3% of the variation in litterfall dry mass using P and Ca, respectively. Third-order polynomials forced through the origin account for 89.3% of the variation using P and 89.2% using Ca (both significant improvements over lines A and B). Significantly less of the total variation in litterfall mass could be accounted for by the amounts of P and Ca in litterfall than by the amount of N.

These results suggest that litterfall mass is more closely coupled with N circulation than with P or Ca over this broad scale. They further suggest that more litterfall dry mass is produced per unit of nutrient at low nutrient levels. While the results in figures 1–3 allow a quantitative examination of the relationships between total dry mass and nutrients in litterfall, however, they do not directly yield the efficiency of nutrient use for litter production. Accordingly, the dry mass of litter produced per kilogram of each nutrient in litterfall (which is equivalent to the inverse of the concentration of each nutrient in litterfall) is plotted against the amount of that nutrient in litterfall in figures 4–6.

The results for nitrogen (fig. 4) are striking. It appears that there is a ratio of dry mass : nitrogen near 60 which communities with high nitrogen circulation approach but do not fall below. Most tropical forests, most temperate forests dominated by symbiotic nitrogen fixers, and a few other nitrogen-rich temperate forests fit into this category. This level could represent a maximum nitrogen concentration in leaves plus twigs of 1.7%, or it could represent the maximum amount of nonhydrolyzable (and hence immobile) nitrogen that trees can accumulate. At lower levels of nitrogen circulation, the dry mass : nitrogen ratio increases exponentially,

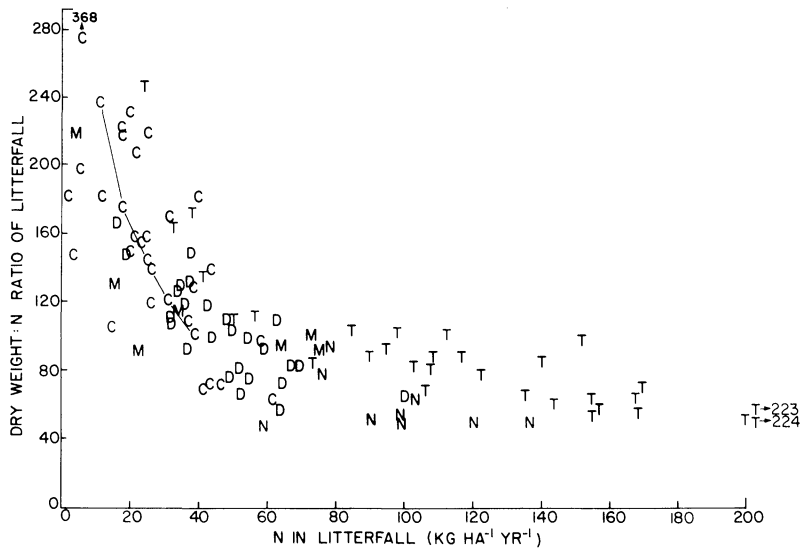


FIG. 4.—The relationship between the amount of nitrogen in fine litterfall and the dry mass to nitrogen ratio of that litterfall. Symbols as in fig. 1.

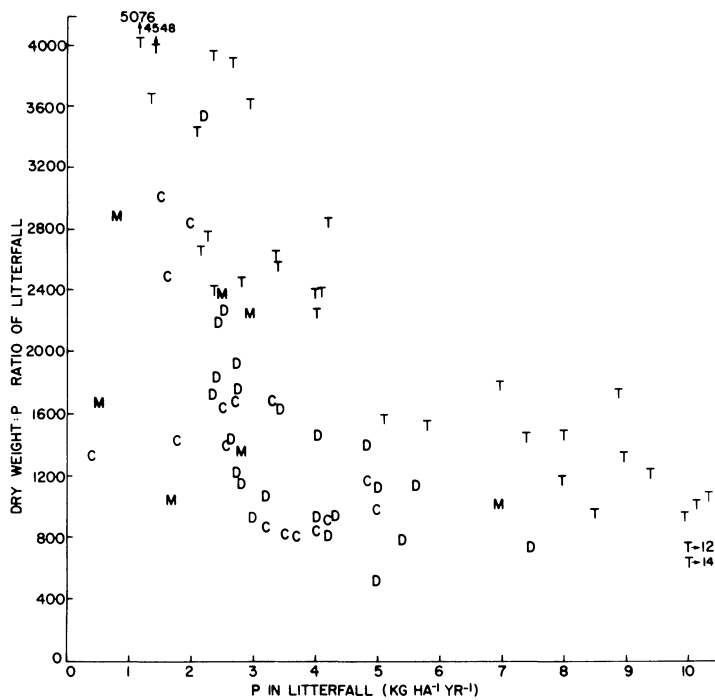


FIG. 5.—The relationship between the amount of phosphorus in litterfall and the dry mass to phosphorus ratio of that litterfall. Symbols as in fig. 1.



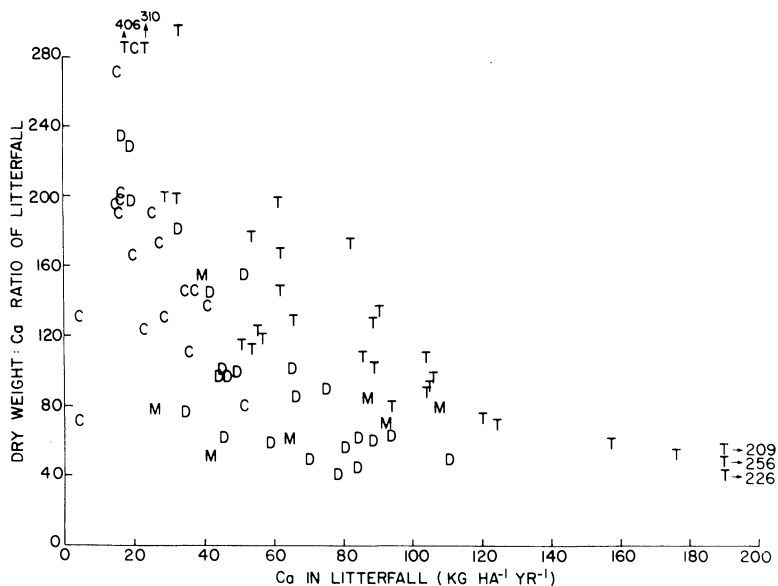


FIG. 6.—The relationship between the amount of calcium in litterfall and the dry mass to calcium ratio of that litterfall. Symbols as in fig. 1.

with values in excess of 200 in several sites. On the average, the efficiency of litter production per unit of nitrogen is greater in coniferous forests than in temperate deciduous forests, where in turn it is greater than in tropical forests. The pattern is continuous across all forest types, however, and there are coniferous forests with dry mass:nitrogen ratios as low as those in most tropical forests and tropical forests with ratios higher than those of many coniferous forests.

The results for phosphorus (fig. 5) and calcium (fig. 6) are rather different. As illustrated above (figs. 2,3), the amount of dry matter produced per unit of phosphorus or calcium is systematically higher in tropical forests. Moreover, among tropical forests there is a significant and rather smooth increase in the dry mass:Ca and especially dry mass:P ratios at lower nutrient levels, such that the pattern for phosphorus and calcium in the tropical forests appears similar to that for nitrogen in all of the sites combined. Most of the tropical forests are high in nitrogen, so the relative efficiency of phosphorus and calcium use in these forests appears particularly interesting.

#### DISCUSSION

Why is there a strong inverse relationship between the amount of a nutrient circulated in litterfall and nutrient use efficiency across biomes for nitrogen (fig. 4) and within the tropical forest biome for phosphorus and calcium (figs. 5,6)? Two logical explanations are that the patterns are an outcome of correlated axes in figures 4–6, or that nutrient use efficiency varies with nutrient availability, and

nutrient circulation in litterfall is a reliable indicator of nutrient availability across the range of sites examined.

The correlation of the axes could cause a relationship to emerge because the  $Y$  axis in figures 4–6 reduces to litterfall mass divided by the  $X$  axis. Consequently, an inverse relationship of the form  $Y = \bar{L}/X$  (where  $\bar{L}$  is the mean litterfall dry mass) would be expected if there were no functional relationship between nutrient circulation and litterfall mass. If the pattern observed simply resulted from autocorrelation, this would imply that nutrient circulation is not related to litterfall production, and that the efficiency of nutrient use is thus biologically unimportant.

Several lines of evidence suggest that the pattern for nitrogen summarized in figure 4 is not simply a consequence of autocorrelation, and these will be discussed below as evidence for a strong correlation between nitrogen circulation in litterfall and nitrogen availability. Perhaps the most important evidence, though, is that the results in figure 1 demonstrate that the pattern of litterfall mass per unit of nitrogen deviates systematically and significantly from line B, the expected value for litterfall dry mass if it is independent of nitrogen circulation.

Correlated axes cannot be easily dismissed as a cause of the phosphorus and calcium results (figs. 5,6). The forest types differ in the amount of litter produced per unit of P or Ca lost (figs. 5,6), and within each forest type (except for Ca in coniferous forests) the results in figures 2 and 3 are difficult to distinguish from a horizontal line at the mean litterfall dry mass for that forest type (line B). There is no significant variation in litter production with P or Ca in litterfall for temperate deciduous forests (figs. 2,3). The results for P and Ca in tropical forests and P in coniferous forests are marginally significant, and then only because a few points have both reduced litterfall mass and low nutrient circulation. These results are consistent with nutrient limitation causing low litter production and very high C:element ratios at very low nutrient levels (figs. 5,6). The majority of the observed pattern in figures 5 and 6 (all the points above  $3 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  P and  $50 \text{ kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  Ca in tropical forest litterfall) may be best explained by autocorrelation, however.

Franken et al. (1979) draw on some of the studies summarized here (table 1) and some unpublished data to suggest that the (P + Ca + K + Mg) content of leaf fall in tropical forests is a good predictor of the total amount of leaf fall, so perhaps inclusion of a broader range of information would lead to the rejection of correlated axes as an explanation for the overall tropical forest patterns (figs. 5,6). I believe that it is more likely that unlike nitrogen, P and Ca availability only affect litter production at very low levels of availability.

The lack of a strong relationship between calcium cycling and litter production is not surprising, since most calcium is present as metabolically inactive and immobile calcium pectate or calcium oxalate (Salisbury and Ross 1978). The pattern for phosphorus is unexpected, however, and it deserves more careful study.

#### NITROGEN AVAILABILITY AND NITROGEN USE EFFICIENCY

I believe that the observed pattern of the nitrogen use efficiency of litter production (fig. 4) occurs primarily because nitrogen circulation in litterfall is a

reliable indicator of nitrogen availability in the range of sites examined. This suggestion is logical if forests are very often nitrogen limited; both nitrogen uptake and circulation should then be a function of nitrogen availability.

I offer four lines of evidence in support of this suggestion:

1. The sites where potential symbiotic nitrogen fixers are dominants or codominants (which includes many of the tropical forests) have a relatively high nitrogen circulation and a relatively low efficiency of litter production. Nitrogen fixers have an essentially unlimited supply of available nitrogen (though at a cost in carbon and energy).

2. The temperate forest sites with relatively large amounts of nitrogen in litterfall and low efficiencies are in regions receiving high levels of anthropogenic fixed nitrogen in rain and snow. This is particularly notable for the three coniferous and three deciduous forests summarized by Cole and Rapp (1980) from the Solling Project, Federal Republic of Germany. All six circulate between 40 and 60 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>, all have organic matter:nitrogen ratios less than 80, and all receive more than 20 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> in precipitation. Nitrogen availability should be considerably enhanced in such sites. I do not know why the deciduous forest at 100 kg N·ha<sup>-1</sup>·yr<sup>-1</sup>, an old oak forest in New Jersey studied by Lang and Forman (1978), is so far above any other temperate forest (fig. 4).

3. Many studies of forest fertilization show that the application of nitrogen increases both foliar N concentrations and forest production. The results of an unusually detailed, long-term study by Miller et al. (1976) on a nutrient-poor Corsican pine plantation in Scotland are summarized by the five points connected by a line in figures 1 and 4. Litterfall and litterfall nutrient contents were measured for 6 yr in control plots and plots which received four levels of nitrogen fertilizer for 3 yr. The increase in nitrogen availability resulting from fertilization progressively increased the amount of nitrogen in litterfall and decreased the nitrogen use efficiency of litter production (although the amount of litter produced increased). The pattern of fertilizer response was very similar to the pattern of change from low-nitrogen to high-nitrogen natural stands (fig. 4).

4. How could sites fail to fit the pattern in figure 4? The combination of low nitrogen circulation and low nitrogen use efficiency (or high litter nitrogen concentration) should be possible if the site has adequate available nitrogen but some other factor strongly limits production. The low-production Mediterranean sites (fig. 4) may provide such a combination. Desert shrub systems should be better, but relatively few recent data are available. Gist et al. (1977) reported values for a "median" cold-winter desert shrub community which, when corrected for a calculation error, yield nitrogen circulation in litterfall of 6.3 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> and a very low dry weight:nitrogen ratio in litterfall of 45. This result suggests that nitrogen availability is adequate but that production and nitrogen circulation are limited by some other factor, probably drought stress. High nitrogen availability is not necessarily a general feature of semi-arid sites, however; Rodin and Bazilevic (1967) summarized results from a number of studies in Syria and the Soviet Union which ranged from 3.1 to 33 kg N·ha<sup>-1</sup>·yr<sup>-1</sup> in aboveground litterfall and from 30 to 92 in litterfall dry mass to litterfall nitrogen ratios. (Wet sites and sites with large numbers of annuals were excluded from these ranges.)

Taken together, these lines of evidence strongly suggest that the nitrogen use

efficiency of litter production varies as an inverse function of nitrogen availability (that is, that litter nitrogen concentration is positively correlated with nitrogen availability). Ideally, nitrogen availability should be measured independently of the amount of nitrogen in litterfall, but direct measures of nitrogen availability in forest soils are not now possible. The instantaneously available nitrogen in soil (ammonium, nitrate, and some dissolved organic nitrogen compounds) is generally present as a relatively small pool which turns over rapidly through addition via microbial breakdown of organic nitrogen compounds and removals via leaching and/or plant and microbial uptake (Robertson and Vitousek 1981). A number of indices for nitrogen availability in forests have been suggested (see the recent review by Keeney 1980), and several methods based on incubations in the field (Ellenberg 1977), laboratory (Keeney 1980; Vitousek et al., in press), or a combination of both (Powers 1980) have been more or less widely adopted. No single method is used widely enough to allow comparisons of apparent nitrogen availability versus nitrogen use efficiency in a wide range of sites, though, and all of these approaches yield only indices of nitrogen availability. Nonetheless, results of the various assays do correlate well with the nitrogen concentration in foliage (Powers 1980) and with the amount of nitrogen in litterfall (Vitousek et al., in press) in a restricted range of sites.

#### *Possible Controlling Mechanisms*

Two mechanisms could cause increased nitrogen use efficiency in low nitrogen forests:

1. Increased nutrient use efficiency in active leaves. Trees in low-nutrient sites have lower concentrations of nitrogen and other nutrients in leaves and twigs, which could mean that on the average they fix more carbon per unit of nitrogen than trees from richer sites. They could do so either by fixing carbon more rapidly (per unit N), or by using a unit of N to fix carbon over a longer period of time (evergreenness; Small 1972; Shaver 1981). This mechanism must underlie at least some of the pattern in figure 4, since communities in sites with relatively small amounts of nitrogen in litterfall also have lower concentrations in active leaves than do communities in sites where more nitrogen circulates through litterfall (Cole and Rapp 1980). Moreover, within a species low foliar nutrient concentrations can be used as a standard indicator of low nutrient availability in a site.

2. Increased reabsorption of nutrients from leaves to stems prior to leaf abscission. Any increase in nitrogen reabsorption in nitrogen-poor stands would cause an increase in the litterfall mass:nitrogen ratio. The nitrogen reabsorbed in this way could subsequently be used to build new leaves or other tissues.

Some evidence suggests that nutrient reabsorption is more effective on nutrient-poor sites. Nye (1961) suggested that the difference in litterfall nitrogen contents between the forest he studied (table 1) and temperate forests was not nitrogen concentrations in active leaves but rather that the tropical trees did not reabsorb nitrogen from leaves before abscission. Turner (1977) experimentally demonstrated that Douglas-fir could adjust the portion of its nitrogen requirement that came from reabsorption depending on the availability of nitrogen in the soil. Stachurski and Zimka (1975) demonstrated that nitrogen reabsorption was con-

siderably less effective in oak and hornbeam trees growing in association with N-fixing alder than it was in the same species growing on a poorer site in association with pine. Miller et al. (1976; personal communication) showed that N-fertilized Corsican pine stands reabsorbed a lower proportion of their foliar N than did unfertilized stands. However, F. Chapin and R. A. Kedrowski (personal communication) reviewed the available literature on reabsorption and found both an absolutely and a proportionally greater reabsorption of nitrogen in species with more nitrogen in foliage, and Chapin (1980) concluded that on the whole the limited available evidence does not support a greater effectiveness of nutrient reabsorption in nutrient-poor sites. This mechanism still probably contributes to the pattern observed (fig. 4), at least in that the high-nitrogen tropical forests do not reabsorb much nitrogen, but better and much broader information on nutrient reabsorption will be necessary to test this possibility more extensively.

At least part of the pattern in nitrogen use efficiency (fig. 4) is clearly due to greater production per unit of nitrogen in situ in low-nitrogen sites, and part is probably also due to more effective reabsorption of nitrogen in such sites. I cannot identify other mechanisms that could contribute to this pattern other than allocation of energy and/or nutrients to other plant parts (discussed below). Regardless of which mechanism proves to be most important in a given site or group of sites, the result of either is an increase in the efficiency of litter production per unit of nitrogen in low nitrogen sites (fig. 4).

#### OTHER PATHWAYS OF BIOMASS AND NUTRIENT LOSS

Both the net biomass increment of trees and belowground litter production also contribute to the overall efficiency of nutrient use in forest ecosystems. Patterns of nutrient use efficiency in the production of these components could modify or reinforce the patterns suggested on the basis of litterfall studies, so I will examine them in a preliminary way here.

Since leaf area (and associate twigs) stabilizes relatively early in succession (Bray and Gorham 1964; Rodin and Bazilevic 1967), the net increment of biomass in older forests is predominantly stem wood. I compared the net increment of stem wood produced in a range of forests with the amount of nutrient in stem wood plus the amount of nutrient in the fine litterfall fraction (fig. 7). The nutrient content of stem wood is generally relatively low (0.1–0.5% N, .01–.05% P), so the amount of nutrient in litterfall usually dominated this comparison. Nitrogen can be reabsorbed from stem wood before it dies and becomes heartwood (Cowling and Merrill 1966; Merrill and Cowling 1966), but the total amounts removed are usually small relative to litterfall.

This comparison does not directly yield the efficiency of wood production per unit nutrient in leaves, since reabsorption from leaves can be important, and more importantly, since evergreens can use several times more of any nutrient in the production of the stem wood increment than they lose annually in litterfall. It should show, however, whether the allocation of carbon to stem wood production reinforces or offsets the patterns for the nutrient use efficiency of litter production described above.

Wood increment is the measurement of most interest in forestry, and an enor-

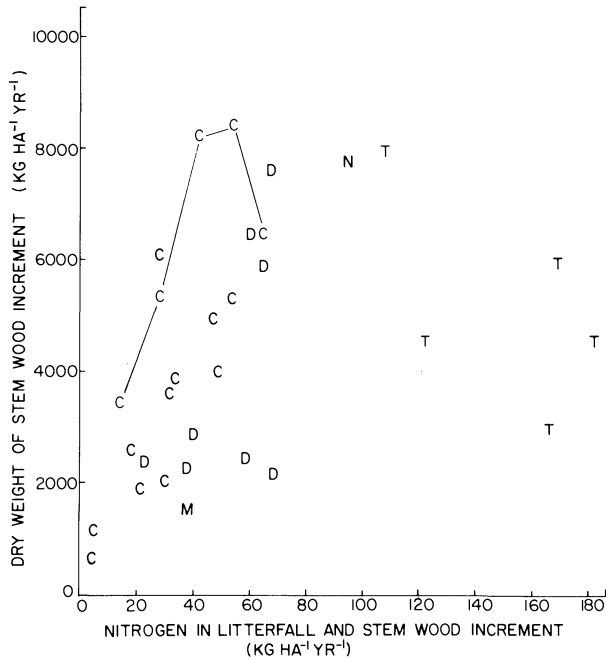


FIG. 7.—The relationship between the amount of nitrogen in litterfall plus the amount of nitrogen in stem wood increment and the dry mass of the stem wood increment. Symbols as in fig. 1. The points connected by short line segments are the results of a fertilization study by H. G. Miller (personal communication).

mous amount of information has been obtained over many years. Sites where the nutrient content of the wood increment and the circulation of nutrients in above-ground biomass have been measured simultaneously are considerably fewer, however. I summarized information from Cole and Rapp (1980), including only those 21 sites for which stem wood and branch increment were reported separately. These sites were supplemented with five tropical sites reported by Bernhard-Reversat (1975, 1977). Comparisons were made for nitrogen, phosphorus, and calcium, but since phosphorus and calcium were at least as variable for stem wood as they were for litterfall (figs. 2,3,5,6), only the results for nitrogen are summarized here.

Since the number of sites considered is relatively small, the results of this analysis must be regarded as grounds for speculation rather than firm conclusions. Moreover, there are more serious possibilities for methodological variations in the calculation of stem wood increment between sites (such as inclusion or exclusion of stem mortality) in these analyses than in the calculations of fine litterfall. Nonetheless, the overall pattern for nitrogen (fig. 7) is interesting, suggesting a relatively high wood production per unit litterfall nitrogen in the two low nitrogen boreal coniferous forests, relatively low wood production in the five high nitrogen tropical forests and the temperate forest dominated by a nitrogen fixer, and no systematic change in wood production/unit nitrogen with changes in nitrogen

circulation (no systematic deviation from a straight line passing through the origin) for most of the temperate forests. Similar results, though with a steeper slope, were observed in the fertilizer response study by Miller et al. (1976) reported above (H. G. Miller, personal communication). These results apparently reinforce the pattern of high nitrogen use efficiency at low nitrogen levels observed for litter production (figs. 1,4). Unfortunately, the extremes in nitrogen availability cannot be separated from other effects on stem wood increments associated with latitude using these results (fig. 7), so the suggestion that wood production is more efficient in terms of light utilization at higher latitudes (Jordan and Murphy 1978) cannot be evaluated for nitrogen use efficiency.

The apparent absence of any systematic change in the relative nitrogen use efficiency of stem wood production among temperate forests (fig. 7) is striking. I expected that the allocation of organic matter to wood production would be greater in a relative as well as an absolute sense in nitrogen-rich sites, since both leaves and (especially) roots might be expected to have a higher priority than wood for the limited available photosynthate under low-nitrogen conditions.

The deviation from the apparent linear trend in several of the temperate sites is extreme. Perhaps the high wood increment in a coniferous forest at  $28 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  is related to the relative youth of the stand (22 yr), but it is not clear why stem wood production is so low in a British deciduous forest at  $68 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$  or in the Hubbard Brook forest (New Hampshire) at  $58 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ .

Information on belowground fine litter inputs in forest ecosystems has only recently become available (Edwards and Harris 1977; Persson 1979; Harris et al. 1980), and insufficient information on fine root senescence and the possibility of nutrient reabsorption from fine roots is available to estimate the nutrient content of belowground litter accurately in any site. Considerable work with short-lived plants (Ingestad 1979; Chapin 1980) and a few studies in forests (Persson 1980; Keyes and Grier 1981) suggest that fine root production is a greater proportion of total production in low-nutrient sites (but see Safford 1974). Moreover, there is evidence that the nutrient concentrations of fine roots can increase substantially following fertilization (Safford 1974). If these rather fragmentary results do prove general, then the nitrogen use efficiency of belowground litter production will be shown to vary in a way similar to aboveground litter production (fig. 4).

In summary, the patterns of nitrogen use efficiency observed for aboveground fine litter production are probably not offset by contrasting patterns in other components of net production. The present results suggest that if anything both wood increment and belowground litter production reinforce the original pattern. More data on these other components in additional sites are necessary, but as a whole, forests appear to be more efficient in net production per unit of nitrogen at low levels of nitrogen availability.

#### ECOSYSTEM-LEVEL SIGNIFICANCE

The patterns of stand nitrogen use efficiency developed here have important implications on the ecosystem level as well. In general, the rate of nitrogen release

from decomposing plant material is highly correlated with the carbon:nitrogen ratio of that material (see Black 1968 for a summary). When the ratio of available carbon (energy) to available nitrogen (protein) is high, decomposers are relatively nitrogen limited, and they retain nitrogen in their biomass. Under these circumstances decomposers can also remove any available nitrogen in the soil solution and incorporate into their biomass. When the carbon:nitrogen ratio of substrate is low (12–20:1), decomposers are not nitrogen limited, and a net release of inorganic nitrogen to the soil solution occurs. The same sort of patterns may exist for the carbon:element ratios of other nutrients, although the critical ratios would be different in each case (Gosz et al. 1973).

The results summarized here show that woody plants in low-nitrogen sites produce litterfall with a much higher carbon:nitrogen ratio than plants in nitrogen-rich sites (fig. 4). (The carbon content of plant litter is reliably about 1/2 the litterfall dry mass.) Such low-nitrogen litter should release nitrogen upon decomposition only after a substantial lag, and it could cause decomposers to take up any available nitrogen from the soil solution. There is indeed evidence that net nitrogen mineralization in forest floor (on either a per gram of litter or a per gram of organic nitrogen basis) is very much less in sites circulating small amounts of nitrogen annually (Stachurski and Zimka 1975; Vitousek et al., in press). The overall effect could be a positive feedback system toward the maintenance and intensification of nitrogen stress in nitrogen-poor ecosystems (Gosz 1981). Litterfall with a high carbon:nitrogen ratio should favor nitrogen retention by decomposers and reduce nitrogen availability in the soil. Low nitrogen availability would then lead to increased nitrogen use efficiency and the production of litter with a still higher carbon:nitrogen ratio (fig. 4). This change could occur by phenotypic changes within a genotype (Miller et al. 1976), by genotype or species replacement, or both (Stachurski and Zimka 1975). A further consequence of this feedback system would be an increase in the resistance to perturbation of the nitrogen cycle (Vitousek et al. 1979; Vitousek et al., in press). On the other hand, it is possible that appropriate levels and timing of fertilization could set up a self-maintaining positive feedback toward higher nitrogen cycling and faster though less efficient tree growth. The long-term fertilization results of Miller et al. (1979), Roberge et al. (1980), and Weetman et al. (1980) may provide some evidence for this possibility.

Finally, the consistency of the observed pattern in nitrogen use efficiency across tropical, temperate deciduous, coniferous, Mediterranean, and fertilized forests needs to be better established, particularly in nitrogen-poor tropical forests like that studied by Herrera and Jordan (1981). If the pattern is indeed general, and if the ecosystem-level implications discussed here are valid, then Jordan and Herrera's (1981) emphasis on examining nutrient cycling in both nutrient-poor (oligotrophic) and nutrient-rich (eutrophic) sites will be most strongly supported. Their conclusion that production and nutrient cycling do not vary much between oligotrophic and eutrophic forests may be questioned in light of the evidence presented here for nitrogen (table 1, figs. 1,4); that conclusion may be affected by their small sample size and their consideration of only calcium among the nutrients. However, their suggestion that the gradient from oligotrophy to eutrophy is an important variable affecting ecosystems in all biomes will be firmly established.



## SUMMARY

Forest ecosystems systematically produce more litterfall dry mass per unit of nitrogen in sites with less aboveground nitrogen circulation. This pattern is observed both within and among tropical, temperate deciduous, coniferous, Mediterranean, and fertilized ecosystems. The differences among sites are probably related to differences in soil nitrogen availability. Patterns of nitrogen use for root and wood production probably reinforce the litterfall results. An examination of phosphorus and calcium use efficiency for litterfall production yields more ambiguous results. The pattern for nitrogen circulation and nitrogen use efficiency in forests has important implications for ecosystem-level properties, including the development of low nitrogen availability in soil.

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