Oecologia (1997) 110:550–556

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On the relationship between nutrient use efficiency and fertility in forest ecosystems

Received: 22 January 1996 / Accepted: 26 December 1996

Abstract The concept of nutrient use efficiency is central in understanding ecosystem functioning because it is the step in which plants can influence the return of the nutrients to the soil pool and the quality of the litter. There are several ways to define nutrient use efficiency, but a common way within ecosystem ecology is as the ratio of litterfall production per unit nutrient to the litterfall nutrient content. However, this ratio is not a valid measurement to examine nutrient use efficiency in relationship to ecosystem fertility because there is a strong autocorrelation between litterfall dry mass per unit of nutrient and the amount of nutrients. More appropriate statistical analysis of the relationship between the fertility of ecosystems and the amount of nutrients in the litterfall are inconclusive, but indicate that, at least in some cases, there is (1) no pattern, (2) higher nutrient use efficiency at intermediate-fertility sites or (3) higher efficiency at higher-fertility sites. There is, however, no indication that nutrient use efficiency is greater in nutrient-poor ecosystems. This conclusion has important consequences for ecosystem nutrient cycling. Given the lack of a clear, consistent relationship between site fertility and litterfall nutrients, there is little likelihood that such a feedback mechanism plays an important role in ecosystem nutrient cycling.

Key words Nutrient use efficiency · Nutrient cycling · Litterfall · Litter quality

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The patterns of nutrient use efficiency in forest ecosystems have important implications for ecosystem productivity and nutrient cycling. Litter quality is partly dependent on the nutrient use efficiency of forest trees and the decomposition of plant material is strongly influenced by the quality of the litter. This can lead to a feedback on litter quality, intensifying the nutrient stress in nutrient-poor environments and limiting the productivity of ecosystems (Vitousek 1982; Shaver and Melillo 1984). Recently, Bridgham et al. (1995) developed a model describing nutrient use efficiency along a nutrient availability gradient and Silver (1994) found a significant, positive relationship between indexes of soil P and plant nutrient use efficiency. Nutrient use efficiency in both these studies was defined as the ratio of litterfall production to litterfall nutrient content. This index, first developed by Vitousek (1982) extended earlier work by Chapin (1980) and proposed that plants in nutrient-poor forest ecosystems are able to produce relatively more organic matter per unit of mineral nutrient taken up than can plants from nutrient-rich habitats.

More recently, Berendse and Aerts (1987) showed that there is a tradeoff between nitrogen productivity and the mean residence time of nitrogen in plants, the two components of nitrogen use efficiency. Based on this relationship, they proposed defining nitrogen use efficiency as the product of these two components. Although a valuable advance, this definition does not address the relationship between nutrient use efficiency and ecosystem fertility. It is this latter relationship, discussed by Vitousek (1982) and many subsequent authors including Pastor et al. (1984), Gholz et al. (1985), Birk and Vitousek (1986), Silver (1994) and Bridgham et al. (1995), that we focus on here.

Because long-lived perennial plants can withdraw nutrients from senescing leaves and other plant parts prior to abscission, Vitousek found that the nutrient use efficiency for a forest correlates inversely with the weighted average nutrient concentration in the aboveground litterfall, root turnover and the organic matter increment in the vegetation (Vitousek 1982). Specifically, he found that a third-order polynomial (forced through the origin) explained more of the variation than a straight line through the origin, which is the expected relationship for litterfall dry mass if nutrient use efficiency does not vary with the amount of nutrient circulated. He visualized this by plotting the inverse of the nutrient concentration in fine litterfall (littermass/nutrient in the litterfall) against the nutrient deposition in the litterfall, yielding a strong inverse relationship that he interpreted as supporting this hypothesis (Fig. 1A). Vitousek's paper (1982) has been widely cited as evidence that there is a strong relationship between availability and nitrogen concentration in aboveground litter (Aber and Melillo 1991) and similar analyses confirmed this relationship (Pastor et al. 1984; Birk and Vitousek 1986; Bridgham et al. 1995). However, the analysis in the original and subsequent articles is problematic on at least two statistical grounds. First, a polynomial regression forced through the origin will always explain more variation than a straight line. Thus, the fact that a polynomial regression explains more variation is not a convincing argument that rejects the hypothesis that there is no relationship between nutrient use efficiency and the amount of nutrient cycling. Secondly, there is a strong autocorrelation between the amount of litterfall and the amount of nutrient deposition in litterfall (Vitousek 1984; Mayer and Rodà 1992; Bridgham et al. 1995). This autocorrelation is more serious than prior investigators have assumed because a variable is plotted against the inverse of the same variable causes a negative relationship by default (Pearson 1897; Atchley et al. 1976; Peters 1991). For example, consider two random datasets x and y, and plot z [calculated as $z = (y/(1000 * x))$], against x – a negative relationship between z and x results (Fig. 1C). Atchley et al. (1976) explored this correlation and found that it depended on the ratio of the coefficient of variation for x and y [i.e. (CV_x/CV_y)] with the highest autocorrelation when the ratio of the coefficients of variation is lowest. The ratio of the coefficients of variation for the tropical dataset of Vitousek (1984) are 0.7 for N and 0.5 for both P and Ca. This results in an expected negative autocorrelation (on a scale from 0 to 1) of approximately 0.9 for N and 0.8 for P and Ca. Consequently, little of ecological significance can be automatically inferred from the negative relationship between the inverse of N concentration in the litterfall and the nutrient deposition in the litterfall shown in Fig. 1A.

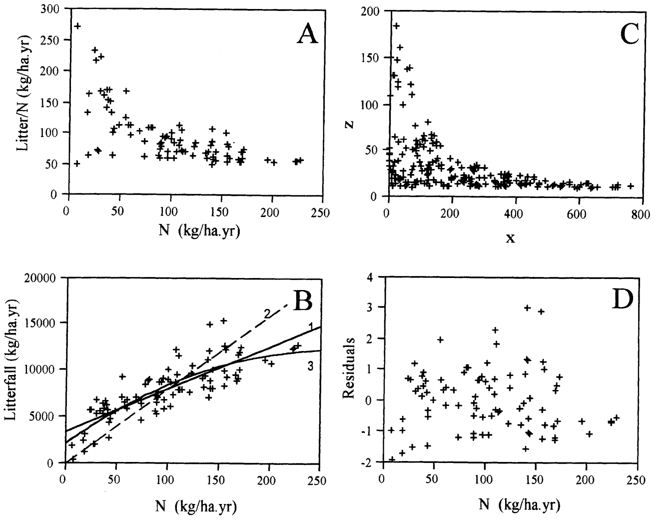

Fig. 1A–D Plots of the litterfall divided by nitrogen and the nitrogen mass (**A**), the litterfall mass and the mass of nitrogen in the litterfall (**B**) with three regression lines (1 = straight regression, 2 = straight regression through the origin and 3 = second-order polynomial regression), two random datasets (**C**), calculated as x = (1000 * random number), y = (random number), $z = (y/x)$ and the residuals of a regression of the litterfall mass against the amount of nitrogen in the litterfall versus the amount of nitrogen in the litterfall (**D**). All data are from Vitousek (1984), except the random data in **C**

Nutrient use efficiency: a reanalysis

One method of avoiding the autocorrelation problem is to perform a regression between the litter mass and the nutrient mass and then analyze the residuals against the variable of interest (Atchley et al. 1976; Atchley and Anderson 1978). We performed this procedure on four datasets: the tropical dataset provided by Vitousek (1982), an extended tropical dataset (Vitousek 1984), a more recent, larger global dataset (Vogt et al. 1986) and a dataset of 40 trees within one stand of *Quercus douglasii* in California studied by Knops et al. (1996). However, there are at least three approaches to this analysis. We performed (1) a straight regression, (2) a straight regression through the origin and (3) a second-order polynomial regression.

Straight regression

We examined the relationship between the residuals and the amount of nitrogen, phosphorus and calcium in the litter (Table 1). None of the correlations between the residuals and nutrient levels approached significance for any dataset. Identical results are obtained if the data are log transformed.

Straight regression through the origin

The regression line should theoretically go through the origin, but we found a significant positive intercept in all but one case. Forcing the regression through the origin therefore is not a good fit for the regression slope and results by default in a negative relationship between the residuals and the variable of interest for all elements. In order to examine if the residuals are significantly different from the artifactual negative relationship that occurs as a consequence of forcing the regression through the origin, we performed randomization tests. In each case, we constructed random datasets by cal-

Table 1 Directional gradients (β) ± standard error (SE β) and the significance for regressions of the litter amount against the amount of nutrients in the litter, and the residuals of this regression against the amount of nutrients in the litter

Dataset	Nutrient	*n*	Litter against nutrient intercept				Residuals against nutrient
				P	Slope	*P*	*P*
Vitousek 1984[a]	N	90	3303 ± 386	0.000	45.7 ± 3.4	0.000	0.994
	P	91	5722 ± 414	0.000	443.2 ± 62.4	0.000	0.962
	Ca	93	5968 ± 425	0.000	21.5 ± 3.5	0.000	0.962
Vogt et al. 1986[a]	N	192	2013 ± 137	0.000	50.0 ± 2.3	0.000	0.953
	P	138	1545 ± 344	0.000	715.8 ± 77.3	0.000	0.992
Knops 1994[b]	N	40	10.3 ± 8.7	0.243	134.9 ± 7.4	0.000	0.985
	P	40	21.1 ± 7.6	0.008	367.0 ± 18.7	0.000	0.992
Vogt et al. 1986 Divided by climate							
Tropical	N	25	4491 ± 1016	0.000	33.7 ± 7.6	0.000	0.981
	P	18	7634 ± 1329	0.000	342.2 ± 187.3	0.086	0.933
Warm temperate	N	33	2011 ± 409	0.000	69.9 ± 11.2	0.000	0.803
	P	26	2869 ± 389	0.000	513.0 ± 104.3	0.000	0.924
Cold temperate	N	115	1884 ± 156	0.000	47.8 ± 3.8	0.000	0.871
	P	81	1354 ± 256	0.000	474.6 ± 62.1	0.000	0.975
Boreal	N	17	1315 ± 501	0.019	47.9 ± 16.9	0.012	0.967
	P	11	1069 ± 523	0.071	784.8 ± 199.4	0.003	0.948
Vogt et al. 1986[a] Divided by leaf duration							
Deciduous	N	73	2145 ± 286	0.000	49.9 ± 3.7	0.000	0.928
	P	52	2046 ± 968	0.040	767.4 ± 182.6	0.000	0.994
Evergreen	N	119	1993 ± 152	0.000	48.4 ± 3.2	0.000	0.925
	P	86	1623 ± 255	0.000	542.0 ± 66.2	0.000	0.986
Vogt et al. 1986 Divided by leaf type							
Broad leaved	N	87	2275 ± 263	0.000	47.7 ± 3.2	0.000	0.958
	P	58	2664 ± 837	0.002	652.9 ± 154.4	0.000	0.979
Needle leaved	N	105	1871 ± 173	0.000	51.9 ± 5.1	0.000	0.705
	P	80	1506 ± 229	0.000	526.0 ± 63.8	0.000	0.991

[a] Fine litterfall, data in kg ha^{-1} $year^{-1}$
[b] Three-year average of the leaf litterfall; all data in g m^{-1} $year^{-1}$

culating the percent of each element in the litterfall, randomizing these values, and then back-calculating nutrient mass for each data point by multiplying the percent of the element by the litterfall mass. Then we compared the slope of the regression of the residuals of the real data with the slope of the randomized data. A total of 500 trials were performed for each dataset. The actual slope of the residuals was considered significant if it fell above or below 97.5% of the slopes of the randomization trials. In no case was the actual slope significantly more negative as expected (Table 2), as predicted by the hypothesis that nutrient use efficiency is greater in nutrient-poor ecosystems. In fact, we found that the slope for nitrogen from the tropical dataset of Vitousek (1984) and the larger global dataset of Vogt et al. (1986) was significantly less steep, implying that forest ecosystems with higher aboveground nitrogen cycling have significantly higher nutrient use efficiency.

Table 2 Directional gradients (β) and the significance for regression of the residuals against the amount of nutrients in the litter. The residuals are calculated from a regression of the litter amount against the amount of nutrients in the litter (forced through the origin). The randomized slope is the average of 500 regressions and was calculated by randomizing the percent nutrient (by dividing nutrient by litterfall mass) and calculating the nutrient mass (by multiplying percent nutrient by the litterfall mass)

Dataset	Nutrient	Actual slope	Randomized slope	*P*	*n*
Vitousek 1984[a]	N	−25.52	−30.05	<0.001	90
	P	−706.6	−782.5	n.s.	91
	Ca	−39.08	−41.22	n.s	93
Vogt et al. 1986[a]	N	−23.99	−31.67	<0.05	192
	P	−282.1	−270.0	n.s.	138
Knops 1994[b]	N	−8.47	−12.90	n.s.	40
	P	−50.32	−36.16	n.s.	40

[a] Fine litterfall; data in kg ha^{-1} $year^{-1}$
[b] Three-year average of the leaf litterfall; all data in g m^{-1} $year^{-1}$

Polynomial regression

Using a second-order polynomial regression to visualize the data, ecosystems of intermediate fertility generally have a higher nutrient use efficiency than both nutrient-poor and nutrient-rich ecosystems (Fig. 1B; identical results are obtained for the other datasets).

In conclusion, a straight regression shows that there is a strong direct correlation between the amount of a nutrient and the amount of litterfall, and this relationship is statistically indistinguishable for both high- and low-fertility sites (Table 1). When we forced the regression through the origin, we found a significantly more positive slope for nitrogen, implying that nutrient-rich ecosystems have a higher nitrogen use efficiency. Lastly, a polynomial regression implies that intermediate ecosystems have a higher nutrient use efficiency. Which of these approaches is best is debatable. Our preference is for the first residual analysis, which is straightforward and involves standard statistical procedures. But regardless of the approach, the conclusion of Vitousek (1982), that "forest ecosystems systematically produce more litterfall dry mass per unit of nitrogen in sites with less aboveground nitrogen circulation" is not supported by any data.

Controlling mechanisms

We found a substantial amount of scatter in the data, so it is useful to see if there is convincing theoretical evidence that the quality of the litter is influenced by site fertility, disproportionally from the amount of litterfall. Vitousek (1982) proposed two mechanisms that could cause increased nitrogen use efficiency in low-nitrogen sites.

(1) Increased nutrient use efficiency in active leaves. Trees can either fix carbon more rapidly (per unit N) or use each unit of N to fix carbon over a long period of time (evergreenness). In general, the rate of photosynthesis in plants is directly related to the rate of CO_2 influx in the leaves, and in most natural ecosystems this rate is most severely limited by the availability of water. Therefore, the rate at which trees fix carbon per unit of nitrogen is predominantly influenced by the water relations of the tree. In addition, the majority of the nitrogen in the leaves is present in rubisco, the enzyme that fixes CO_2. This implies that the first step in the photosynthesis, in which rubisco is the key element, is the limiting step in photosynthesis. Thus, photosynthetic rates depend primarily on the water relationship of the plant and secondarily on the amount of rubisco, which is linearly related to the amount of nitrogen in the leaf. This results in a strong linear correlation between photosynthetic rates and leaf nitrogen (Field and Mooney 1986; Reich et al. 1991, 1992). Photosynthetic rates per unit of nitrogen differ between evergreen and deciduous tree species, with evergreens having substantially lower rates of photosynthesis per unit of leaf nitrogen (Reich et al. 1995). However, evergreens tend to occur in nutrient-poor ecosystems, implying that nutrient-poor ecosystems have a lower nutrient use efficiency than nutrient-rich ecosystems (Schulze 1982). All of these measurements are based on rates of photosynthesis per unit nutrient, whereas the litterfall leaves reflect the net primary productivity. Net primary productivity is not directly correlated with photosynthetic rates, because respiration and other factors like herbivory can influence it. To our knowledge, it has not yet been determined if the nutrient use efficiency of leaves, over their entire lifetime, is the same as or different from these instantaneous measurements.

Evergreen species occur in two contrasting environments. The first group occurs in areas where the temperature and/or water availability do not limit growth in any predictable period of the year, such as the wet tropics (Schulze 1982; Woodward 1987). Here, evergreen species outcompete deciduous species due to their ability to photosynthesize year round. The second group of evergreen species tends to occur in climates where the growing season is too short to recoup the investment in deciduous leaves, or in water-stressed environments. This bimodal distribution implies that water and temperature, rather than nutrient stress, are the important factors in the distribution. This hypothesis is supported by Kikuzawa (1991), who showed that this bimodal distribution can be explained on a cost-benefit basis based on photosynthetic rates, construction and maintenance cost of leaves. We found no evidence within a group of similar forest types of a relationship between nutrient use efficiency and the fertility of the ecosystem (Table 1), and the slopes of the regression of litterfall against N or P did not differ significantly for the two groups [nitrogen; deciduous litter = 2145 (SE 286) + 49.9 (SE 3.7) * N and evergreen litter = 1993 (SE 152) + 48.4 (SE 3.2) * N; phosphorus: deciduous litter = 2046 (SE 968) + 767 (SE 182) * P and evergreen litter = 1623 (SE 255) + 542 (SE 66) * P]. Thus, there is no evidence supporting the hypothesis that species have evolved evergreenness as an adaptation to increase the total amount of carbon gain per unit of N or P.

(2) Increased reabsorption of nutrients from leaves prior to leaf abscission. Most evidence does not support this mechanism as being higher in nutrient-poor sites (Aerts 1990; Del Arco et al. 1991). In contrast, Chapin (1980) showed that reabsorption is more related to the nutrient status of the foliage and that high nutrient levels lead to a larger proportional retranslocation. Retranslocation of nutrients within evergreens is generally lower than within deciduous species (Chapin and Kedrowski 1983; Aerts 1990; Del Arco et al. 1991), even though the nutrient levels in evergreen species are in general substantially lower than in deciduous species (Loveless 1961, 1962).

In summary, there appears to be no evidence that either increased nutrient use efficiency or increased resorption of nutrients from leaves prior to abscission play a role in influencing the relationship between site fertility and nutrient use efficiency as measured in the amount of nutrients in the litter versus the amount of litter.

Does the quality of the litter provide an estimate of the nutrient use efficiency?

There are numerous factors confounding the analysis of the nutrient use efficiency among communities. Most importantly, different species with different physiological traits are present in different sites (Chapin 1980; Pastor et al. 1984; Chapin et al. 1986) and exploit different sources of nitrogen (Schulze et al. 1995). Species can differ strongly in growth rates, leaf longevity, retranslocation rates, leaching losses, rates of herbivory and litter quality due to phenolics and lignin. All these factors influence the relationship between the amount of litter and the amount of a given nutrient in the litter. However, these factors are not necessarily related to the fertility of a given ecosystem. In addition, climate, due to temperature and rainfall limitation, has a strong influence on both plant growth and species distribution. These factors can potentially influence the relationship between the amount of litter and the amount of nutrients in the litter and any analysis ignoring this information may be misleading (Vogt et al. 1986; Aerts and de Caluwe 1994).

Most studies examining nutrient use efficiency in relation to fertility compare different sites. However, different sites do not differ only in fertility, but also in species composition and environmental factors. This might lead to misleading conclusions, because it is likely that the species composition and environmental factors also influence the nutrient use efficiency. One way to circumvent this is by examining the litterfall of a single stand of trees with differences in both litterfall and the amount of nutrients in the litterfall between the individual trees. We used data that were collected as part of an ecosystem study on the effect of epiphytic lichens on ecosystem nutrient cycling (Knops et al. 1996) in central coastal California. Litterfall was collected monthly for a 3-year period, beginning in March 1990, with five collectors (diameter 50 cm) placed stratified random under the canopy of each of 40 trees. Litterfall was dried at 80°C and sorted into leaves and other categories. Nitrogen and phosphorus were analyzed by standard autoanalyzer techniques, following Kjeldahl digestion on samples pooled per tree and across a year. Retranslocation was calculated from the nutrient levels of leaves collected in August minus the nutrient levels in fall leaf litterfall on a leaf weight basis. Soil samples were collected from five stratified random locations under the same trees, analyzed with the same methods as the litter samples and averaged per tree (see Knops 1994, for more extensive methods).

We failed to find a relationship between the residuals [of regression between litter mass and nutrient mass and either nitrogen or phosphorus (Table 1)]. Litterfall and the amount of nitrogen and phosphorus in the litter were

Table 3 Directional gradients (β) ± standard error (SE β) and the significance for regression (retranslocation is calculated as summer percent nutrient minus fall percent nutrient divided by summer percent nutrient; only significant regression slopes are included in this table)

Dependent variable	Independent variable	Regression	Significance	r^2
Litter 1990	N litter 1990	129.0 ± 9.9	0.000	0.817
Litter 1991	N litter 1991	119.5 ± 13.8	0.000	0.663
Litter 1992	N litter 1992	125.8 ± 7.0	0.000	0.896
Litter 1990	P litter 1990	376.5 ± 19.3	0.000	0.909
Litter 1991	P litter 1991	245.5 ± 20.6	0.000	0.789
Litter 1992	P litter 1992	433.9 ± 36.2	0.000	0.791
Litter 1990	N soil	98.5 ± 34.1	0.006	0.180
Litter 1991	N soil	73.8 ± 25.9	0.007	0.176
Litter 1992	N soil	118.3 ± 37.5	0.003	0.207
Litter 1990	P soil	–	0.836	–
Litter 1991	P soil	–	0.586	–
Litter 1992	P soil	–	0.318	–
N litter 1990	N soil	0.730 ± 0.235	0.004	0.202
N litter 1991	N soil	0.456 ± 0.180	0.016	0.145
N litter 1992	N soil	0.866 ± 0.284	0.004	0.196
P litter 1990	P soil	–	0.745	–
P litter 1991	P soil	–	0.205	–
P litter 1992	P soil	–	0.173	–
Litter 1990	N retranslocation 1990	–	0.979	–
Litter 1991	N retranslocation 1991	–	0.466	–
Litter 1992	N retranslocation 1992	–	0.985	–
Litter 1990	P retranslocation 1990	–	0.258	–
Litter 1991	P retranslocation 1991	–	0.210	–
Litter 1992	P retranslocation 1992	–	0.425	–
N litter 1990	N retranslocation 1990	–	0.997	–
N litter 1991	N retranslocation 1991	–	0.476	–
N litter 1992	N retranslocation 1992	–	0.871	–
P litter 1990	P retranslocation 1990	–	0.124	–
P litter 1991	P retranslocation 1991	–	0.875	–
P litter 1992	P retranslocation 1992	–	0.244	–
N Soil	N retranslocation 1990	−0.020 ± 0.007	0.006	0.163
N Soil	N retranslocation 1991	–	0.975	–
N Soil	N retranslocation 1992	–	0.211	–
P Soil	P retranslocation 1990	–	0.412	–
P Soil	P retranslocation 1991	–	0.251	–
P Soil	P retranslocation 1992	–	0.164	–

both strongly correlated with each other in all three years. The amount of litterfall and the amount of nitrogen in the litterfall were both significantly related to the amount of total soil nitrogen but not soil phosphorus (Table 3). This implies that the amount of nitrogen in the soil that a tree exploits influences both the amount of litterfall and the amount of nitrogen in the litterfall, but that a tree does not produce more litterfall dry mass per unit of nitrogen or phosphorus when soil nutrients are limited.

This conclusion is further supported by the retranslocation of both nitrogen and phosphorus (Table 3). Nitrogen retranslocation was not correlated among the individual trees over the 3 years and varied little among trees and among years: from 62 ± 1% (1990, range 53–70), 72 ± 1% (1991, range 66–79) to 64 ± 1% (1992, range 47–73). Phosphorus retranslocation was positively correlated among the trees and varied substantially more, both among trees and among years: from −2 ± 3% (1990, range −48–39), −15 ± 4% (1991, range −68–34) to 29 ± 3% (1992, range −35–62). However, there was no positive relationship between the retranslocation of either nitrogen or phosphorus and the amount of litter, the amount of nitrogen, or phosphorus in the litter and the amount of nitrogen, or phosphorus in the soil. This confirms that there is a relationship between soil fertility and the amount of litterfall, at least for nitrogen, but that the relationship is linear and there is no direct influence of soil fertility on retranslocation of either nitrogen or phosphorus. Consequently, these data offer no support for the hypothesis that soil fertility has a disproportionate influence on the nutrient content of the litterfall.

Components of nutrient use efficiency

It is often assumed that there is a biological advantage for plant species in nutrient-poor systems to have a higher nutrient use efficiency than species in nutrient-rich ecosystems and that species growing in poor nutrient conditions are relatively more productive for a given unit of nutrient. However, this ignores a possible tradeoff between the two components of nutrient use efficiency: nutrient productivity and the mean residence time of nutrients (Berendse and Aerts 1987). Recent experiments with herbaceous plants suggest that species from nutrient-rich ecosystems can also be more productive than species from nutrient-poor ecosystems (Boot and den Dubbelden 1990) and that the mean residence time of nitrogen may be the critical component of nutrient use efficiency that correlates with ecosystem fertility (Aerts 1990; Aerts and van der Peijl 1993; Aerts and de Caluwe 1994). These results suggest that even if there is no overall relationship between nutrient use efficiency and ecosystem fertility, there might be a more general relationship between mean nutrient residence time or nutrient productivity and ecosystem fertility. Additional data are needed to test these possibilities for tree species and forest ecosystems.

Acknowledgements We thank Brad Shaffer for pointing out the correct way to analyze ratio data, Dennis Young for statistical advice, Rien Aerts, John Barthell, Terry Chapin, Shahid Naeem, Anne Royalty, Bill Schlesinger, D.E. Schulze, David Tilman, Peter Vitousek and Dave Wedin for reviewing the manuscript. J.M.H.K. and W.D.K were supported by the University of California's Integrated Hardwoods Range Management Program and the site data of *Q. douglasii* were collected with support from NSF grants BSR-89-07405 (Arizona State University) and BSR-89-07689 (Duke University).

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