

John Pastor · Scott D. Bridgham

## Nutrient efficiency along nutrient availability gradients

Received: 3 March 1998 / Accepted: 31 August 1998

**Abstract** The validity of nutrient use efficiency as a central concept in ecosystem ecology has recently been subject to challenge based upon arguments over autocorrelation of data, interpretation of graphical approaches, and appropriate statistical analyses. Much of the confusion on the measurement and interpretation of nutrient use efficiency results from the lack of a sound theoretical basis with which to examine experimental results. In this paper, we develop a theory of nutrient use efficiency based upon fundamental mass balance, present a graphical approach to appropriate testing of alternative hypotheses to avoid problems of autocorrelation in data, and suggest critical areas where experiments must be performed to distinguish among hypotheses. We show that nutrient use efficiency (production per unit nutrient uptake) must be distinguished from nutrient response efficiency (production per unit nutrient available). In contrast to the monotonic increase of nutrient use efficiency with decreasing nutrient availability originally proposed in the 1982 model of P.M. Vitousek, nutrient response efficiency is unimodal with maximum efficiency at intermediate levels of nutrient availability. However, nutrient use efficiency dynamics at low nutrient availability cannot yet be theoretically defined. We also show theoretically which plant traits control responses of ecosystem nutrient use or nutrient response efficiency along gradients of nutrient availability. Finally, we show how our model naturally leads to species replacement along nutrient availability gradients.

**Key words** Nutrient use efficiency · Nutrient response efficiency · Nutrient availability · Litterfall · Production

### Introduction

Nutrient use efficiency emerged as a central concept in ecosystem ecology with the work of Vitousek (1982, 1984), which defined it as net primary production per unit nutrient uptake or resource acquired by vegetation. Because of a general lack of comprehensive data, Vitousek (1982, 1984), as well as ourselves (Bridgham et al. 1995) and many others, used litterfall and its nutrient content as surrogate measures for net primary production and nutrient uptake, respectively. Vitousek then operationally defined nutrient use efficiency as annual litterfall/nutrient content of litterfall and graphed it against the nutrient content of litterfall on the  $x$ -axis to see how efficiency changes with nutrient uptake by vegetation. Because plant nutrient uptake in ecosystems is characteristically proportional to soil nutrient availability, the  $x$ -axis is also generally interpreted as reflecting a gradient of nutrient availability. Vitousek (1982, 1984) provided data suggesting that nutrient use efficiency increases monotonically as either nutrient availability or nutrient uptake declines.

These seminal papers used exploratory statistical analysis to discover patterns in nutrient use efficiency along resource availability gradients. As such, these patterns invite us to present hypotheses for their underlying mechanisms. However, one must be cautious about drawing conclusions from such analyses. First, the data are obtained from the literature, and the sites and measurement methods may have been chosen for reasons other than examining patterns of nutrient use efficiency. There is thus the real possibility of a bias in the data, particularly with respect to site selection.

Secondly, the various interpretations of what the  $x$ -axis represents raise problems of autocorrelation of the data, as discussed by Knops et al. (1997) and Vitousek (1997). The autocorrelation arises because litterfall dry

---

J. Pastor (✉)  
Biology Department and Natural Resources Research Institute,  
University of Minnesota,  
Duluth, MN 55811, USA  
email: jpastor@sage.nrri.umn.edu;  
Tel: +1-218-7204271; Fax: +1-218-7209412

S.D. Bridgham  
Department of Biological Sciences,  
University of Notre Dame,  
Notre Dame, IN 46556, USA

mass/litterfall nutrient content is plotted against litterfall nutrient content, which results in plotting  $1/x$  against  $x$ . This problem does not result solely from the use of litterfall surrogates, as graphing net primary production/nutrient uptake relative to nutrient uptake still gives rise to autocorrelation. Problems of autocorrelation in the use and analysis of ratios are also discussed by Atchley et al. (1976), Atchley and Anderson (1978), and Packard and Boardman (1988).

Thirdly, ratios are problematic, because they may increase unbounded as the denominator goes to zero. In the case of nutrient use efficiency, this would lead to infinite efficiency as zero nutrient uptake is approached, and productivity would be undefined when no nutrients are incorporated into litterfall, clearly a biologically meaningless result. Therefore, mechanisms must also be specified that prevent efficiency from increasing in an unbounded manner.

Fourthly, there is controversy over how to best interpret the axes, slope, and intercept of productivity-nutrient uptake graphs, with various parties deriving fundamentally opposite conclusions from the same datasets (Bridgham et al. 1995; Knops et al. 1997; Vitousek 1997).

Thus, the theoretical underpinnings of one of the central concepts of ecosystem ecology have become confounded with problems of how to best graph and statistically analyze data. Simply gathering more data in new experiments or the literature will not solve these problems.

We believe that much of the confusion on the measurement and interpretation of nutrient use efficiency results from the lack of a sound theoretical basis with which to examine empirical results. The purpose of this paper is to provide a theoretical basis for various measures of nutrient efficiency and their behavior along nutrient availability gradients. This theory partitions nutrient efficiency into its various components and demonstrates their behavior along nutrient availability gradients while avoiding the problems of autocorrelation raised by Knops et al. (1997) and the problems of ratios raised by Atchley et al. (1976), Atchley and Anderson (1978) and Packard and Boardman (1988).

The theory provides a list of mutually exclusive, *a priori* hypotheses that distinguish between various patterns of productivity in relation to nutrient availability on the one hand and the corresponding efficiency-availability relationships on the other hand. Statistical analysis can then be used to verify one of the *a priori* hypotheses and reject the others, in contrast to the use of a *posteriori* exploratory statistics to discover patterns. We will then show how statistical analyses of these hypotheses avoid the problems of autocorrelation discussed by Knops et al. (1997) and Vitousek (1997). Moreover, we demonstrate that the dynamics of *nutrient response efficiency* (production per unit nutrient available) along nutrient availability gradients must be considered separately from those of *nutrient use efficiency* (production per unit nutrient uptake). Both

Vitousek (1982, 1984) and Knops et al. (1997) implicitly assume that the dynamics of these two efficiency indices are coincident along fertility gradients, but we demonstrate that the conclusions of Vitousek (1982, 1984) about a monotonic increase in nutrient use efficiency with decreasing nutrient availability cannot hold for nutrient response efficiency. Finally, the theory pinpoints the regions where crucial experiments are required to distinguish between these mutually exclusive hypotheses, and also suggests a new hypothesis of the causes of species replacement along nutrient availability gradients.

---

### A theoretical approach to nutrient efficiency

First, we extend our previous analysis of ecosystem nutrient efficiency (Bridgham et al. 1995) to include the work of Berendse and Aerts (1987), so that we may have a theoretical foundation from which to view the results of Knops et al. (1997) and Vitousek (1997). This theoretical relationship will also provide a mathematical definition of nutrient response efficiency with which to examine its behavior along nutrient availability gradients without the problem of autocorrelation.

Berendse and Aerts (1987) considered two terms in deriving nutrient use efficiency (NUE). The first was the relative nutrient uptake rate ( $L_n$ :  $\text{g N}^{-1}$  in the plant  $\cdot \text{year}^{-1}$ ) for which the inverse is the residence time of a unit nutrient in the plant. The second term was the nutrient productivity of the ecosystem ( $A$ , units of dry mass  $\text{g}^{-1}$  nutrient uptake  $\text{year}^{-1}$  or the rate dry-matter production ( $P$ ) per unit nutrient acquired by the plant ( $R_{ac}$ ). The concept of nutrient productivity was originally introduced by Agren (1983). For generality, we use  $R$  to stand for any limiting abiotic resource, although in this paper we will refer specifically to limiting nutrients unless otherwise specified. Berendse and Aerts (1987) then defined nutrient use efficiency as:

$$NUE = \frac{A}{L_n} = \frac{P}{R_{ac}} \quad (1)$$

This equation simply reduces to productivity ( $P$ ,  $\text{g C m}^{-2} \text{ year}^{-1}$ ) divided by the rate of resource uptake or acquisition by plants ( $R_{ac}$ ,  $\text{g N m}^{-2} \text{ year}^{-1}$ ). This equation is ecologically useful because it explicitly considers tradeoffs between nutrient productivity and the ability of plants to retain and recycle nutrients internally.

Combining the previous work of Shaver and Melillo (1984) and Miller (1979), Bridgham et al. (1995) found it useful to define two other terms to describe the efficiency with which nutrients are used for net primary production. Nutrient response efficiency (NRE) is the product of nutrient use efficiency ( $P/R_{ac}$ ) and nutrient uptake efficiency, which is the proportion of potentially available nutrients in the environment ( $R_{av}$ ,  $\text{g nutrient m}^{-2} \text{ year}^{-1}$ ) that plants actually take up ( $R_{ac}/R_{av}$ ):

$$NRE = \frac{P}{R_{av}} = \frac{P}{R_{ac}} \cdot \frac{R_{ac}}{R_{av}} = \frac{A}{L_n} \cdot \frac{R_{ac}}{R_{av}} \quad (2)$$

Thus, nutrient response efficiency depends on productivity ( $P$ ), nutrient productivity ( $A$ ), the residence time of the plant nutrient pool ( $1/L_n$ ), the nutrient uptake rate ( $R_{ac}$ ) and the abilities of different plants to compete for available nutrients ( $R_{ac}/R_{av}$ ).

Equations 1, 2 indicate that nutrient response efficiency can be affected by numerous factors such as tissue nutrient concentration, carbon and nutrient allocation within the plant, nutrient resorption from leaves before senescence, residence time of various vegetative parts, the kinetics of root uptake, nutrient productivity, and storage of nutrient reserves. Additionally, separate consideration of nutrient uptake efficiency, nutrient response efficiency, nutrient use efficiency, residence time of nutrients in plants, and nutrient productivity can yield important insights into the competitive abilities of different species along fertility gradients (Shaver and Melillo 1984; McGraw and Chapin 1989; Aerts and de Caluwe 1994).

As Knops et al. (1997) and Vitousek (1997) fundamentally disagreed about the graphical interpretation of nutrient use efficiency, it is fruitful to consider this subject further. They graphed productivity ( $P$ ) on the  $y$ -axis relative to nutrient uptake by vegetation on the  $x$ -axis, and discussed the biological meaning of linear models fitted to these data. However, from Eqs. 1 and 2, nutrient uptake is a combination of the inverse of nutrient productivity ( $A$ ), the inverse of residence time ( $L_n$ ), and productivity ( $P$ ):

$$\text{Nutrient uptake} = \frac{g \text{ Nutrient} \cdot \text{yr}}{g C} \cdot \frac{1}{\text{yr}} \cdot \frac{g C}{m^2 \cdot \text{yr}} = \frac{P}{NUE} \quad (3)$$

More simply, we see that the  $x$ -axis in the discussion of Knops et al. (1997) and Vitousek (1997) is the inverse of nutrient use efficiency times productivity. Therefore, the slope of the productivity-nutrient uptake graph is simply NUE. A linear solution to this graph as discussed by Knops et al. (1997) and Vitousek (1997) therefore requires a constant nutrient use efficiency across a nutrient-uptake gradient. This is the only possible interpretation of a linear solution, despite the extensive arguments expended by Knops et al. (1997) and Vitousek (1982, 1984, 1997) to explain the linearity of this graph. However, the data describing this relationship are typically nonlinear (cf. Vitousek 1982, 1984; Bridgham et al. 1995; Knops et al. 1997), and below we develop the theoretical implications of these nonlinearities. Additionally, it is clear from this equation that not only is a graph of NUE versus nutrient uptake autocorrelated, but so is a graph of productivity versus nutrient uptake.

Let us now consider graphical approaches for nutrient response efficiency. By rearrangement of Eq. 2, productivity at a given level of resource availability [ $P(R_{av})$ ] can be defined as:

$$P_{R_{av}} = R_{av} \cdot \left[ \frac{P}{R_{av}} \right] + 0 \quad (4)$$

The explicit addition of zero is not trivial, but makes the point that nutrient response efficiency is the slope of a line from the origin to a given point on a separate function for  $P(R_{av})$  that defines the relationship between productivity and nutrient availability (for example, a Monod function). Note that in Eq. 4 nutrient response efficiency changes with nutrient availability; how it changes depends on the functional response of productivity to nutrient availability specified by another function, such as a Monod function. Repeated application of Eq. 4 to each point on  $P(R_{av})$  generates a family of lines between the origin and every point on  $P(R_{av})$ . This is the tool we need to examine corresponding relationships between productivity and nutrient availability on the one hand and nutrient response efficiency and nutrient availability on the other hand.

---

### A general theorem of ecosystem nutrient response

We now consider how different functional relationships between productivity and resource availability determine the shape of the resource response efficiency-nutrient availability curves. From two reasonable biological assumptions, we prove a theorem that resource response efficiency is unimodal along a gradient of a limiting resource. This is in contrast to Vitousek's original (1982, 1984) findings that nutrient use efficiency appears to increase monotonically with declining nutrient availability, uptake, or circulation in litterfall. We use an intuitive and graphical approach below, but this theorem is proved in formal mathematical terms in the Appendix. In our previous paper (Bridgham et al. 1995), we used a Monod model to demonstrate the behavior of this theorem, but here we demonstrate that the theorem holds for any function given two simple assumptions. The theory also holds for other limiting resources besides nutrients, such as water and light. We also show that nutrient use efficiency must follow the same dynamics as nutrient response efficiency at high nutrient availability (or uptake), but it may or may not follow dynamics similar to nutrient response efficiency at low nutrient availability. Finally, we suggest some statistical tests of these patterns that avoid the problems of autocorrelation raised by Knops et al. (1997).

Five different relationships between productivity and resource availability along with the corresponding relationship between resource response efficiency and resource availability are shown in Fig. 1. Figure 1a is the null model, namely that productivity is unrelated to resource (nutrient) availability. One might also expect this for extremely low-nutrient environments, where plants have a low physiological potential to respond to increased nutrient availability (Chapin et al. 1986). By applying Eq. 4 to Fig. 1a and mentally drawing lines from the origin to the horizontal line in Fig. 1a, the

**Fig. 1 a,c,e,g,i** Net primary production ( $P$ ) as a function of resource availability ( $R$ ).

**b,d,f,h,j** Resource response efficiency ( $E$ ) as a function of resource availability.  $R_{\min}$  is the minimum amount of resource that will yield positive growth.

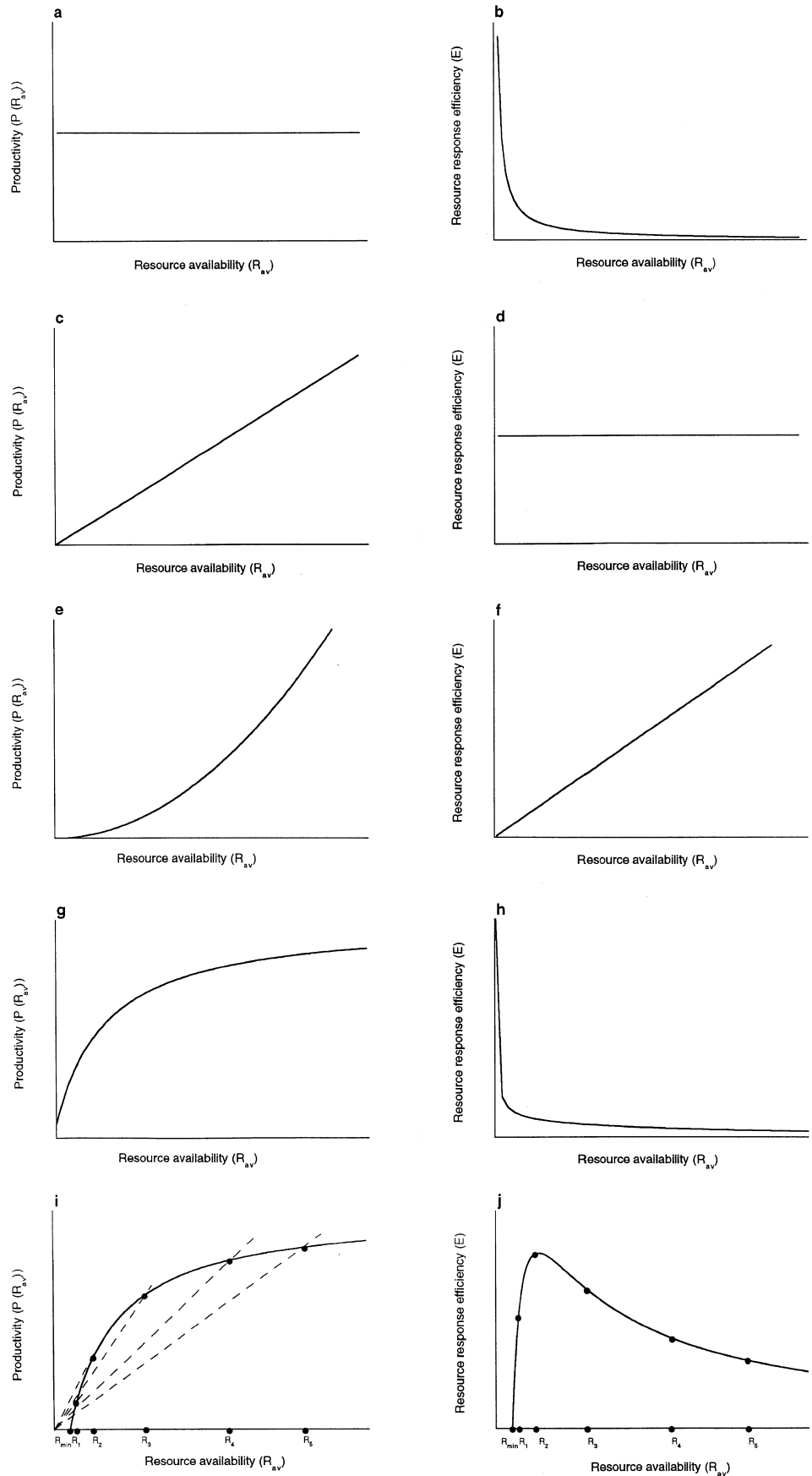
**a,b** Hypothesis: productivity and resource availability are unrelated. Resource response efficiency increases monotonically with declining resource availability.

**c,d** Hypothesis: productivity increases linearly with increasing resource availability. Resource response efficiency is then constant across a resource availability gradient.

**e,f** Hypothesis: resource response efficiency increases linearly with resource availability, requiring productivity to increase exponentially.

**g,h** Hypothesis: productivity increases with resource availability to a horizontal asymptote, but with a positive  $y$ -intercept. Resource response efficiency then increases monotonically with declining resource availability.

**i,j** Hypothesis: Productivity increases with resource availability to a horizontal asymptote, but there is a minimal resource availability at which any production can occur. Resource response efficiency is then unimodal (see Appendix for proofs). See text for explanation of lines radiating from the origin.



reader can see that the slope of Eq. 4 (resource response efficiency at a given level of resource availability) will change as shown in Fig. 1b. If productivity increases linearly with resource availability (Fig. 1c), then resource response efficiency is constant with increasing resource availability (Fig. 1d) because the slope of the functional response in Fig. 1 is the same as the slope of Eq. 4. Conversely, if resource response efficiency increases at a constant rate with increasing resource availability (Fig. 1f), then productivity increases exponentially with increasing resource availability (Fig. 1e). If productivity saturates with increasing resource availability but is positive even at zero resource (i.e., has a positive  $y$ -intercept; Fig. 1g), then we again obtain a monotonic increase in resource response efficiency with declining resource availability (Fig. 1h).

Note that a monotonic increase in resource response efficiency with decreasing nutrient availability results from both a null relationship between productivity and resource availability (Fig. 1a) and a saturating response with a positive  $y$ -intercept (Fig. 1g). This is the response inferred by Vitousek (1982, 1984) from his graphs of litterfall nutrient use efficiency/nutrient circulation in litterfall. Thus, a monotonic increase in resource response efficiency with decreasing availability is ambiguous with respect to the corresponding relationship between productivity and resource availability. Secondly, both hypotheses are of limited biological interest. Figure 1a is probably only relevant to very infertile ecosystems composed of plants that are physiologically incapable of responding to increasing nutrient availability (Chapin et al. 1986), or to ecosystems that are already nutrient-saturated environments. Furthermore, a positive productivity at zero availability of a limiting resource (Fig. 1g) makes no sense. The other cases considered so far (Fig. 1c,e) may reflect only a limiting range of resource availability, and clearly cannot continue unbounded, otherwise we end up with infinite productivity at infinite resource availability.

This leaves us with the final case (Fig. 1i,j), which is general and based on biologically reasonable assumptions. Our first assumption is the law of diminishing returns; i.e., at some finite amount of resource availability, a resource is no longer limiting and further increases in that resource will cause no further increase in production. This assumption states that the productivity-resource availability graph in Fig. 1i approaches a limit of a horizontal asymptote. We do not consider the case of negative growth at toxic resource concentrations. The second assumption is that net primary productivity ( $P$ ) is zero at some minimum positive resource availability ( $R_{\min}$ ) and that productivity increases if resource availability is greater than  $R_{\min}$ . In Fig. 1i, this assumption states that the  $x$ -intercept (i.e.,  $R_{\min}$ ) must be positive.

That net growth must be positive and growth increment must decline with increased availability of a limiting resource (assumption 1) are biologically obvious. It is also clear that diminishing nutrient response efficiency

with increasing nutrient availability (or diminishing nutrient use efficiency with increasing nutrient uptake) must lead to a horizontal asymptote for production.

The concept of a minimum positive resource availability at which net production must be zero (i.e.,  $R_{\min}$  in assumption 2) may not at first seem intuitively obvious. However, there are many well-known examples of a minimum resource availability being required before net growth can begin – e.g., the photosynthetic compensation point of light (Larcher 1980). This assumption is also implicit in the  $R^*$  theory of Tilman (1982), as well as the minimal cell quota for algae proposed by Droop (1973), and has also been demonstrated for tree response to increased nutrient availability by Mitchell and Chandler (1939).

We apply Eq. 4 to the productivity-resource availability relationship in Fig. 1i by drawing lines from the origin to several key points on the curve. This results in the corresponding changes in the slope of Eq. 4 (resource response efficiency), which are graphed in Fig. 1j. There are two important points to be drawn from Fig. 1j. First, if the two assumptions are met, then resource response efficiency is unimodal along resource availability gradients. Second, the maximum resource response efficiency occurs at the level of resource availability where a line drawn from the origin is tangent to the productivity-resource availability function. This theorem, proved formally in the Appendix, shows that, so long as the two assumptions are satisfied, the growth function  $P(R_{\text{av}})$  requires the corresponding unimodal resource response efficiency function  $E(R)$  in Fig. 1j, regardless of the specific function used for  $P(R_{\text{av}})$ .

The shape of the resource response efficiency function is also intuitive. It is clear that resource response efficiency at  $R_{\min}$  must be zero because productivity is zero. At some small increment of resource availability above  $R_{\min}$ , efficiency is positive ( $R_1$  in Fig. 1j). Therefore, resource response efficiency increases as resource availability increases from  $R_{\min}$  to  $R_1$ . The law of diminishing returns states that the increment of production must also decrease as resource availability approaches saturation and becomes non-limiting. Further increments in resource availability cause smaller and smaller increases in production. Therefore, resource response efficiency must decrease as resource availability increases near the limit of the horizontal asymptote of production response (from  $R_2$  to  $R_4$  in Fig. 1j). Thus, maximum resource response efficiency must occur at some point between  $R_{\min}$  and some resource level at which plant growth is no longer limited (Fig. 1j).

Bridgham et al. (1995) verified the patterns of saturating response with positive  $R_{\min}$  (Fig. 1i) and the corresponding unimodal response efficiency curves (Fig. 1j) for litterfall and aboveground net primary production relative to numerous measures of soil nutrient availability, such as total phosphorus, resin-sorbed phosphorus, isotopically exchangeable phosphorus, extractable phosphorus, and nitrogen mineralization.

These empirical tests were based on data from pocosin wetlands, old-growth conifer and hardwood forests, and the data set of Vitousek (1984) on tropical forests augmented with these two other data sets.

Now let us consider the dynamics of resource use efficiency along a resource uptake axis. Vitousek (1982, 1984, 1997); Knops et al. (1997); and Bridgham et al. (1995) considered the resource uptake axis to also represent a resource availability axis, and all three previously considered that resource use efficiency and resource response efficiency would have similar dynamics along a resource availability gradient.

Our assumption that the productivity curve along a resource availability axis must approach a horizontal asymptote at non-limiting resource availability (Fig. 1g,i) also holds for productivity along a resource uptake axis. Thus, resource use efficiency must also decrease as non-limiting resource levels are attained in the environment. In these regions of intermediate to high resource availability and uptake, our model in Fig. 1i,j agrees qualitatively with that of Vitousek (1982, 1984).

However, the dynamics of resource use efficiency at very low resource availability remain unclear. If resource uptake must also be zero at zero productivity, then resource use efficiency becomes undefined if the production-resource uptake curve passes through the origin. However, Redfield (1958), Droop (1973), Bridgham et al. (1995) and Elser et al. (1996) suggest that simple stoichiometric ratios of biologically important molecules require a minimum amount of each nutrient in specific proportions before a unit of a biologically essential molecule – protein for example – can be made. This stoichiometry imposes an  $R_{\min}$  at the molecular level (i.e., the amount of nutrients required for a single organism to exist). However, productivity at  $R_{\min}$  is greater than zero because organisms occur in incremental units. Therefore, the production-resource uptake curve may not pass through the origin but instead must stop at the smallest unit of production and the corresponding unit of uptake required to produce an organism.

At this point, without further assumptions, we cannot derive a unique theoretical foundation for the dynamics of resource use efficiency at very low resource availability, in contrast to our theorem of resource response efficiency. Resource use efficiency could continue to increase with lower resource availability to the limits of the stoichiometry of biological molecules (Vitousek's model with a stopping rule), or it could decrease with diminishing resource availability, similar to resource response efficiency as demonstrated here and in Bridgham et al. (1995).

If resource response efficiency decreases (the model of Bridgham and colleagues) and resource use efficiency increases (the Vitousek model) at low nutrient availability, then the mass balance in Eqs. 1 and 2 says that this must be due to lower resource uptake efficiency. There are numerous possible mechanisms for such a result. Studies have found that microbes are much more

competitive for nutrients than plants at very low nutrient availability (Richardson and Marshall 1986; Walbridge 1991), and the geochemical sorption sink for phosphorus can be very strong in highly weathered, low-phosphorus soils. Additionally, the diffusion rate to the root surface is the rate-limiting step in nutrient uptake by plants (Chapin 1980), and this would be expected to become an increasing constraint at low nutrient availability. Under these conditions, plants would be less effective at competing for the potentially available nutrient pool.

However, empirical data in Bridgham et al. (1995) from numerous terrestrial ecosystems suggests that nutrient response efficiency and nutrient use efficiency both decrease at very low nutrient availability. This would be expected if, at low nutrient availability, greater proportions of production were allocated to root and leaf tissue at the expense of woody tissue. Since wood has low nutrient concentrations, increased proportional allocation to leaves and roots under extreme nutrient limitations would automatically decrease nutrient use efficiency (Grubb 1989). This mechanism would yield the same sort of unimodal response of nutrient use efficiency along nutrient uptake gradients as demonstrated here for nutrient response efficiency along nutrient availability gradients.

Although the empirical identification of  $R_{\min}$  for different resources, organisms, and ecosystems poses experimental challenges, the assumption of a required  $R_{\min}$  is biologically reasonable and poses no theoretical difficulties. The potential departure of the behaviors of nutrient use efficiency and nutrient response efficiency occurs only at extremely low nutrient availability, so experimental efforts should focus on such nutrient poor ecosystems. Nutrient use efficiency can still follow the Vitousek model, but this requires additional assumptions (i.e., stoichiometric constraints) to bound the increase in nutrient use efficiency as nutrient uptake declines. However, nutrient use efficiency need not necessarily follow the Vitousek model, and in fact we have shown that in some cases it does not (Bridgham et al. 1995).

Before moving on to a new implication of our theorem, we wish to suggest appropriate statistical tests for distinguishing among the different patterns in Fig. 1, while avoiding the problems of autocorrelation raised by Knops et al. (1997). Each of the patterns of resource response efficiency in the right-hand panels of Fig. 1 is autocorrelated because  $P/R_{\text{av}}$  is plotted against  $R_{\text{av}}$ . Autocorrelation does not mean that they are biologically uninteresting, only that statistical tests of these patterns are problematic. However, the productivity-resource availability relationships are not autocorrelated. Therefore, one should statistically test the slopes and  $y$ -intercepts of empirical relations between productivity and resource availability to verify one of the various alternative hypotheses in the left-hand panels of Fig. 1 and disprove the rest. Equation 4 and the proofs in the Appendix rigorously associate each pattern of resource

response efficiency with a particular pattern of productivity along resource availability gradients. The corresponding efficiency curve on the right-hand panels is then required. Note that no statistical test need or should be done on the efficiency curves in the right-hand panels. We have argued above that only Fig. 1i,j apply generally across a broad range of resource availability. Therefore, although the other hypotheses (Fig. 1a–h) may be statistically verified within a limited range of data for resource availability, extrapolation of such conclusions outside this range leads to problems of either infinite production or infinite resource response efficiency and so are biologically flawed.

If, however, one wishes to determine how resource use efficiency ( $P/R_{ac}$ ) changes with resource availability, then one could statistically test directly each of the curves on the right-hand panels of Fig. 1. In this case, since there is no autocorrelation between  $P/R_{ac}$  and  $R_{av}$ , such statistical tests would be valid. The corresponding curves in the left-hand panels would then graph productivity against resource availability as a consequence of the changes in resource use efficiency along resource availability gradients. However, in contrast to resource response efficiency curves, the left-hand panels are now autocorrelated, as demonstrated in Eq. 3. Thus, no statistics should be done on the left-hand panels for resource use efficiency. Furthermore, it is essential that nutrient availability be measured directly, and nutrient uptake not be used as its surrogate, to avoid problems with autocorrelation in examination of nutrient use efficiency. Reich et al. (1997) provide an example of such a test for productivity /litterfall N (N use efficiency) against N mineralization (N availability) in hardwood and conifer stands. Within the range of their data, N use efficiency is not correlated with N mineralization (our Fig. 1d), which then implies that productivity and uptake increase linearly with increasing N mineralization (our Fig. 1c), which they also find.

### New implications of the nutrient response efficiency theorem

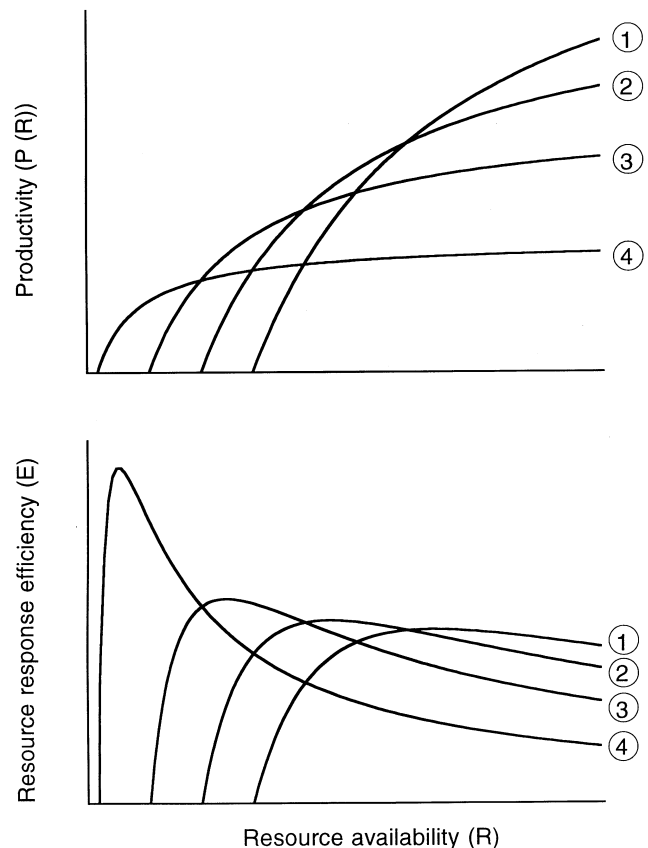
Our resource response efficiency theorem is logically consistent with the known response of production to increasing resource availability. As required by the theorem, we have shown examples of ecosystems which are inefficient at using nutrients at low nutrient availability (Bridgman et al. 1995). Nevertheless, such ecosystems appear to be quite rare. Why is this phenomenon of declining nutrient response efficiency at low levels of nutrient availability so rare, and if it is, could we then simply dismiss it as a special case?

We suggest that the theorem itself contains the seeds of an answer if we add an additional assumption that maximum productivity at high levels of nutrient saturation is positively correlated with  $R_{min}$ . That is, there may be a tradeoff between high productivity at high levels of nutrient availability and ability to survive

at low levels of nutrient availability. Numerous examples in the literature suggest that such a tradeoff happens in both terrestrial (Mitchell and Chandler 1939; Chapin et al. 1986) and aquatic ecosystems (Droop 1973; Sterner and Hessen 1994) and is associated with species replacement along nutrient availability gradients.

Now consider an ecosystem or a species that has a high productivity at high levels of nutrient availability, but also has a high  $R_{min}$ . At a nutrient availability  $R < R_{min}$ , this species or ecosystem cannot exist, but some other species or ecosystem with a lower  $R_{min}$  could. Given the correlation between  $R_{min}$  and maximum productivity, the two growth curves will cross (Fig. 2a). Now consider a third species or ecosystem that can survive at a still lower  $R_{min}$  but has a lower maximum productivity than either of the other two species or ecosystems (Fig. 2a). It is obvious that we can continue this progression *ad infinitum*.

Studies on algal response to nutrient availability typically use Monod functions for the relationships in Fig. 2a. The species replacement shown in Fig. 2a and observed in algal systems (Droop 1973; Sterner and Hessen 1994) is obtained by decreasing the ratio of



**Fig. 2 a** Net primary productivity ( $P$ ) response of four plant species or ecosystems to change in resource availability ( $R$ ). It is assumed that species or ecosystems with higher maximum  $P$  have a higher  $R_{min}$ . **b** Resource response efficiency ( $E$ ) of these four species or ecosystems to change in resource availability

maximum productivity ( $P_{\max}$ ) to the half-saturation constant ( $k_M$ ) of Monod functions.

These prior studies have not framed the problem in terms of changes in nutrient response efficiency along nutrient availability gradients. Our nutrient response efficiency theorem allows us to specify the sequence of efficiency curves along the nutrient availability gradient (Fig. 2b) that are consistent with the productivity response curves in Fig. 2a. In every case, as nutrient availability declines, one species or ecosystem that is most efficient at higher levels of nutrient availability is replaced by another that is more efficient than the preceding one, or perhaps the preceding one dies because it cannot physiologically adjust to declining resource response efficiency with increasing resource limitations. If the switch from one species or ecosystem to another occurs just below the peak response efficiency of that species with greater  $R_{\min}$ , then it would be rare to find the decline in response efficiency with decreasing nutrient availability within a given ecosystem or species – it would simply be replaced by another, more efficient one. It is only for species or ecosystems that can grow at very low nutrient availabilities that we can detect the lower decline in nutrient response efficiency that distinguishes our model from that of Vitousek.

Again, extremely infertile ecosystems are critical areas where we should focus our research to further our understanding of nutrient efficiency. We demonstrated decreasing nutrient response and nutrient use efficiency with lower nutrient availability, as well as species and ecosystem replacement, along declining nutrient-availability gradients in North Carolina peatlands and in Wisconsin forests (Bridgham et al. 1995). Additionally, we showed that the nutrient-poor tropical forests included in the paper of Vitousek (1994) also have decreasing nutrient use efficiency with lower nutrient availability.

Vitousek (1982, 1984) has also empirically demonstrated species or ecosystem replacement along declining nutrient availability gradients in his model. However, this is a purely phenomenological finding that is not required by his model – different species or ecosystems could also be randomly distributed along the Vitousek model line or replace one another arbitrarily. With the additional assumption of a correlation between  $R_{\min}$  and maximum productivity, it is a logical consequence of our model and the nutrient response efficiency theorem proposed here. Because our theorem unifies changes in efficiency with changes in productivity along nutrient availability gradients without problems of unbounded efficiency at the lower end, and because it predicts that ecosystems should follow replacement sequences along nutrient availability gradients, we feel that it is more fundamental than the original Vitousek (1982, 1984) model, regardless of the criticisms of Knops et al. (1997) toward the latter model. It also sets up the testable hypothesis that the various components of nutrient efficiency in ecosystems, as detailed in Eqs. 1–4, may respond differently to changing resource availability gradients.

## Conclusion

We agree with Vitousek (1997) that it is time that the debate on nutrient use efficiency progressed past use of litterfall indices for productivity and nutrient uptake. There is a great need for empirical studies that quantitatively measure each of the terms in Eqs. 1–4 in a variety of plant species and ecosystems. In a more general sense, it is paramount that reasonable biological models be fit to data and the theoretical implications be understood in empirical ecosystem studies. Empiricists often criticize models that are divorced from real world data, but problems also arise when data are divorced from theory.

**Acknowledgements** We thank Robert Sterner for his insights on nutrient efficiency in ecosystems. His comments substantially improved an earlier draft of this manuscript. Sterner also hosted an all-day bagels and coffee discussion on efficiency in ecological systems, in which we benefited from insightful comments by Yosef Cohen, Kathy McTavish, John Schampel, and Andrea Plevan. Kathy McTavish and Göran Ågren also gave insightful comments on the proofs in the Appendix. Peter Vitousek, Jean Knops, Knute Nadelhoffer, and an anonymous reviewer made valuable comments on a previous manuscript, which helped us greatly.

## Appendix

A general theorem of nutrient response efficiency in relation to production and nutrient availability

Here we provide two proofs of our theorem. Proof 1 relies on the assumptions of a minimal resource required before productivity can begin as well as the assumption of a saturating response of productivity to increasing resource availability, and uses small discrete changes in  $P$  and  $R$ . Proof 2 also relies on the assumption of a saturating response, but instead replaces the assumption of a minimal resource availability with the more general assumption that productivity must decline to zero faster than resource availability, and uses continuous changes in  $P$  and  $R$ . Proof 2 is more general in that it also applies to sigmoidal as well as Monod-type functions with an  $R_{\min}$ , but both prove that resource response efficiency is unimodal along resource availability gradients.

### Proof 1

#### Theorem

For every differentiable growth function,  $P(R)$ , which is continuous in the interval  $[0 \leq R < \infty]$  and which satisfies the following two conditions:

A.  $P(R) > 0$  for all  $R > R_{\min}$  and  $P(R) < 0$  for all  $R < R_{\min}$ , where  $R_{\min}$  is a minimum positive resource availability and  $R$  is a real number; and

B.  $\lim \Delta P(R) = 0$  in the interval  $[R_{\min} < R < \infty]$ , (i.e., the law of diminishing returns); as  $R \rightarrow \infty$  the corresponding efficiency function,  $E(R) = P(R)/R$ , increases to a maximum then declines in the interval  $[R_{\min} < R < \infty]$ .

#### Proof

$P(R_{\min}) = 0$  by condition A and therefore  $E(R_{\min}) = 0$ . Now increment  $R$  by a small amount  $\Delta R$  to produce  $R_1$  (Fig. 1i). Then

$P(R_1) > P(R_{\min})$  by condition A and  $E(R_i) > 0$ . Therefore  $\Delta E_{[R_{\min}, R_1]} > 0$ . Now consider some arbitrarily large  $R_2 = R_{\min} + d\Delta R$ , where  $d$  is a large integer. Increment  $d$  by 1 to produce  $R_3$ , then increment  $d$  by 2 to produce  $R_4$ . By condition B,  $\Delta P_{[R_2, R_3]} > \Delta P_{[R_3, R_4]}$  and eventually  $\Delta P \rightarrow 0$  with further increments to  $R$ . However, the denominator ( $R$ ) of  $E(R)$  continues to increase by a constant amount ( $\Delta R$ ). Therefore,  $E(R_{\min} + nd\Delta R) > E(R_{\min} + (n+1)d\Delta R)$  for some large  $n$ . Therefore,  $\Delta E < 0$  in the interval  $[R_{\min} + nd\Delta R, R_{\min} + (n+1)d\Delta R]$ . Since  $\Delta E_{[R_{\min}, R_1]} > 0$  and  $\Delta E_{[R_{\min} + nd\Delta R, R_{\min} + (n+1)d\Delta R]} < 0$ , then  $\Delta E = 0$  somewhere in the interval  $[R_{\min}, R_{\min} + (n+1)d\Delta R]$ .  $E(R)$  must therefore increase to a maximum and then decline in this same interval. Q.E.D.

Proof 2

*Theorem*

For every differentiable growth function,  $P(R)$ , which is continuous in the interval  $[0 \leq R < \infty]$  and which satisfies the following two conditions:

A.  $\lim_{R \rightarrow 0} P(R) = 0$  and  $P(R) \rightarrow 0$  faster than  $R \rightarrow 0$  where  $R$  is a real number; and

B.  $\lim_{R \rightarrow \infty} \frac{\partial P}{\partial R} = 0$  (i.e., the law of diminishing returns); the corresponding efficiency function,  $E(R) = P(R)/R$ , increases to a maximum then declines in the interval  $[R_{\min} < R < \infty]$ .

*Proof*

Condition A implies that there exists an  $R_{\min} > 0$  such that  $P/R_{\min} = 0$ . Condition B implies that  $P/R \rightarrow 0$  as  $R \rightarrow \infty$ . For all intervening  $R$  in the interval  $[R_{\min}, \infty]$ ,  $R > 0$  and  $P > 0$ , so  $P/R > 0$ .  $P/R$  is the resource-dependent slope of the function:

$$P(R) = (P/R)_R \cdot R + 0$$

which generates a family of lines between the origin and every point on  $P(R)$ . Since  $P/R = 0$  for  $R_{\min}$  and  $\infty$  and is  $> 0$  in the open interval  $(R_{\min}, \infty)$ , it must reach a maximum in the closed interval  $[R_{\min}, \infty]$ . Since the slope of  $P(R)$  in the above equation increases to that maximum then decreases in that interval, then by Rolle's Theorem the change in the slope must be zero somewhere in that interval. Therefore the change in efficiency with respect to resource availability is unimodal. Q.E.D.

## References

- Aerts R, Caluwe H de (1994) Nitrogen use efficiency of *Carex* species in relation to nitrogen supply. *Ecology* 75:2362–2372
- Ågren GI (1983) Nitrogen productivity of some conifers. *Can J For Res* 13:494–500
- Atchley WR, Anderson D (1978) Ratios and the statistical analysis of biological data. *Syst Zool* 27:78–83
- Atchley WR, Gaskins CT, Anderson D (1976) Statistical properties of ratios. I. Empirical results. *Syst Zool* 25:137–148
- Berendse F, Aerts R (1987) Nitrogen-use-efficiency: a biologically meaningful definition? *Funct Ecol* 1:293–296
- Bridgham SD, Pastor J, McClaugherty CA, Richardson CJ (1995) Nutrient-use efficiency: a litterfall index, a model, and a test along a nutrient-availability gradient in North Carolina peatlands. *Am Nat* 145:1–21
- Chapin FS III (1980) The mineral nutrition of wild plants. *Annu Rev Ecol Syst* 11:233–260
- Chapin FS III, Vitousek PM, Van Cleve K (1986) The nature of nutrient limitation in plant communities. *Am Nat* 127:48–58
- Droop MR (1973) Some thoughts on nutrient limitation in algae. *J Phycol* 9:264–272
- Elser JJ, Dobberfuhl DR, MacKay NA, Schampel JH (1996) Organism size, life history, and N:P stoichiometry. *Bio Science* 46:674–684
- Grubb PR (1989) The role of mineral nutrients in the tropics: a plant ecologist's view. In: Proctor J (ed) *Mineral nutrients in tropical forest and savanna ecosystems*. (British Ecological Society special publication 9) Blackwell, Oxford, pp 417–440
- Knops JMH, Koenig WD, Nash TH III (1997) On the relationship between nutrient use efficiency and fertility in forest ecosystems. *Oecologia* 110:550–556
- Larcher W (1980) *Physiological plant ecology*, 2nd edn. Springer, Berlin Heidelberg New York
- McGraw JB, Chapin FS III (1989) Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. *Ecology* 70:736–749
- Miller PC (1979) Quantitative plant ecology. In: Horn DJ, Stairs GR, Mitchell RD, (eds) *Analysis of ecological systems*. Ohio State University Press, Columbus, pp 179–231
- Mitchell HL, Chandler RF (1939) The nitrogen nutrition and growth of certain deciduous trees of northeastern United States (Black Rock Forest Bulletin 11). Cornwall on the Hudson, New York
- Packard GC, Boardman TJ (1988) The misuse of ratios, indices, and percentages in ecophysiological research. *Physiol Zool* 61:1–9
- Redfield AC (1958) The biological control of chemical factors in the environment. *Am Sci* 46:205–221
- Reich PD, Grigal D, Aber JD, Gower ST (1997) Nitrogen mineralization and productivity in 50 hardwood and conifer stands on diverse soils. *Ecology* 78:335–347
- Richardson CJ, Marshall PE (1986) Processes controlling movement, storage, and export of phosphorus in a fen peatland. *Ecol Monogr* 56:279–302
- Shaver GR, Melillo JM (1984) Nutrient budgets of marsh plants: efficiency concepts and relation to availability. *Ecology* 65:1491–1510
- Serner RW, Hessen DO (1994) Algal nutrient limitation and the nutrition of aquatic herbivores. *Annu Rev Ecol Syst* 25:1–29
- Tilman D (1982) *Resource competition and community structure*. Princeton University Press, Princeton
- Vitousek PM (1982) Nutrient cycling and nutrient use efficiency. *Am Nat* 119:553–572
- Vitousek PM (1984) Litterfall, nutrient cycling, and nutrient limitation in tropical forests. *Ecology* 65:285–298
- Vitousek PM (1997) On regression and residuals: response to Knops et al. (1997) *Oecologia* 110:557–559
- Walbridge MR (1991) Phosphorus availability in acid organic soils of the lower North Carolina coastal plain. *Ecology* 72:2083–2109