

NUTRIENT-USE EFFICIENCY: A LITTERFALL INDEX, A MODEL,  
AND A TEST ALONG A NUTRIENT-AVAILABILITY GRADIENT  
IN NORTH CAROLINA PEATLANDS

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*Abstract.*—The efficiency of using nutrients to produce new biomass may be an important adaptation of plants to infertile habitats. We distinguish resource-use efficiency (production per unit resource uptake) from resource-response efficiency (production per unit resource availability) and employ Monod functions to investigate changes in these two efficiencies along resource gradients. The model predicts increasing nutrient efficiency with decreasing nutrient availability or uptake to some optimum resource level, but further nutrient deficiency causes a decrease in nutrient efficiency. We tested this model along a natural fertility gradient in three North Carolina peatland communities, using the ratio of litterfall production to litterfall nutrient content as an index of nutrient-use efficiency and the ratio of litterfall production to various measures of soil nutrient pool size as an index of nutrient-response efficiency. The model did an excellent job of describing both nutrient efficiencies, and, as predicted, efficiency decreased at suboptimal nutrient levels in infertile pocosin peatlands. Additionally, we tested the generality of our model in northern and tropical forests. Our model described the results in both data sets well, and nutrient-use efficiency declined at suboptimal concentrations for the primary limiting nutrient. Thus, the model appears to work on numerous different ecosystems and to be relatively scale invariant, working from local resource gradients to regional and global scales.

Increasing the efficiency of using nutrients to produce new biomass may be an important competitive strategy for plants adapted to infertile environments. Nutrient-use efficiency has commonly been defined as the amount of production per unit nutrient used (Chapin 1980). In short-lived plants this value is simply the inverse of tissue concentration, but in perennial plants it is most appropriately defined as total net primary production (above- and belowground) per unit nutrient absorbed annually (Hirose 1975; Vitousek 1982; Birk and Vitousek 1986). In a woodland, nutrient-use efficiency can functionally be considered as the mass of organic matter lost (in litterfall and root turnover) or stored (biomass increment) per unit nutrient lost or stored (Vitousek 1982).

Increased nutrient-use efficiency with decreasing nutrient availability has been

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demonstrated in both single species (Ingestad 1979; Veerkamp et al. 1980; Chapin et al. 1982; Gray and Schlesinger 1983; Shaver and Melillo 1984; Birk and Vitousek 1986) and mixed communities (Vitousek 1982, 1984; Pastor et al. 1984). Nutrient-use efficiency also increases with age in pine forests (Gholz et al. 1985). Additionally, nutrient-use efficiency is greater in coniferous forests than deciduous forests because of slower leaf turnover and lower leaching losses in coniferous forests (Cole and Rapp 1981; Schlesinger 1991). Nutrient-use efficiency may exert important ecosystem controls; for example, high nutrient-use efficiency drives infertile systems toward even greater nutrient deficiency because low litter nutrient content and reduced nutrient mineralization rates depress nutrient circulation (Pastor et al. 1984; Shaver and Melillo 1984; Vitousek 1984; Chapin 1986).

An exact accounting of nutrient-use efficiency requires accurate belowground estimates of production, but this is time-consuming to measure, and alternative methods often yield highly disparate results (Milchunas and Lauenroth 1992; Nadelhoffer and Raich 1992). Vitousek (1982, 1984) used aboveground litterfall alone to determine patterns of relative nutrient-use efficiency in world forests. He found that the nitrogen (N) and phosphorus (P) efficiency of litter production declined with increasing return of N and P in litterfall, which supports the hypothesis that communities from infertile environments will use nutrients more efficiently than those from fertile environments.

However, his analyses lacked a formal theoretical basis and were confounded by autocorrelation between the amount of nutrients cycled in litterfall (an index of nutrient availability) and the ratio of litter production to litter nutrient content (nutrient-use efficiency). Additionally, a mechanistic understanding of adaptations of perennial plants to maximize nutrient-use efficiency must not only consider tissue nutrient concentrations but also allocation of production to various tissues (Pastor and Bockheim 1984), nutrient resorption from leaves during senescence (Small 1972; Flanagan and Van Cleve 1983; Shaver and Melillo 1984; Schlesinger et al. 1989; Pugnnaire and Chapin 1993), turnover time of vegetative parts (Small 1972; Cole and Rapp 1981), the kinetics of root uptake (Barber 1981; Gray and Schlesinger 1983; Birk and Vitousek 1986; Schlesinger et al. 1989), carbon fixation per unit plant nutrient (Birk and Vitousek 1986), and mobilization of stored nutrient reserves (Miller 1979). Some of these factors, such as resorption and turnover time in leaves, are implicitly considered using litterfall as an index for production.

Despite these limitations, Vitousek's articles were a breakthrough in the theory of plant-nutrient interactions and have been extensively cited. Litterfall has subsequently been successfully used as an index of nutrient-use efficiency in other forested ecosystems (Pastor et al. 1984; Birk and Vitousek 1986).

However, an intuitive definition of nutrient-use efficiency and the expression of this as the inverse of tissue nutrient concentration has made interpretation of previous results problematic (Chapin 1980). Furthermore, it is generally assumed that increased efficiency with decreased nutrient availability continues unbounded; in fact, models have been derived with this explicit assumption (Berendse and Aerts 1987). But it has not been shown that this is a logical consequence of the response of production to decreased nutrient availability in any

formal (mathematical) sense, and this prediction has not been tested in sites of extremely low nutrient availability.

We develop a mathematical model of nutrient-use efficiency and explore the behavior of this model with different assumptions of nutrient uptake by plants. We additionally define a nutrient-response efficiency based on soil nutrient availability to avoid autocorrelation as described above. Model predictions are tested against litterfall data from three freshwater peatland communities along a nutrient-availability gradient on the lower coastal plain of North Carolina. Additionally, we explore the generality of our model with data from the literature. Nutrient-response efficiency is examined in edaphic climax forests on Blackhawk Island, Wisconsin (Pastor et al. 1984), where data on aboveground net primary production and net N mineralization avoid assumptions inherent in using litterfall and soil nutrient pool sizes as surrogates for production and soil nutrient flux density, respectively. Finally, we reanalyze the data in Vitousek (1984) to test the applicability of the model on a global scale.

#### PRODUCTION AND RESOURCE AVAILABILITY—THEORY

There have been a number of attempts to formalize mathematically the concept of nutrient-use efficiency as proposed by Chapin (1980), Vitousek (1982), and others cited above. These stem mainly from the concept of N productivity, or the rate of dry-matter production per unit N in the plant (Ingestad 1979). Berendse and Aerts (1987) showed that nutrient-use efficiency is equal to the N productivity times the mean residence time of N in the plant. This reduces mathematically to productivity per unit N lost in litter, the same definition proposed by Chapin (1980), Vitousek (1982), and others. Ågren (1983) refined the concept of N productivity further as the amount of nutrient committed to growth of foliage, or photosynthetic apparatus. He then showed mathematically that N productivity in a plant decreases as productivity, and presumably availability of limiting nutrient, increases because of self-shading in the plant. This is essentially the pattern found by Vitousek (1982).

Nevertheless, difficulties remain with these previous attempts at providing a formal basis for nutrient-use efficiency. First, the formulation of Berendse and Aerts (1987) allows one to calculate nutrient-use efficiency at some particular combination of production and nutrient residence time; it does not address how nutrient-use efficiency changes along nutrient-availability gradients. Ågren (1983) goes further in this regard; his model predicts that nutrient-use efficiency declines with increasing nutrient availability. However, at a vanishingly small availability, when nutrient limitation is most intense and therefore nutrient-use efficiency most critical in sustaining productivity, his formulation becomes undefined (i.e., division by zero in his eq. [4a]).

We require a formal mathematical statement of how nutrient-use efficiency changes along nutrient-availability gradients that is at least consistent with, and preferably derived from, a model of how productivity changes along nutrient-availability gradients. Here, we consider nutrient availability to be the rate of resupply of a limiting resource from the external environment, identical to the

concept of resource-flux density (Ingestad 1979; Chapin et al. 1986). Recycling of nutrients internal to the plant by retranslocation from senescing leaves provides an additional nutrient pool for production and is one mechanism to increase nutrient-use efficiency, but “new” nutrients external to the plant are also needed unless production ceased and zero loss from the plant could be achieved. We therefore focus on nutrient flux density from the environment as the most important component of nutrient limitations to growth. However, nutrient flux density is often difficult to measure, especially for P because of its important geochemical cycle, and various indexes, such as total pool size of plant available forms, have often been substituted (Chapin et al. 1986; Binkley and Hart 1989; Walbridge 1991). This operational substitution of measurements does not affect our theoretical arguments so long as the correlation between the indexes and flux data holds.

The response of a particular species to resource availability is determined by its resource-use ( $PR/R_{ac}$ ) and its resource-uptake ( $R_{ac}/R_{av}$ ) efficiencies:

$$\frac{PR}{R_{av}} = \frac{PR}{R_{ac}} \times \frac{R_{ac}}{R_{av}}, \quad (1)$$

where  $PR$  is production,  $R_{ac}$  is the amount of resource acquired, and  $R_{av}$  is resource availability. The resource-uptake efficiency ( $R_{ac}/R_{av}$ ) was previously defined by Shaver and Melillo (1984). The ratio of production to resource availability ( $PR/R_{av}$ ) was introduced by Miller (1979), and we call this term the *resource-response efficiency*.

Both  $R_{av}$  and  $R_{ac}$  have rarely been examined in nutrient-efficiency studies (Pastor et al. 1984; Shaver and Melillo 1984), but alternative use of the two resource terms may give different relative production efficiencies. For example, efficiency may differ depending on how resources are defined in cases in which plants from infertile environments have greater nutrient storage in live tissue (Chapin 1980). This discrepancy may be especially important in studies in which nutrient concentrations in particular biomass pools, for example, litterfall (Vitousek 1982, 1984), rather than nutrient uptake ( $R_{ac}$ ) are actually determined. Additionally, changes in the kinetics of nutrient uptake by roots over nutrient-availability gradients (Barber 1981; Gray and Schlesinger 1983; Birk and Vitousek 1986; Schlesinger et al. 1989) may yield different nutrient-use and nutrient-response efficiencies. The resource-response efficiency ( $PR/R_{av}$ ) is therefore a useful complement to resource-use and resource-uptake efficiencies for analyzing ecosystem and species responses to resource gradients. This ratio integrates the ability of a species to acquire resources with its ability to use them in growth once acquired. It is also particularly useful in a whole-ecosystem context in which total production is the sum total of all species' responses to resource availability.

Plants generally show a characteristic production response to gradients of resource availability. Production increases with resource availability, but eventually increases in production diminish with further resource availability until a maximum is reached ( $PR_{max}$ ) as another resource becomes more limiting. Production can be zero at zero nutrient availability or at some low but positive nutrient availability, which we term  $R_{min}$ . These two alternatives have important consequences for nutrient efficiency, as discussed below. A third alternative, that of positive production at zero or negative nutrient availability, is not possible. We

believe that zero production at some low but positive nutrient availability is the only logical alternative; that is, some minimum amount of nutrients is required to sustain an ecosystem. There are numerous empirical examples of  $R_{\min}$  for limiting nutrients (Mitchell and Chandler 1939; Droop 1973; Ingestad 1979; Tilman 1982). More fundamentally,  $R_{\min}$  is implicit in the characteristic elemental stoichiometry of organisms (Redfield 1958). That is, a unit of biomass, be it protein, DNA, or ATP, must be produced with a stoichiometry of  $C_x N_y P_z$ . In other words, a unit of biomass cannot be produced without at least  $z$  units of P.

Production at a given resource availability can be approximated by a Michaelis-Menten equation for resource uptake, if one assumes a direct coupling between uptake of a limiting resource and production (Monod 1942):

$$PR = \frac{(R_{ac} - R_{\min})PR_{\max}}{R_{ac} - R_{\min} + \alpha}, \quad (2)$$

where  $\alpha$  is the amount of resource in excess of  $R_{\min}$  that will yield a production of  $0.5 PR_{\max}$ , or the half-saturation constant with respect to  $R_{ac}$ .

Response curves (fig. 1) differ among species according to their resource requirements (Mitchell and Chandler 1939; Kramer and Decker 1944; Kozłowski 1949; Loach 1967; Small 1972; Larcher 1975; Aber et al. 1979; Tilman 1982). We refer to species adapted to infertile environments as tolerant and species that only occur in relatively fertile environments as intolerant (Mitchell and Chandler 1939; Aber et al. 1979). The growth rates of tolerant species (curves *B* and *C*, fig. 1A) are less affected by low resource availabilities than those of intolerant species (curve *A*, fig. 1A). The  $R_{\min}$  of tolerant species is therefore lower than that of intolerants. Tolerants also reach their maximum growth rate at lower resource availabilities than do intolerants (Chapin 1980, 1991). In other words, they become saturated at lower resource availabilities than intolerants. In terms of equation (2), intolerants have higher  $\alpha$ ,  $R_{\min}$ , and  $PR_{\max}$  than tolerant species (fig. 1A).

Resource-use efficiency is readily calculated by dividing equation (2) by resource uptake:

$$\frac{PR}{R_{ac}} = \frac{(R_{ac} - R_{\min})PR_{\max}}{(R_{ac} - R_{\min} + \alpha)R_{ac}}. \quad (3)$$

By differentiation of equation (3), it can be shown that the maximum, and therefore optimal, production per unit resource acquired will occur at the resource level,  $R_{opt}$ :

$$R_{opt} = R_{\min} + R_{\min}(\alpha/R_{\min})^{0.5}. \quad (4)$$

Note that  $R_{opt}$  does not depend on  $PR_{\max}$  but depends strongly and directly on  $R_{\min}$ . Also,  $R_{opt}$  is lower for tolerant than intolerant species as a result of differences in  $R_{\min}$ . Plots of  $PR/R_{ac}$  relative to  $R_{ac}$  for hypothetical tolerant and intolerant species are shown in figure 1B. Resource-response efficiency may be similarly derived substituting  $R_{av}$  for  $R_{ac}$ .

Several key points emerge from figure 1. First, the amount of production per unit resource acquired will necessarily be zero when production is zero (i.e., at  $R_{ac} = R_{\min}$ ). Second, when  $R_{\min}$  is positive (curves *A* and *B*), resource-use effi-

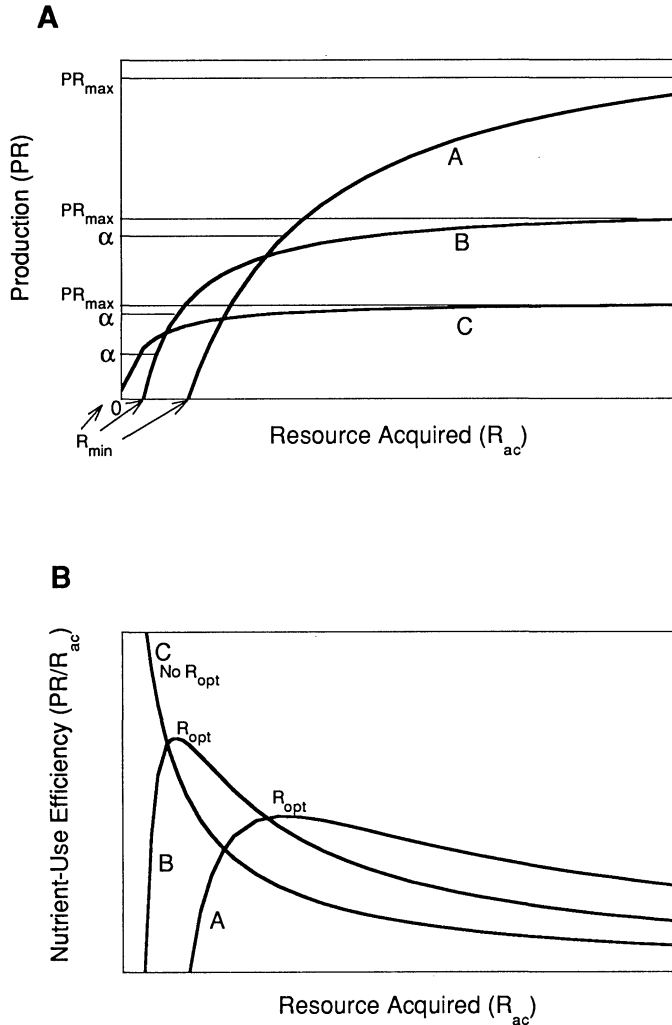


FIG. 1.—Predictions of the Monod model for (A) production and (B) nutrient-use efficiency relative to a resource acquired by a plant or ecosystem. Curve A represents a species intolerant of infertile conditions; curve B, a species tolerant of infertile conditions with a positive  $R_{min}$ ; and curve C, a species tolerant of infertile conditions with a  $R_{min} \leq 0$ .

ciency will first increase sharply to a maximum as  $R_{ac}$  becomes greater than  $R_{min}$  but will eventually decline as increases in production diminish. Third, as  $R_{min}$  declines and approaches zero in plant communities with increasing tolerance to low nutrient conditions,  $R_{opt}$  also approaches zero (also see eq. [4]). However, as long as  $R_{min}$  is greater than zero, there is a finite, maximum value for resource-use efficiency. Only when  $R_{min}$  is less than or equal to zero can resource-use efficiency increase without an upper limit (curve C). Ingestad (1977, 1979) experimentally found concave downward curves similar to A and B for birch and spruce

response to N availability, but Vitousek (1982, 1984) hypothesized an unbounded increase in resource-use efficiency with declines in resource availability. However, the unbounded increase makes little biological sense because (1) the stoichiometric constraints on plants outlined above dictate that  $R_{\min}$  must be greater than zero, (2) an infinite efficiency at zero production is incongruous, and (3) a negative resource availability is not possible.

It is clear from figure 1 that data on responses from very infertile environments are required to distinguish among the curves. We tested our Monod model of nutrient-use efficiency with field data from a nutrient-availability gradient in North Carolina peatlands that includes extremely infertile communities. These data allow examination of  $R_{\min}$  to determine whether resource use efficiency declines as  $R_{ac}$  approaches zero.

## METHODS

### *Sites*

Several different peatland plant communities occur on the coastal plain of the southeastern United States, despite the subdued topography. These communities are most readily distinguished by differing height and biomass of the aboveground vegetation, ranging from stunted shrub thickets to swamp forests, and also represent a natural nutrient-availability gradient (Walbridge 1991; Bridgham and Richardson 1993). We studied carbon and nutrient relationships in three of these peatland communities in the Croatan National Forest, Craven County, North Carolina (34°55'N latitude, 77°5'W longitude). Short pocosins are highly nutrient deficient and are dominated by low-statured (< 1.5-m height), evergreen-to-deciduous shrubs; tall pocosins are somewhat less nutrient deficient and are dominated by taller shrubs of a similar species composition; and gum swamps are relatively nutrient rich and have a full-sized, deciduous tree canopy. Additional details concerning the study sites are given elsewhere (Bridgham 1991; Bridgham and Richardson 1991, 1993).

### *Litterfall and Soil Nutrients*

Four 0.1-ha (20 × 50-m) plots were established in each community. Five litter traps were placed just above the soil surface in each plot in September 1988. The contents were collected approximately biweekly in the autumn and monthly otherwise through December 1989. The area of the litter traps varied among communities in order to maximize the collecting surface without undue disturbance of the vegetation. Wooden-frame traps with a fiberglass screen bottom (1.5-mm mesh) were used in the gum swamp (1 m × 1 m) and the tall pocosin (0.75 m × 0.75 m). A PVC pipe 15.2 cm in diameter and 3.0 m long was used in the short pocosin. The pipe was cut in half lengthwise and perforated with holes at closely spaced intervals, and screen was placed at its lowest end. Litter was divided into leaves, wood, and miscellaneous (e.g., fruits, flower parts, unidentifiable fragments) components, except for the last three collections in the autumn of 1989 when just bulk litter was measured. The litter was oven-dried at 70°C

before weighing. Only the results from fine litterfall (i.e., without wood) are discussed here, as newly fallen wood does not necessarily represent annual production and occurs mostly with storm events.

The leaf and miscellaneous fractions were composited from all litter traps within a plot quarterly from January to September 1989 for nutrient analyses. From October through December 1989, bulk, unsorted litter was collected for nutrient analyses, but at this time of year leaves are by far the dominant input. The appropriate seasonal nutrient concentrations of each fraction were multiplied by the monthly inputs to arrive at nutrient return to the soil from litterfall.

Three soil samples to 30-cm depth were taken from each plot with a stainless steel box corer (C. J. Richardson, unpublished design), which caused minimal compaction of peat, and composited. Large roots were removed from the samples by hand before further processing, and subsamples for bulk density and total nutrient concentrations were dried at 70°C.

Dried samples of litter and soil were digested in concentrated H<sub>2</sub>SO<sub>4</sub> and 30% H<sub>2</sub>O<sub>2</sub> (Lowther 1980). Nitrogen and phosphorus were measured with standard autoanalyzer techniques (Orion Scientific Instruments 1984), and calcium was measured with atomic adsorption spectrophotometry (Perkin Elmer 1982).

### Modeling

We followed the strategy of Vitousek (1982, 1984) and used nutrient circulation in litterfall to explore nutrient-use efficiency across the nutrient-availability gradient in the three North Carolina peatlands. In terms of our model, litterfall is an index of aboveground production ( $PR$ ); nutrient return in litterfall is an index of the amount of a nutrient acquired for production, or nutrient uptake ( $R_{ac}$ ); and the mass:nutrient return ratio of litterfall, or the inverse of nutrient concentration, is an index of nutrient-use efficiency ( $PR/R_{ac}$ ). Additionally, the ratio of litterfall mass:soil nutrient pool size ( $PR/R_{av}$ ) is an index of nutrient-response efficiency. We examined N, P, and Ca return because these nutrients are primarily cycled in litterfall (Vitousek 1982). Nitrogen and phosphorus in particular are the nutrients most likely to limit growth in forested ecosystems (Waring and Schlesinger 1985).

Litterfall was regressed against nutrient return in litterfall or soil nutrient availability with equation (2) and the nonlinear estimation program Nonlin in SYSTAT, minimizing residual sums of squares (SYSTAT 1992). Both the Simplex and Quasi-Newton curve-fitting routines converged on the same values in all cases. Estimates were obtained for  $PR_{max}$ ,  $\alpha$ , and  $R_{min}$  using this procedure. If  $R_{min}$  is greater than zero, then efficiency curves *A* and *B* in figure 1*B* hold; if  $R_{min}$  is zero or negative, then curve *C* holds. The coefficient of variation ( $r^2$ ) reported for the nonlinear estimation was calculated as

$$r^2 = 1 - \frac{\text{residual sum of squares}}{\text{total sum of squares}}. \quad (5)$$

## RESULTS

### Nutrient-Use Efficiency

Litter production increased asymptotically with P, N, and Ca return (fig. 2). The extremely infertile short pocosin had the lowest litterfall and nutrient return,



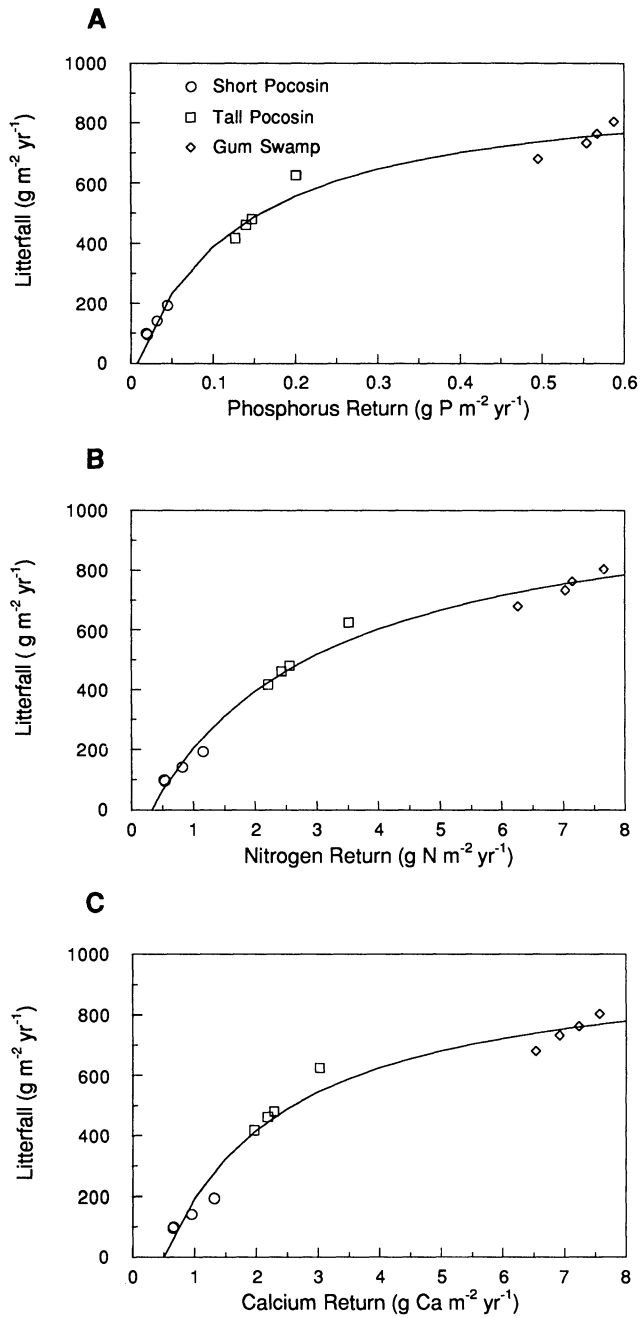


FIG. 2.—Litterfall and nutrient return in litterfall for (A) phosphorus, (B) nitrogen, and (C) calcium in three peatland communities in North Carolina. Lines are model predictions from eq. (2).

while litterfall in the relatively fertile gum swamp approached the asymptote. The Monod model (eq. [2]) closely fit the data with  $r^2 > 0.99$ , and  $R_{\min}$  was positive for all three nutrients.

The mass:P ratio of litterfall widened with lower P return (fig. 3A), which indicates greater nutrient-use efficiency with lower nutrient circulation. Note that the model lines in figure 3 were not fit to the resource-use efficiency data, but rather parameters were derived from the data in figure 2 and then overlaid on the data in figure 3. Equation (3) described the mass:P ratio of litterfall well, but all the short pocosin sites had P return values very close to the predicted value for maximum nutrient-use efficiency ( $R_{\text{opt}}$ ; eq. [4]) of  $0.03 \text{ g P m}^{-2} \text{ yr}^{-1}$ . Therefore, the decrease in nutrient-use efficiency at suboptimum resource values as predicted by the model with a positive  $R_{\min}$  was not evident. However, the nutrient-use efficiency curves and the data did show an optimum efficiency for N and Ca, with lower efficiencies to either side of this point (fig. 3B, C). The mass:N ratio was lowest in the gum swamp but approximately equal in the short and tall pocosins despite significantly lower N return in the short pocosin. The mass:Ca ratio was actually lower in the short pocosin than in the tall pocosin, with the short pocosin again having a lower Ca return. The values for  $R_{\text{opt}}$  were 1.3 and 1.5 g nutrient returned  $\text{m}^{-2} \text{ yr}^{-1}$  for N and Ca, respectively.

#### *Nutrient-Response Efficiency*

We also examined the relationship between the North Carolina litterfall data and several methods of measuring soil nutrient pool sizes, a proxy for nutrient availability or nutrient flux density, and calculated the nutrient-response efficiencies ( $P/R_{\text{av}}$ ) from equation (1). The three communities had significantly different total soil P concentrations (Bridgham 1991; Bridgham and Richardson 1993), and litterfall was strongly correlated with total soil P (fig. 4A). It is clear from these data that litterfall in the gum swamp is on the asymptote of the relationship between production and nutrient availability (fig. 4A). Hence, greater P availability will not cause greater production (or at least litterfall) in the gum swamp but will for the pocosin sites. Equation (2) again provided an excellent fit to the data ( $r^2 = .97$ ), and  $R_{\min}$  was positive. Both equation (3) and the data showed an optimum P availability at  $12.3 \text{ g P m}^{-2}$  with declines in resource-response efficiency at levels both higher and lower than this optimum (fig. 4B).

Total soil N and Ca concentrations were not significantly different between the short and tall pocosins (Bridgham 1991; Bridgham and Richardson 1993) and thus did not adequately describe the soil nutrient gradient. Equation (2) would not converge for total soil N and litterfall (data not shown). Total soil Ca predicted litterfall only moderately well ( $r^2 = 0.86$ ), and there was no relationship with Ca response efficiency (data not shown).

Walbridge (1991) measured isotopically exchangeable P and anion-exchangeable P with resin bags in the same peatland complex in the Croatan National Forest as our study but in different plots. We compared our mean litterfall values for each of the three communities with his P availability data. Excellent fits between isotopically exchangeable P and resin-bag P and litterfall were found with the Monod model, again with a positive  $R_{\min}$  (fig. 5). Additionally, P response

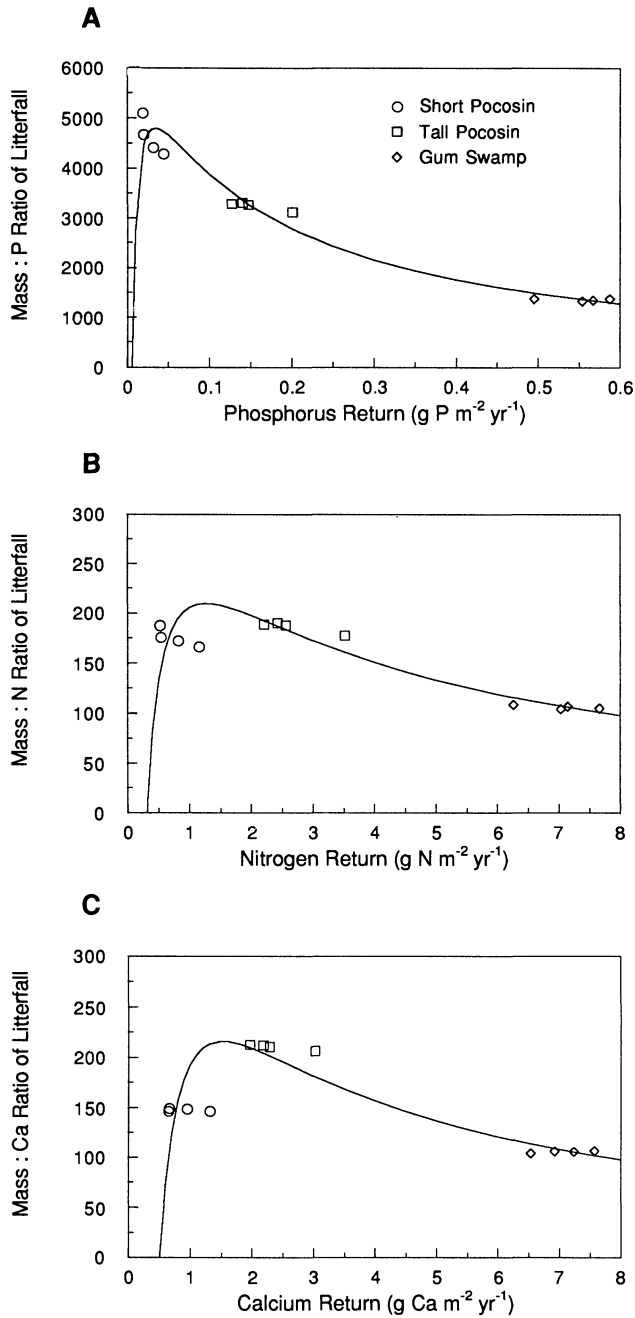


FIG. 3.—The mass:nutrient return ratio relative to nutrient return in litterfall for (A) phosphorus, (B) nitrogen, and (C) calcium in three peatland communities in North Carolina. Lines are model predictions from eq. (3). Note that the model lines were not fit to the data in this figure, but rather parameters were derived from the data in fig. 2.

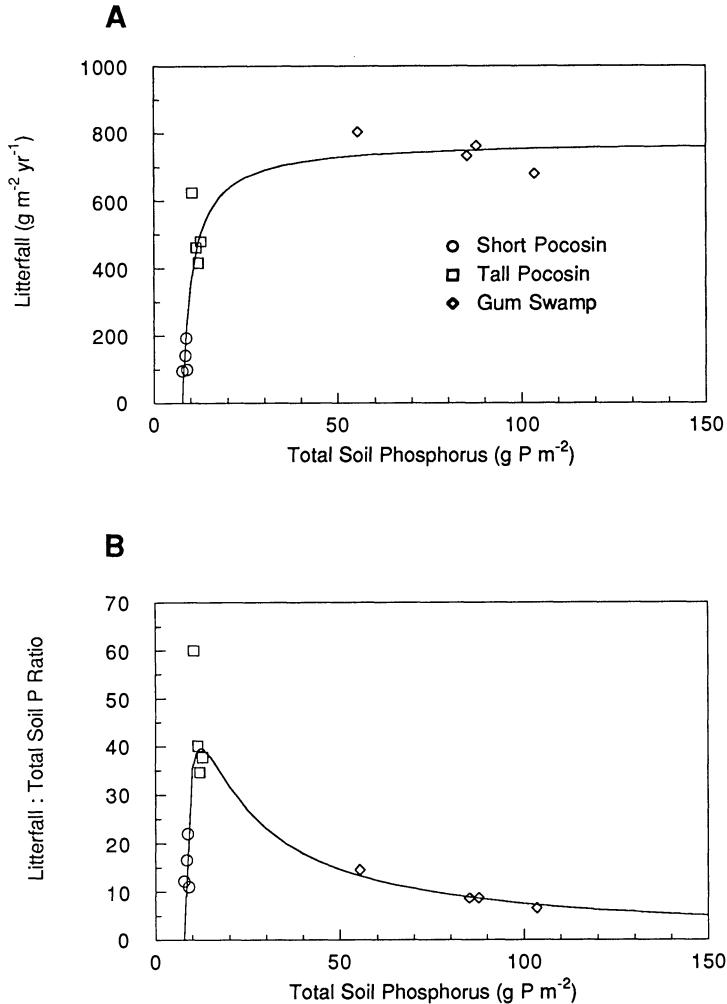


FIG. 4.—(A) Litterfall and (B) the litterfall:total soil phosphorus ratio relative to total soil phosphorus in three peatland communities in North Carolina. Lines are model predictions from eqq. (2) and (3), respectively.

efficiency, including the decline in the short pocosin at suboptimal P availability, was also well described with equation (3) (fig. 5).

Thus, total soil P, isotopically exchangeable P, and resin-bag P all effectively differentiated P availability among the three communities, provided high predictive power of aboveground production (as litterfall), and demonstrated that nutrient-response efficiency decreases at suboptimal P availability in the short pocosin. It is notable that only small differences in soil nutrient availability between infertile communities, such as the short and tall pocosins, can cause relatively large changes in vegetation response, such as in plant biomass, litterfall production, nutrient cycling in litterfall, and nutrient-response efficiency.

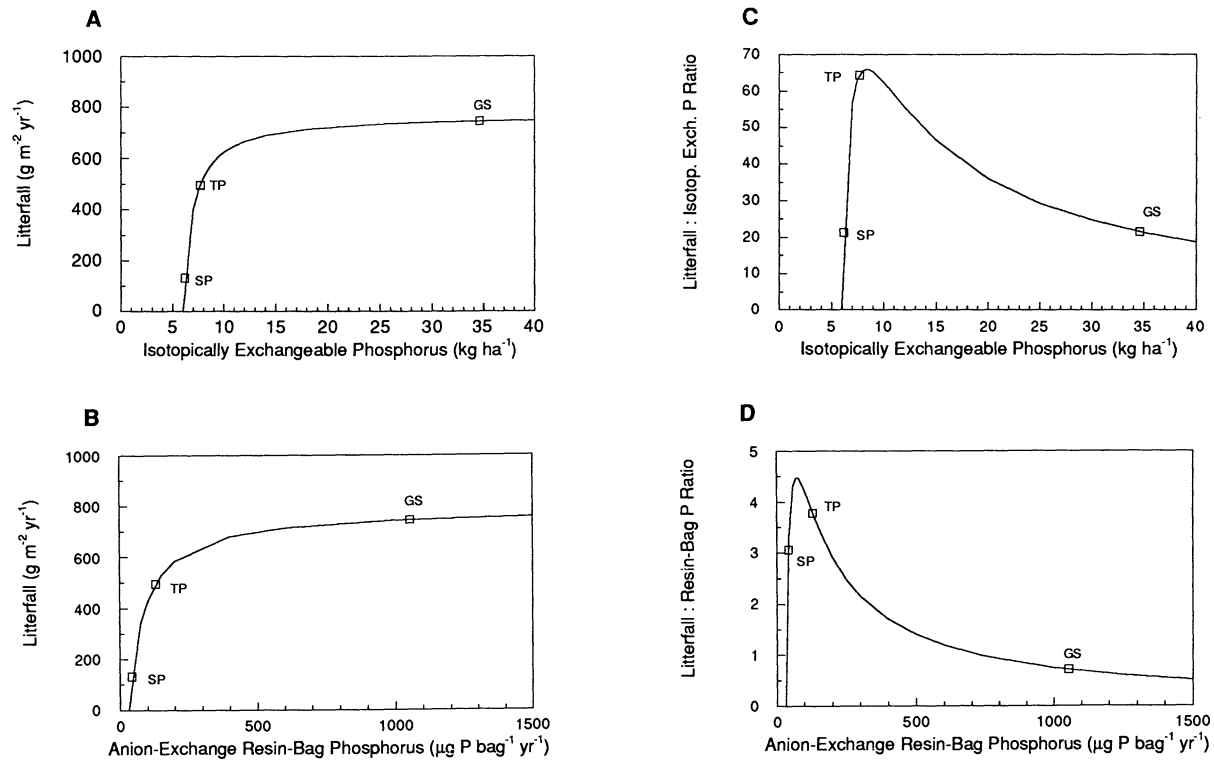


FIG. 5.—Average litterfall relative to (A) isotopically exchangeable phosphorus and (B) anion-exchange resin-bag phosphorus, (C) the litterfall:isotopically exchangeable phosphorus ratio relative to isotopically exchangeable phosphorus, and (D) the litterfall:anion-exchange resin-bag phosphorus ratio relative to anion-exchange resin-bag phosphorus in three peatland communities in North Carolina. *SP*, Short pocosin; *TP*, tall pocosin; and *GS*, gum swamp. Lines in A and B are model predictions from eq. (2), and lines in C and D are model predictions from eq. (3). The two phosphorus availability indexes are from Walbridge (1991).

TABLE 1  
PHOSPHORUS-UP TAKE EFFICIENCY INDEXES

Site	P Return/ Total Soil P*	P Return/ Extractable P*	P Return/IEP†	P Return/AER†
Short pocosin	.034 (.007) <sup>b</sup>	4.2 (.9) <sup>b</sup>	.047	.007
Tall pocosin	.134 (.020) <sup>a</sup>	33.8 (7.7) <sup>a</sup>	.199	.012
Gum swamp	.071 (.012) <sup>b</sup>	9.5 (4.2) <sup>b</sup>	.159	.005

\* Values are mean  $\pm$  SE. Values within a column with the same superscript letter are not significantly different ( $P > .05$ , Fisher's protected least significant difference).

† IEP is isotopically exchangeable phosphorus and AER is anion-exchange resin-bag phosphorus, from Walbridge 1991. Because means were used, no statistical comparisons were possible.

### *Nutrient-Uptake Efficiency*

We determined P-uptake efficiency ( $R_{ac}/R_{av}$ ) by dividing the P return in litterfall by four different measures of soil nutrient availability (table 1). In each case the tall pocosin had the highest P-uptake efficiency.

### *Blackhawk Island—Northern Edaphic Climax Forests*

An intensive study of plant production relative to nutrient dynamics in several climax forest stands that had grown under different edaphic conditions on Blackhawk Island, Wisconsin, has been reported elsewhere (Pastor et al. 1984). Aboveground net primary production (ANPP) and net N mineralization were measured, so N-response efficiency could be determined without using litterfall and nutrient pool sizes as surrogates for production and nutrient flux density, respectively. As with the North Carolina data set, the Monod model performed excellently in describing the relationship between production and nutrient availability (fig. 6A;  $r^2 = 0.999$ ). The value for  $R_{min}$  was positive, with an optimum nutrient-response efficiency ( $R_{opt}$ ) at an N mineralization rate of 32.9 kg ha<sup>-1</sup> yr<sup>-1</sup> (fig. 6B). A hemlock stand had close to this optimum nutrient-response efficiency, but a decrease in efficiency, as predicted by the model, occurred in a red pine stand. Thus the Monod model and our hypothesis of a positive  $R_{min}$ , with its ecological consequences for reduced nutrient efficiencies under very limiting nutrient conditions, appears to hold for northern temperate forests.

### *A Reevaluation of the 1984 Vitousek Data*

Our tests above of the ability of the Monod model to predict nutrient-use and nutrient-response efficiencies were done on the scale of local nutrient-availability gradients. The original analyses of nutrient-use efficiency with litterfall by Vitousek (1982, 1984) were done on a regional to global scale, and to test the applicability of the Monod model on this larger scale we reanalyzed the data presented in Vitousek's 1984 article. Sites that were either young successional stands (< 15 yr old), often of exotic planted species, or savanna sites that would be predominantly water limited were eliminated from the analysis (P. Vitousek, personal communication). In these sites, litterfall (and production in general) may

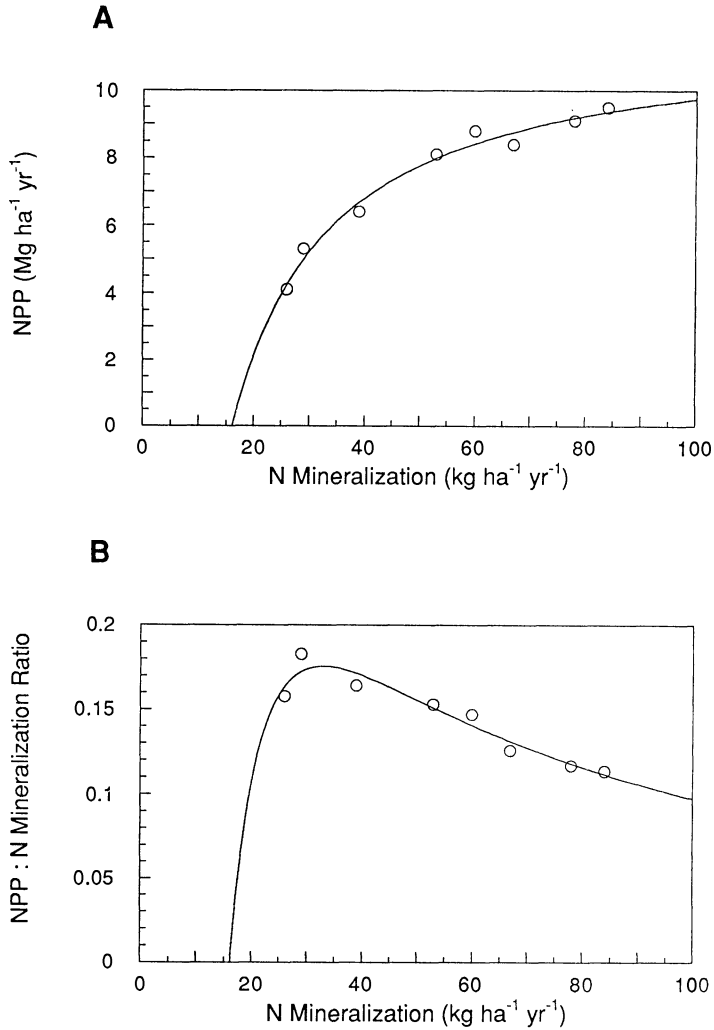


FIG. 6.—Data from edaphic forested climax communities on Blackhawk Island, Wisconsin (Pastor et al. 1984). Lines in *A* and *B* are model predictions from eqq. (2) and (3), respectively. *NPP* is aboveground net primary production, and *N Mineralization* is net N mineralization with the buried bag technique.

not be limited by nutrient availability. Additionally, we added our North Carolina sites to Vitousek's 1984 data.

Equation (2) predicted the overall relationship between litterfall and nutrient return relatively well for P and N ( $r^2 = 0.95\text{--}0.97$ ; fig. 7*A, B*). The value for  $R_{\min}$  was positive for P but negative for N. The short pocosin sites had the lowest litterfall and nutrient-return values in the combined data sets, and the tall pocosin sites had values similar to the most nutrient-deficient tropical stands. The combined data sets gave an increased  $R_{\text{opt}}$  for P ( $0.043 \text{ g P m}^{-2} \text{ yr}^{-1}$ ) relative to the

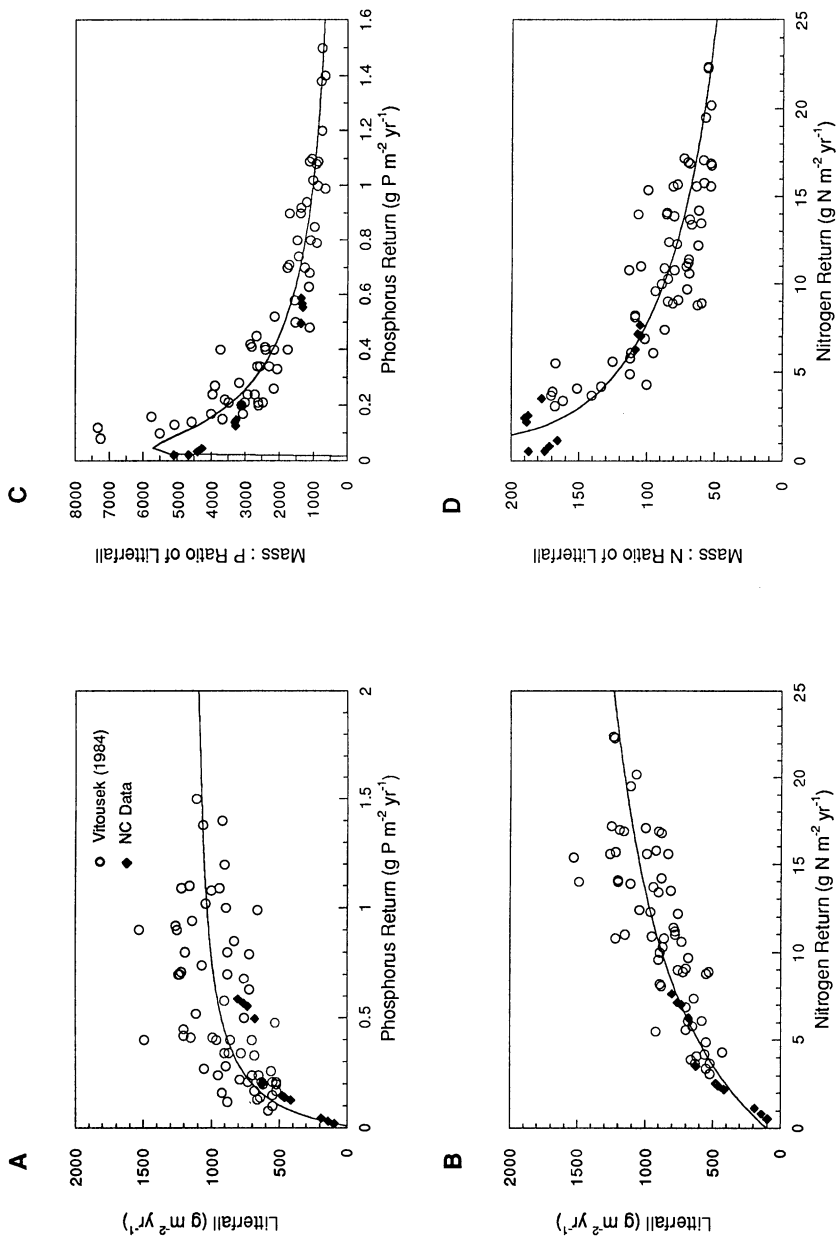


Fig. 7.—Data from world tropical forests (Vitousek 1984) (open circles) and from the North Carolina sites (solid diamonds). Lines in A and B are model predictions from eq. (2), and lines in C and D are model predictions from eq. (3).



North Carolina data alone ( $R_{opt} = 0.034 \text{ g P m}^{-2} \text{ yr}^{-1}$ ), with the result that the short pocosin sites were now on the decreasing leg of the P-use efficiency curve at decreasing values of P return (fig. 7C). Phosphorus-use efficiency in the short pocosin sites was approximately equal to that obtained at  $R_{opt}$  when only the North Carolina peatland sites were considered (fig. 3A). Two stands, a terra firme forest in Venezuela and a dipterocarp forest in Malaysia, were clearly outliers in the analysis with a P-use efficiency ratio approximately 1,600 units higher than the calculated maximum P-use efficiency of 5,720 at  $R_{opt}$ .

The value for  $R_{min}$  for N was positive when the North Carolina sites were considered alone (fig. 3B). The negative  $R_{min}$  obtained with the combined data sets poorly described N-use efficiency in the short and tall pocosins (fig. 7D), and the negative  $R_{min}$  may well be caused by the large scatter of points with higher N return. The tropical data are obviously biased against sites with low litterfall and nutrient return when compared to the North Carolina peatland sites.

#### DISCUSSION

We used a local nutrient-availability gradient in shrub and forested peatlands in North Carolina to test a proposed litterfall index of production and nutrient-use efficiency (Vitousek 1982). Pocosins are extremely nutrient-deficient shrub peatlands and provided a robust test of relationships between litterfall and nutrients at an end of the spectrum where few data points have previously been available and where critical tests of different resource efficiency models are required. The Monod model effectively separated the communities in terms of production and the efficiency of nutrient use.

Litterfall (an index of production) increased with nutrient return in litterfall (an index of nutrient uptake) for P, N, and Ca until an asymptote was approached in the fertile gum swamp (fig. 2), which indicated a shift to other controlling factors (e.g., light). The value for  $R_{min}$  was positive for all three nutrients, supporting curves A and B in figure 1 as the most realistic alternatives in real ecosystems. The Monod model predicts that with a positive  $R_{min}$  nutrient-use efficiency should increase with decreasing nutrient availability to some optimum but that under suboptimal conditions nutrient-use efficiency should decrease. The model's predictions were corroborated for N and Ca in litterfall, with the ratio of mass to nutrient return in litterfall (an index of nutrient-use efficiency) increasing with decreasing nutrient return for N and Ca until an optimal level ( $R_{opt}$ ) was achieved (fig. 3). Below this optimal level the ratio decreased. The mass:P ratio of litterfall in the most infertile community, the short pocosin, was approximately equal to  $R_{opt}$ , so no decrease in P-use efficiency was observed at suboptimal resource uptake levels.

Nutrient-response efficiency defines changes in production due to nutrient availability. We compared several methods of measuring soil nutrient availability, each of which samples a somewhat different soil pool and integrates over a different time span. Total soil nutrients represent a long-term potentially available pool, especially in peat-based systems in which the majority of the nutrients are in organic form (Richardson and Marshall 1986; Walbridge 1991; Bridgman and

Richardson 1993). Isotopically exchangeable nutrients represent an instantaneous "available" soil pool, while resin bags measure the available nutrient pool integrated over time, thus incorporating the kinetics of P released from less available, insoluble forms (Stevenson 1986).

Nutrient-use and -response efficiencies generally responded similarly along the resource gradient regardless of method of measurement. Total soil P, isotopically exchangeable P, and anion-exchangeable resin-bag P were highly correlated with litterfall and the ratio of litterfall to nutrient availability (figs. 4, 5). Additionally,  $R_{\min}$  was positive and P-response efficiency declined in the highly infertile short pocosin sites with all three P-availability indexes.

We found much better relationships between nutrient availability and nutrient-response efficiency for P than for N and Ca. Nutrient-addition experiments have shown that pocosin vegetation is primarily P limited, with N occasionally colimiting (Woodwell 1958; Maki 1974; MacCarthy and Davey 1976; Wilbur and Christensen 1983; Simms 1987). Additionally, the N:P ratio of annual nutrient return in litterfall significantly widens along the resource gradient from 12.5 in the gum swamp, to 17.5 in the tall pocosin, to 26.4 in the short pocosin, which indicates the increasing importance of P as a limiting nutrient (Bridgham and Richardson 1993).

The tall pocosin had the greatest P-uptake efficiency for all four nutrient-availability methods used (table 1), and P-uptake efficiency showed the same relative dynamics as the P-use and -response efficiencies. It appears that a positive  $R_{\min}$  implies a decrease in multiple measures of nutrient efficiency for plant communities in infertile ecosystems with nutrient availability below some optimum level. The tall pocosin appears to be close to this optimum nutrient availability for efficiency of uptake and use of nutrients, but even greater nutrient deficiency in the short pocosin causes a reduction in nutrient efficiency. The exception to this was that the short pocosin had P return in litterfall approximately equal to  $R_{\text{opt}}$ , so no decrease in P-use efficiency was evident at suboptimal resource uptake levels.

The use of litterfall mass as an index of productivity and the nutrient content of litterfall as an index of nutrient uptake has numerous assumptions, as discussed previously. Additionally, our three measures of nutrient availability in the North Carolina peatlands represent pools rather than fluxes. The Blackhawk Island data (Pastor et al. 1984) directly measured aboveground net primary productivity and N flux. Thus, we were able to test the Monod model without the assumptions inherent in using litterfall and nutrient pool sizes and additionally to test the model on a very different set of communities. This edaphic forest climax gradient had a positive  $R_{\min}$  and showed the most nutrient-deficient community, a red pine stand, on the downward slope of N-response efficiency at suboptimal nutrient availability. Additionally, it is important that  $R_{\min}$  ( $16.2 \text{ kg ha}^{-1} \text{ yr}^{-1}$ ) is somewhat lower than most reported rates of N uptake in temperate closed-canopy forests (Cole and Rapp 1981), which indicates that it is biologically reasonable. This second local nutrient-availability gradient strongly supports our results from North Carolina peatlands: the Monod model accurately predicts production and nutrient-response efficiency relative to nutrient availability,  $R_{\min}$  is a positive

quantity, and nutrient-response efficiency will decrease at suboptimal nutrient availability.

On a global scale using Vitousek's (1984) data, the Monod model continued to perform well at predicting production and nutrient-use efficiency (fig. 7). Thus the model worked from a local to global scale, with numerous different input parameters, and appears to be scale invariant. Phosphorus, the limiting nutrient in most tropical forests (Vitousek 1984), showed a positive  $R_{\min}$  with the combined tropical and North Carolina peatland sites. The value for  $R_{\min}$  was negative for both P and N when only the tropical data were examined, but the results of different nutrient-efficiency models (fig. 1) are discriminated only at low values of production and nutrient acquisition. The values for short pocosins are much lower than those in the tropical forest data, and inclusion of the pocosin sites corroborated our hypothesis that nutrient efficiency must decrease at low, suboptimal concentrations of limiting nutrients.

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