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ESSAY REVIEW

Nutrient resorption from senescing leaves of perennials: are there general patterns?

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Summary

1 Possible patterns in nutrient resorption efficiency (% of the leaf nutrient pool resorbed) from senescing leaves of perennials were examined at both the intra- and the interspecific level. Most of the data used originated from studies with evergreen and deciduous shrubs and trees.

2 Combining all data, mean nutrient resorption efficiency was 50% for N ($n = 287$) and 52% for P ($n = 226$). N resorption efficiency of evergreen shrubs and trees (47%) was significantly lower than in deciduous shrubs and trees (54%), whereas P resorption efficiency did not differ significantly between these growth-forms (51 and 50%, respectively). Although nutrient resorption is an important nutrient conservation mechanism at the species level, it does not differ strongly between growth-forms.

3 Mean N and P concentrations in leaves of deciduous shrubs and trees were about 60% higher than in evergreen species. There were only small differences in mean resorption efficiency and nutrient concentrations in leaf litter of deciduous species were therefore much higher than in evergreens. This implies that, in comparison with deciduous species, the low nutrient concentrations in mature leaves of evergreens contribute far more to nutrient conservation than does nutrient resorption.

4 Relations between leaf nutrient status and leaf nutrient resorption were absent or very weak. Assuming that leaf nutrient status reflects nutrient availability, this implies that nutrient resorption is only weakly controlled by nutrient availability.

5 At the intraspecific level, nutrient resorption was not very responsive to increased nutrient availability. There was no response in 63% of the experiments analysed (covering 60 spp.), whereas in 32% there was a decrease in N resorption in response to increased nutrient availability. For P (37 species analysed) there was no response in 57% of the cases and in 35% of the cases P resorption decreased upon enhanced nutrient supply. Evergreen shrubs and trees showed especially low responsiveness.

6 This review shows that there are no clear nutritional controls on nutrient resorption efficiency. Future research should focus on the biochemical basis of variation in nutrient resorption efficiency and on the factors, other than nutrient availability, that control nutrient resorption efficiency.

Keywords: deciduous, evergreen, leaf chemistry, leaf litter, nutrient conservation

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Introduction

Leaf senescence can be defined as 'the series of events concerned with cellular disassembly in the leaf and the mobilization of materials released during this process' (Thomas & Stoddart 1980). These events involve considerable *de novo* synthesis of proteolytic enzymes and other substances (Thomas & Stoddart 1980; Noodén & Leopold 1988). The primary value of leaf senescence to plant fitness is that certain breakdown products can be re-used. In this review I will use the term 'nutrient resorption' for the process by which nutrients are mobilized from senescing leaves and transported to other plant tissues (cf. Killingbeck

1986). Terms such as 'nutrient (re)translocation' or 'nutrient re-absorption' are also used for this process. Resorption of nutrients from senescing leaves enables plants to re-use these nutrients and as such it is a major nutrient-conservation mechanism (Chapin 1980; Chabot & Hicks 1982; Aerts 1990), which has important implications at both the population level and the ecosystem level.

At the population level, it has been postulated that low nutrient loss rates can increase the fitness of plant populations in nutrient-poor environments (Grime 1979; Chapin 1980; Berendse & Aerts 1987; Aerts 1990; May & Killingbeck 1992). Recent models have shown that such low loss rates lead to clear advantages in habitats where plant growth is nutrient-limited: low nutrient loss rates lead to a higher equilibrium biomass (Aerts & Van der Peijl 1993) and they lead to competitive replacement of species with higher nutrient loss rates (Berendse 1994). At the ecosystem level, nutrient resorption from senescing leaves has important implications for element cycling. The nutrients which are resorbed during senescence are directly available for further plant growth, which makes a species less dependent on current nutrient uptake. Nutrients which are not resorbed, however, will be circulated through litterfall. The litter must be decomposed and the nutrients contained in that litter must be remineralized to become once again available for plant uptake. As these processes can take several years (Staaf & Berg 1982; Berg 1986) the nutrients contained in litterfall must be, in the short term, considered as losses to the plant population.

One of the paradigms of plant ecology is that species from nutrient-poor environments have a higher nutrient resorption efficiency than species characteristic of nutrient-rich environments. However, Chapin (1980) pointed out that there is actually little evidence to support this claim. During the past 15 years numerous papers have appeared in which nutrient resorption from senescing leaves of perennials was considered as an adaptation to low soil fertility. In these studies very different relationships between soil fertility and nutrient resorption were found. In some studies, nutrient resorption increased with increasing soil fertility, in some the opposite trend was found and in others there was no relation at all. There are two important reasons for this apparent lack of any pattern in the relation between soil fertility and nutrient resorption from senescing leaves. (1) In many studies only one or only a few species from a specific plant community were studied but very general conclusions were drawn from this limited data set. This is a dangerous approach, because it might be that in specific communities in which most species have relatively similar leaf traits the relation between soil fertility and nutrient resorption is very different from broad general relationships (cf. Reich 1993). (2) In many studies species growing in nutrient-poor habitats were compared with species growing in nutrient-rich habitats. In this way, phenotypic responses to different levels of soil fertility and interspecific differences are confounded. This is the more so, as very often the dominant growth-form also changes with changes in soil fertility. A well-known aspect of this is the increasing dominance of evergreen species with decreasing levels of soil fertility (Monk 1966; Aerts 1995).

In this review three major questions are treated: (1) What range of N and P resorption can be observed from senescing leaves of perennials? (2) Is there a consistent interspecific difference in nutrient resorption between species belonging to different growth-forms (evergreen shrubs and trees, deciduous shrubs and trees, forbs, graminoids)? (3) Is there, at the phenotypic level, a consistent difference in nutrient resorption between high- and low-fertility sites?

Data acquisition and data handling

I have used data on nutrient resorption from a wide variety of studies, attempting to avoid geographical bias, although most of the data originate from the USA and Europe. I focus on the resorption of N and P, as these nutrients are the most important growth-limiting nutrients in many terrestrial ecosystems (Chapin 1980; Vitousek & Howarth 1991). Resorption data are presented as nutrient resorption efficiency, which is defined as the amount of nutrients resorbed during senescence and is expressed as a percentage of the amount present in the leaves prior to senescence. In the literature, the amounts of nutrients are expressed in various ways. The two most widely used estimates are: (1) amounts expressed as total nutrient pools in the entire canopy (as is very often done in forestry studies); or (2) as the total amount of nutrients per leaf or per unit leaf area. Both approaches are reliable estimates of nutrient resorption, because they correct for possible changes in specific leaf mass (*SLM*: leaf mass per unit leaf area) during senescence as a result of resorption of (soluble) carbon compounds. In a few studies, however, the amounts are expressed as concentrations (nutrients per unit leaf mass), thus ignoring possible changes in *SLM* during senescence. These estimates of nutrient resorption may therefore be biased. However, since loss of leaf mass during senescence is mostly in the range of 0–10% (Chapin *et al.* 1990), the errors in these estimates are relatively small. The three types of estimates are, respectively, referred to as 'pool', 'concentration on area basis' and 'concentration on mass basis'.

A major problem in the analysis of nutrient resorption in relation to soil fertility is that it is hard to quantify soil fertility. In most of the studies reviewed here, no attempt at all was made to do so and in only very few studies was soil fertility quantified (e.g. Walbridge 1991; Escudero *et al.* 1992a,b). Thus, it was not possible to relate nutrient resorption to a standard measure of soil fertility. Therefore I chose the following approaches: (1) assuming that leaf nutrient concentration reflects soil nutrient availability I related nutrient resorption to leaf nutrient concentration; (2) in accordance with generally accepted ecological theory (cf. Monk 1966; Small 1972; Chapin 1980; Aerts 1995) I assumed that evergreen species are mainly confined to nutrient-poor soils and that deciduous species are dominant on nutrient-rich soils. Thus I made a comparison of nutrient resorption between growth-forms. I distinguished the following categories: evergreen shrubs and trees, deciduous shrubs and trees, forbs, and graminoids. The categories forbs and graminoids are of course not confined solely to low- or high-nutrient soils, but I included them to see if they deviate from the patterns observed in the woody species. At the intraspecific level I analysed studies in which nutrient availability was experimentally increased or in which species were studied along natural gradients of soil nutrient availability.

Most studies on nutrient resorption from senescing leaves were performed in forest ecosystems. This is most certainly due to the strong impact that this process has on nutrient cycling and thereby on stand fertility and stand productivity. As a result, there are very many data on nutrient resorption from senescing foliage of evergreen and deciduous trees, and only few data on forbs and graminoids. Therefore, the data do not allow strong conclusions about nutrient resorption from foliage of forbs and graminoids.

There appeared to be a wide variety in the number of parameters determined in the various studies. In some a detailed account was given of soil nutrient availability at the growing sites for each species, together with data on leaf nutrient concentrations and nutrient resorption data. In contrast there were studies in which nutrient resorption for only one nutrient was the sole parameter presented. As a result, the number of data points for the different parameters I discuss in this review is not constant. All analyses were performed for both the entire data set and for each growth-form separately.

The data

N AND P RESORPTION IN SPECIES BELONGING TO DIFFERENT GROWTH-FORMS

The studies used are listed in Appendix 1. For brevity, only the maximum values reported in each study are presented. There is a tremendous variation in maximum N and P resorption. Table 1 shows the mean N and P concentration in mature leaves and the N and P resorption from senescing leaves, calculated both for the entire data set and for each growth-form separately. The N concentration in mature leaves of evergreen shrubs and trees and of graminoids is significantly lower than in deciduous shrubs and trees and in forbs. The largest difference (62%) is between mean N concentration in evergreen and deciduous shrubs and trees. A similar pattern is observed for the P concentration in mature leaves, despite the fact that there are only weak or nonsignificant correlations between N and P concentrations in mature leaves (Table 2). Thus, the data show that there are large differences in N and P concentration between growth-forms.

Mean N and P resorption from senescing leaves is 50 and 52%, respectively, (Table 1). Thus, on average about half of the N and P contained in leaves can be re-used after senescence of those leaves although there is much variability. The coefficients of variation in N resorption for the different growth-forms are between 24 (graminoids) and 52% (forbs) and for P resorption between 22 (graminoids) and 71% (forbs). N resorption from senescing leaves differs significantly between growth-forms. Mean N resorption in evergreens and in forbs is significantly lower than in deciduous shrubs and trees and graminoids. So, contrary to general ecological belief, it appears that N resorption is lower in evergreens compared with deciduous species. However, the relative difference is small (13%). For P resorption the pattern is somewhat different: mean P resorption in evergreen and deciduous shrubs and trees and in forbs is not significantly different, but they are lower than in graminoids. Correlation analysis showed that in all growth-forms N and P resorption are significantly correlated, but the correlation in woody species and especially in deciduous shrubs and trees is rather low (Table 2).

The data show that N and P resorption were not clearly related to the nutrient status of the leaf (Table 3). Over the entire data set there was no relation at all between N resorption and the N concentration in mature leaves (Table 3). Only for forbs and graminoids were there positive, if weak, relationships: for these groups N resorption increases with increasing N concentration of the leaves. When the entire data set was considered, there was a negative relation between P resorption and P concentration in the leaf. However, only 9% of the variance was explained by the regression model. Similar weak relations were also found for evergreen and deciduous shrubs and trees. For forbs and graminoids there was no relation at all. Thus, the data show that the relationship between nutrient status and N and P resorption from mature leaves is at best weak.

INTRASPECIFIC DIFFERENCES IN N AND P RESORPTION IN RELATION TO SITE FERTILITY

There are significant differences in N and P resorption between growth-forms, but the differences are relatively small. The next question I tried to answer is whether there are consistent differences at the phenotypic level in nutrient resorption between high- and low-fertility sites. The studies used here are listed in

Table 1 Mean (± SD) nitrogen and phosphorus concentration in mature leaves of perennials, and N and P resorption efficiency. Numbers of observations are shown in parentheses. Different letters within a column indicate statistical difference between growth-forms ($P < 0.05$)

	Concentration (mg g^{-1})		Resorption efficiency (%)	
	N	P	N	P
All data	18.3 ± 7.4 (241)	1.33 ± 0.81 (179)	50.3 ± 17.3 (287)	52.2 ± 22.1 (226)
Evergreen shrubs and trees	13.7 ± 5.2^{a} (95)	1.02 ± 0.56^{a} (74)	46.7 ± 16.4^{a} (108)	51.4 ± 21.7^{a} (88)
Deciduous shrubs and trees	22.2 ± 7.4^{b} (95)	1.60 ± 0.92^{b} (78)	54.0 ± 15.9^{b} (115)	50.4 ± 19.7^{a} (98)
Forbs	22.2 ± 5.8^{b} (29)	1.86 ± 0.72^{b} (14)	41.4 ± 21.4^{a} (33)	42.4 ± 30.3^{a} (18)
Graminoids	16.0 ± 4.0^{a} (22)	0.95 ± 0.51^{a} (13)	58.5 ± 14.2^{b} (31)	71.5 ± 16.0^{b} (22)

Table 2 Pearson correlation coefficients (r) for the correlations between N and P concentration in mature leaves and between N and P resorption from those leaves

Data	r	d.f.	P
N and P concentrations			
All data	0.37	171	< 0.0001
Evergreen shrubs and trees	0.32	73	< 0.005
Deciduous shrubs and trees	0.23	69	< 0.05
Forbs	0.04	12	
Graminoids	0.52	11	< 0.05
N and P resorption			
All data	0.67	217	< 0.0001
Evergreen shrubs and trees	0.68	86	< 0.0001
Deciduous shrubs and trees	0.48	89	< 0.0001
Forbs	0.90	16	< 0.0001
Graminoids	0.90	20	< 0.0001

Table 4 Summary of the phenotypic response in nutrient resorption from senescing leaves upon enhanced nutrient supply. For each type of response the percentage of the total response is indicated. n is the number of species examined

		Response to increased availability		
	n	None	Increase	Decrease
Nitrogen				
All data	60	63	5	32
Evergreen shrubs and trees	24	75	4	21
Deciduous shrubs and trees	12	58	0	42
Forbs	10	80	20	0
Graminoids	14	36	0	64
Phosphorus				
All data	37	57	8	35
Evergreen shrubs and trees	19	73	11	16
Deciduous shrubs and trees	8	38	0	62
Forbs	6	50	17	33
Graminoids	4	25	0	75

Appendix 2. I separated the data by growth-form. In 63% of the cases, N resorption from senescing leaves does not change in response to increased nutrient supply (Table 4). In about one-third of the studies a decrease in nutrient resorption is found. Nitrogen resorption from senescing leaves is least influenced by nutrient availability in evergreen shrubs and trees and in forbs. Nor is phosphorus resorption very responsive to increased nutrient supply: in 57% of the cases there was no response, whereas in 35% of the cases there was a decrease of P resorption upon enhanced nutrient supply. It is difficult to draw any conclusion about the responsiveness of the different growth-forms, because the number of observations for deciduous shrubs and trees and for forbs and graminoids is low. Nevertheless, the data suggest that P resorption from leaves of evergreen shrubs and trees is not very responsive to changes in nutrient availability.

Table 3 Relations between percentage nutrient resorption (R) and nutrient concentration (C) in mature foliage

Data	Regression	r^{2}	d.f.	P
Nitrogen				
All data	$R_N = 0.337\ C_N + 42.46$	0.02	239	
Evergreen shrubs and trees	$R_N = 0.294\ C_N + 41.44$	0.01	93	
Deciduous shrubs and trees	$R_N = 0.057\ C_N + 51.07$	0.00	93	
Forbs	$R_N = 1.554\ C_N + 4.88$	0.19	27	< 0.01
Graminoids	$R_N = 1.957\ C_N + 26.89$	0.36	20	< 0.005
Phosphorus				
All data	$R_P = -8.45\ C_P + 61.84$	0.09	178	< 0.0001
Evergreen shrubs and trees	$R_P = -18.32\ C_P + 69.62$	0.22	73	< 0.0001
Deciduous shrubs and trees	$R_P = -6.14\ C_P + 59.50$	0.08	76	< 0.01
Forbs	$R_P = 16.09\ C_P + 4.73$	0.17	12	
Graminoids	$R_P = -8.85\ C_P + 79.69$	0.07	11	

Discussion

ARE THERE GENERAL PATTERNS?

The aim of this review was to examine whether there are general patterns in nutrient resorption from senescing leaves of perennials. This issue has been addressed quite often before, but the data used were always very limited in size and/or failed to distinguish between interspecific differences and phenotypic responses. My data set does not suffer from these problems and therefore more general conclusions can be drawn. However, there are three points which merit attention: (1) The data on nutrient resorption efficiency compiled from the literature were not always expressed in the same way. However, as already explained in the section on 'Data acquisition and data handling' the effect on the patterns presented in this review is probably very small. (2) In all the parameters I examined there was considerable variability. This implies that the values and relationships found in small-scale studies in which a particular species or species groups from a specific habitat are studied can deviate from the patterns observed in this large-scale survey. (3) The data for forbs and graminoids are limited, so for these growth-forms conclusions cannot be that strong. Therefore, I will confine the discussion of my data mainly to evergreen and deciduous shrubs and trees.

About half of the N and P contained in mature leaves is resorbed during senescence (Table 1). This suggests that nutrient resorption is an important nutrient conservation mechanism, because a large part of the nutrient capital of plants is contained in the leaves (Chapin 1980). It must be emphasized, however, that there is large variability in the data and that there are no or relatively minor differences between growth-forms, except that P resorption is higher in graminoids. However, due to the limited data set for graminoids, it is uncertain whether this is generally true. Thus, the data show that high nutrient resorption from senescing leaves is characteristic for most species and that species from nutrient-poor sites (evergreens) have not adapted to low soil fertility by having a high nutrient resorption efficiency. Thus, the conclusions drawn by Chapin (1980) based on the limited amount of data available at that time have not been altered by the studies which have appeared during the past 15 years.

There was also no clear effect of nutrient availability in soil on nutrient resorption at the phenotypic level (Table 4): in most cases there was no relationship. However, due to the increases in both leaf mass and leaf nutrient concentrations in mature leaves in response to fertilization, the absolute amount of nutrients resorbed during senescence increases with fertility in most cases (e.g. Birk & Vitousek 1986; Nambiar & Fife 1991; Munson *et al.* 1995). As a result, a larger proportion of the annual nutrient requirement of (forest) stands is then supplied by nutrients which are resorbed from senescing foliage.

The lack of a clear relation between nutrient availability and nutrient resorption both at the interspecific and at the phenotypic level is also reflected in the very weak (low r^2-values) or absent relations between leaf nutrient status and nutrient resorption (Table 3). These very weak or absent relations are also found in studies with a limited set of species (e.g. Chapin & Kedrowski 1983; Birk & Vitousek 1986; Lajtha & Klein 1988; del Arco *et al.* 1991; Escudero *et al.* 1992a).

It has been suggested that in low-nutrient environments there is selection on plant features which lead to low nutrient loss rates (Grime 1979; Chapin 1980; Aerts 1990; Aerts & Van der Peijl 1993; Berendse 1994). As high nutrient resorption efficiency is clearly not characteristic of species of low-nutrient environments, this raises the question how these species reduce their nutrient losses. In a study with evergreen and deciduous woody species in Central Spain, Escudero *et al.* (1992a) showed that leaf longevity was far more important as a nutrient conservation mechanism than high resorption efficiency. Reich *et al.* (1995) arrived at a similar conclusion in a study with evergreen and deciduous woody species of an oligotrophic Amazonian forest. These observations are not very surprising, because the variation usually observed in leaf life span is much larger than that in resorption efficiency. It should be emphasized, however, that the long leaf life span of evergreens is not only important as a nutrient conservation mechanism, but also as a way to improve the carbon balance (Greenway *et al.* 1992; Jonasson 1992, 1995). Nutrient losses can also be reduced by the synthesis of tissues with low nutrient concentrations (Aerts 1990), a feature which is clearly characteristic of evergreens (Table 1). Nutrient concentrations in other tissues of evergreens are also low compared with other growth-forms (Aerts 1995). Thus, evergreen species appear to reduce their nutrient losses mainly by having leaves with a long life span and low nutrient concentrations, and *not* by a high resorption efficiency.

THE BIOCHEMICAL BASIS OF VARIATION IN NUTRIENT RESORPTION

Nutrient resorption can vary widely both within and between species. High resorption efficiency is dependent on many factors, including the relative pool sizes of mobile and insoluble nutrients and the presence of an appropriate nutrient sink. Thus, to understand possible patterns in nutrient resorption we need to know more about the biochemical basis of variation in nutrient resorption. Chapin & Kedrowski (1983), in a study with deciduous and evergreen Alaskan tree species, found no major differences in patterns of N and P distribution among the most important chemical fractions. During autumn senescence the organic

N and P fractions were hydrolysed and inorganic P and amino acid N were resorbed from the leaves of deciduous species prior to abscission. Hydrolysis of nucleic acids and phospholipids contributed 40–47% and 26–38%, respectively, to the total P resorbed from senescing leaves. Hydrolysis of proteins and subsequent resorption as amino acids was equivalent to 82–91% of the N resorbed from senescing leaves.

Pugnaire & Chapin (1993) showed that N resorption efficiency from senescing leaves was positively related to the ratio between soluble and insoluble N. A surprising aspect of their study was that plants with a low total tissue N had the highest proportion of soluble N. Although Pugnaire & Chapin (1993) provide some possible explanations for this pattern, it is not very clear if this is indeed a widespread phenomenon and what the causes might be. Low resorption efficiency in species from infertile sites may partly be explained as a consequence of an antiherbivory mechanism (Aerts 1990). Herbivory, which would increase nutrient losses and would reduce photosynthetic carbon gain, is reduced in plants growing at infertile sites because they generally contain higher amounts of phenolic compounds than do plants from more fertile habitats (Haukioja *et al.* 1985; Nicolai 1988). High concentrations of phenolic compounds may lead to precipitation of proteins prior to protein hydrolysis, which reduces nutrient resorption (Chapin & Kedrowski 1983).

In conclusion, to understand the biochemical basis of variation in nutrient resorption we need to know the controls on the ratio of soluble and insoluble compounds in senescing leaves and the factors that control hydrolysis of organic compounds.

CONTROLS ON NUTRIENT RESORPTION

I found little evidence for nutritional controls on nutrient resorption efficiency: there were no or only small differences between growth-forms, there was no relation with leaf nutrient status, and at the phenotypic level there was only a weak response of nutrient resorption to increased nutrient supply. The most clear nutritional control on nutrient resorption is found when plants are grown at abnormally high leaf nutrient concentrations, where nutrient resorption efficiency is low (Chapin & Moilanen 1991).

Several possible controls have been proposed. Nambiar & Fife (1991) showed for *Pinus radiata* that nutrient resorption from leaves (needles) was closely linked with shoot production (sink strength). In their study, Nambiar & Fife (1991) mainly discussed nutrient resorption from nonsenescing needles during the growing season. However, as Chapin & Moilanen (1991) clearly point out, even if differences in sink strength exert an important ecological control over nutrient resorption efficiency *during the growing season*, it is less clear that sink strength will differ in an ecologically predictable fashion during autumn senescence of deciduous species. In their study with *Betula papyrifera* they found that the rate of phloem transport (source–sink interactions) was the most important factor governing nutrient resorption efficiency. Chapin & Moilanen *et al.* (1991) suggest that controls over phloem transport are more important than controls over breakdown of nutrient-containing fractions in the leaf as determinants of nutrient resorption efficiency.

Soil moisture availability may also be an important determinant of nutrient resorption efficiency (Boerner 1985; del Arco *et al.* 1991; Escudero *et al.* 1992a). Boerner (1985) found that during a drought summer in Ohio N resorption was most closely correlated to soil moisture, and P resorption to soil P availability. This differential dependence among elements on moisture levels was the underlying reason for differences in the relation between nutrient resorption efficiency and soil nutrient availability of N and P for a variety of woody species. Del Arco *et al.* (1991) studied the effects of site characteristics on N resorption efficiency from leaves of woody species in Spain. Patterns in resorption efficiency were determined by the duration of the leaf abscission period, with the species exhibiting gradual leaf fall having the lowest percentage of nutrient resorption. Gradual leaf fall seems to be an adaptation to water stress in regions with an arid or semiarid climate. The species that occupied the more xeric sites thus showed lower nutrient resorption efficiency. Factors related to N availability showed no clear effect on the resorption efficiency. Based on results from the same study site, Escudero *et al.* (1992a) concluded that improvement of resorption efficiency would entail the modification of leaf abscission patterns and its costs in terms of water use efficiency would probably be unacceptable under conditions of low water availability.

These studies clearly show that there is a need for more research on the controls on nutrient resorption efficiency. However, as Nambiar & Fife (1991) emphasized, there is unlikely to be a single explanation for variation in nutrient resorption efficiency.

NUTRIENT RESORPTION, NUTRIENT USE EFFICIENCY AND LEAF LITTER DECOMPOSITION

I found no clear differences in nutrient resorption between growth-forms, but there were large differences in nutrient concentrations in mature leaves prior to senescence. These differences may have large implications for leaf-level nutrient use efficiency (*NUE*: productivity per unit nutrient uptake) and leaf litter decomposition. I calculated mean leaf litter nutrient concentrations by multiplying the mean concentration data from Table 1 by the mean percentage of the nutrients not resorbed during senescence. The inverse of these litter concentrations was used as an

Table 5 Leaf litter nutrient concentrations and leaf-level nutrient use efficiency (*NUE*) of different growth-forms, calculated from the data presented in Table 1

	Concentrations in litter (mg g^{-1})		Leaf-level *NUE* (g g^{-1})	
	N	P	N	P
Evergreen shrubs and trees	7.30	0.50	137	2017
Deciduous shrubs and trees	10.21	0.79	98	1260
Forbs	10.79	1.07	93	933
Graminoids	6.64	0.27	151	3693

index of leaf-level nutrient use efficiency (Vitousek 1982; Aerts 1990).

Leaf-level efficiency of N and P use are much higher in the evergreens and graminiods compared with the other growth-forms (Table 5). Thus, evergreens and forbs produce more leaf mass per unit of N or P taken up. This is an important adaptation to low soil fertility, but it must be emphasized that patterns in leaf-level *NUE* do not necessarily correspond with whole-plant level *NUE* (Aerts 1990, 1995). As we have already seen, the differences in leaf-level *NUE* between growth-forms are not due to differences in nutrient resorption efficiency, but are due to differences in the nutrient concentrations in mature leaves prior to senescence.

In many terrestrial ecosystems, nutrient release from decomposing litter is the major source of nutrients for plant growth (Taylor *et al.* 1989). Leaf litter N and P concentrations are much lower in evergreens and graminoids than in deciduous shrubs and trees and forbs (Table 5). This has direct implications for litter decomposition rates and nutrient release, because decomposition and nutrient release from litter are very often positively related to the N or P concentrations in the litter and negatively related to the C/N or the C/P ratio (Witkamp 1966; Coulson & Butterfield 1978; Berg & Staaf 1980; Taylor *et al.* 1989). Thus, from my data it can be predicted that leaf litter from evergreens and graminoids will decompose slower and release less nutrients than the litter from other growth-forms. As evergreens dominate on nutrient-poor soils, this implies that there might be a positive feedback between low soil fertility and dominance of evergreens (cf. Hobbie 1992; Aerts 1995).

Conclusions and future directions

This review shows that nutrient resorption is, at the species-level, an important nutrient conservation mechanism: about half of the N and P contained in mature leaves are resorbed during senescence. There are no or only minor differences in nutrient resorption efficiency between growth-forms. Evergreen species do not reduce nutrient losses by a high resorption efficiency, but by the synthesis of leaves with low nutrient concentrations and with a long life span. As there were no or only weak relations between leaf nutrient concentrations and nutrient resorption efficiency, it can be concluded that nutrient resorption is only weakly controlled by nutrient availability. This conclusion is supported by the observation that at the phenotypic level nutrient resorption efficiency was not very responsive to increased nutrient availability.

Future research should focus on the mechanisms and the controls of variation in nutrient resorption efficiency. Thus, to understand the biochemical basis of variation in nutrient resorption we need to know the controls on the ratio of soluble and insoluble compounds in senescing leaves and the factors that control hydrolysis of organic compounds during leaf senescence. Furthermore, research effort should be spent on the importance of sink strength, phloem transport rate, and water availability as controls on nutrient resorption efficiency.

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Appendix 1
Studies used in the analysis of resorption data

Study	Species description	Growth-forms	Maximum resorption (%)		Measured as*
			N	P	
Small (1972)	Peat bog shrubs and trees from the boreal zone	Evergreen	73	98	Concentration^{M}
		Deciduous	68	80	Concentration^{M}
Stachurski & Zimka (1975)	Tree species from the temperate zone	Deciduous	64	ND†	Concentration^{A}
		Evergreen	77	ND	Concentration^{A}
Morton (1977)	*Molinia caerulea* in a wet heathland in the temperate zone	Graminoid	75	83	Concentration^{M}
Staaf (1982)	*Fagus sylvatica* in the boreal zone	Deciduous	72	70	Concentration^{A}
Gray (1983)	Shrubs from chaparral vegetation in the USA	Evergreen	63	68	Concentration^{A}
		Deciduous	56	42	Concentration^{A}
Boerner (1984)	Trees from the temperate zone	Deciduous	64	79	Concentration^{M}
Boerner (1985)	*Hamamelis virginiana* in the temperate zone	Deciduous	72	58	Concentration^{A}
Boerner (1986)	Perennial forest herbs in the temperate zone	Forbs	40	32	Concentration^{A}
Chapin & Kedrowski (1983)‡	Tree species from many habitats	Evergreen	72	80	Pool
		Deciduous	75	81	Pool
Birk & Vitousek (1986)	*Pinus taeda*, warm temperate zone	Evergreen	58	ND	Concentration^{M}
Pfadenhauer & Twenhöven (1986)	Species from peatlands in the temperate zone	Graminoids	64	77	Pool
Ganzert & Pfadenhauer (1986)	*Schoenus ferrugineus* in a fen in the temperate zone	Graminoid	28	34	Pool

Study	Species description	Growth-forms	Maximum resorption (%)		Measured as*
			N	P	
Berendse *et al.* (1987)	Wet-heathland species from the temperate zone	Evergreen	42	54	Pool
		Graminoid	59	81	Pool
Nambiar & Fife (1987)	*Pinus radiata*, in the Mediterranean zone of Australia	Evergreen	39	58	Pool
Killingbeck & Costigan (1988)	Understorey shrubs in the temperate zone	Deciduous	70	59	Concentration^{A}
Lajtha & Klein (1988)	*Larrea tridentata*, a desert species in the USA	Evergreen	54	65	Concentration^{A}
Aerts (1989)	Dry-heathland species from the temperate zone	Evergreen	52	69	Concentration^{A}
		Graminoid	75	87	Concentration^{A}
Aerts & Berendse (1989)	Wet-heathland species from the temperate zone	Evergreen	36	25	Concentration^{A}
		Graminoid	73	88	Concentration^{A}
Aerts & De Caluwe (1989)	*Molinia caerulea* in a wet heathland in the temperate zone	Graminoid	74	81	Concentration^{A}
Schlesinger *et al.* (1989)	High-altitude trees and shrubs in California and Nevada	Evergreen	71	66	Concentration^{A}
Chapin & Moilanen (1991)	*Betula papyrifera* in the Arctic	Deciduous	65	45	Pool
Nambiar & Fife (1991)	Temperate conifers (mainly *Pinus radiata* in Australia)	Evergreen	49	52	Concentration^{A}
Shaver & Chapin (1991)	Several Arctic vegetation types	Deciduous	79	80	Concentration^{A}
		Forbs	53	78	Concentration^{A}
		Graminoids	71	81	Concentration^{A}
Son & Gower (1991)	Trees from the temperate zone	Deciduous	83	72	Concentration^{A}
		Evergreen	55	55	Concentration^{A}
Walbridge (1991)	Pocosin (evergreen shrub bog) in the temperate zone	Evergreen	72	87	Concentration^{A}
Berendse & Jonasson (1992)‡	Arctic tundra shrubs, forbs and graminoids	Deciduous	69	70	Pool/ Concentration^{M}
		Evergreen	74	86	Pool
		Forbs	81	88	Pool
		Graminoids	78	92	Pool
Escudero *et al.* (1992a)	Mediterranean tree species	Evergreen	50	61	Pool
		Deciduous	69	76	Pool
Escudero *et al.* (1992b)	*Quercus ilex*, in the Mediterranean zone	Evergreen	37	ND	Pool
Helmisaari (1992)	*Pinus sylvestris* stands in eastern Finland	Evergreen	82	87	Pool
Hendricks & Boring (1992)	Herbaceous legumes in a burned pine forest, Georgia, USA	Forbs	52	ND	Concentration^{A}
Jaramillo & Detling (1992)	Grass species from native semiarid grass prairie	Graminoids	68	ND	Concentration^{M}
Konings *et al.* (1992)	*Carex* species from the temperate zone	Graminoids	57	67	Pool
Mayor & Rodà (1992)	*Quercus ilex*, in the Mediterranean zone	Evergreen	33	43	Concentration^{M}
Minoletti & Boerner (1993)	*Polystichum acrostichoides* in the temperate zone	Forb§	58	62	Concentration^{M}
Negi & Singh (1993)	Tree species in the central Himalaya	Deciduous	75	ND	Concentration^{A}
		Evergreen	60	ND	Concentration^{A}
Aerts & De Caluwe (1994)	*Carex* species from the temperate zone	Graminoids	58	ND	Concentration^{A}
Bowman & Conant (1994)	Three alpine populations of *Salix glauca*	Deciduous	64	ND	Concentration^{M}
Dalla-Tea & Jokela (1994)	*Pinus elliottii* and *P. taeda* in Florida, USA	Evergreen	65	69	Concentration^{A}
Lodhiyal *et al.* (1994)	*Populus deltoides* in central Himalaya	Deciduous	65	50	Concentration^{M}
Näsholm (1994)	*Pinus sylvestris* in the boreal zone	Evergreen	50	ND	Concentration^{A}
Bowman *et al.* (1995)	Forbs and graminoids from alpine tundra	Forbs	75	ND	Concentration^{M}
		Graminoids	58	ND	Concentration^{M}
Reich *et al.* (1995)	Tropical tree species in Amazonian rain forest	Deciduous	55	71	Concentration^{A}
		Evergreen	39	64	Concentration^{A}
Jonasson (1995)	*Rhododendron lapponicum* in subarctic tundra	Evergreen	53	36	Concentration^{A}
Sabaté *et al.* (1995)	*Quercus ilex*, in the Mediterranean zone	Evergreen	52	62	Concentration^{A}

*Concentration^{A}: based on changes in nutrient concentration per unit leaf area; Concentration^{M}: based on changes in nutrient concentration per unit leaf mass; Pool: based on changes in foliar nutrient pools.

†ND: not determined; ‡and other studies cited in this paper; §Ferns are included in the category Forbs.

Appendix 2

Summary of studies in which the phenotypic response in nutrient resorption to natural variation in soil nutrient availability or to experimentally increased nutrient supply was studied.

Study	Type	Species	Nutrient resorbed	Response of nutrient resorption to increased availability	Resorption measured as*
Evergreen shrubs and trees					
Birk & Vitousek (1986)	Natural gradient	*Pinus taeda*	N	None†	Concentration[M]
	Fertilization with sludge	*Pinus taeda*	N	None	Concentration[M]
Nambiar & Fife (1987)	N fertilization	*Pinus radiata*	N	Increase	Pool
			P	None	Pool
Lajtha & Klein (1988)	NP fertilization	*Larrea tridentata*	N, P	None	Concentration[A]
Chapin & Shaver (1989)‡	NP fertilization	*Ledum palustre*	N	Slight decrease	Pool
			P	Slight increase	Pool
		Empetrum nigrum	N	Slight decrease	Pool
			P	Decrease	Pool
Lajtha & Whitford (1989)	N fertilization	*Larrea tridentata*	N	None	Concentration[M]
Schlesinger *et al.* (1989)	Natural gradient	*Pinus jeffreyi*	N,P	None	Concentration[A]
		Arctostaphylos patula	N,P	None	Concentration[A]
		Pinus monophylla	N,P	None	Concentration[A]
		Juniperus osteosperma	N,P	None	Concentration[A]
		Amelanchier alnifolia	N,P	None	Concentration[A]
Nambiar & Fife (1991)	NP fertilization	*Pinus radiata*	N,P	None	Concentration[A]
Walbridge (1991)	Natural gradient	*Cyrilla racemiflora*	N,P	None	Concentration[A]
		Pinus serotina	N,P	None	Concentration[A]
		Zenobia pulverulenta	N,P	None	Concentration[A]
		Lyonia lucida	N,P	None	Concentration[A]
		Persea borbonia	N,P	None	Concentration[A]
Escudero *et al.* (1992b)	Natural gradient	*Quercus ilex*	N	None	Pool
Helmisaari (1992)	N fertilization	*Pinus sylvestris*	N,P	None	Pool
Dalla-Tea & Jokela (1994)	NPK fertilization	*Pinus elliottii*	N,P	Decrease	Concentration[A]
		Pinus taeda	N,P	Decrease	Concentration[A]
Näsholm (1994)	N fertilization	*Pinus sylvestris*	N	None	Concentration[A]
Sabaté *et al.* (1995)	Natural gradient	*Quercus ilex*	N	Decrease	Concentration[A]
			P	Increase	Concentration[A]
Deciduous shrubs and trees					
Stachurski & Zimka (1975)‡	Natural gradient	*Carpinus betulus*	N	Decrease	Concentration[A]
		Quercus robur	N	Decrease	Concentration[A]
Staaf (1982)	Natural gradient	*Fagus sylvatica*	N,P	None	Concentration[A]
Boerner (1984)	Natural gradient	*Quercus prinus*	N,P	None	Concentration[M]
		Quercus alba	N,P	Decrease	Concentration[M]
		Acer rubrum	N,P	Decrease	Concentration[M]
		Fagus grandifolia	N,P	Decrease	Concentration[M]
Boerner (1985)	Natural gradient	*Hamamelis virginiana*	N	None	Concentration[A]
			P	Decrease	Concentration[A]
Chapin & Shaver (1989)‡	NP fertilization	*Betula nana*	N,P	None	Pool
Chapin & Moilanen (1991)	Natural gradient	*Betula papyrifera*	N	None	Pool
Bowman & Conant (1994)	Natural gradient	*Salix glauca*	N	None	Concentration[M]
Nelson *et al.* (1995)	N fertilization	*Liquidambar styraciflua*	N	None	Pool
			P	Decrease	Pool
Forbs					
Boerner (1986)	Natural gradient	*Geranium maculatum*	N	Increase	Concentration[A]
			P	None	Concentration[A]
		Polygonatum pubescens	N,P	Increase	Concentration[A]
Chapin & Shaver (1989)‡	NP fertilization	*Polygonum bistorta*	N	None	Pool
			P	Decrease	Pool
Minoletti & Boerner (1993)	Natural gradient	*Polystichum acrostichoides*§	N,P	None	Concentration[M]
Bowman (1994)	N, P, NP fertilization	'Dry alpine tundra' (F + G)	N	None	Pool
			P	Decrease upon P fertilization	Pool
		'Wet alpine tundra' (F + G)	N,P	None	Pool
Bowman *et al.* (1995)	N fertilization	*Acomastylis rossii*	N	None	Concentration[M]
		Bistorta vivipara	N	None	Concentration[M]
		Artemesia scopulorum	N	None	Concentration[M]
		Bistorta bistortoides	N	None	Concentration[M]

Study	Type	Species	Nutrient resorbed	Response of nutrient resorption to increased availability	Resorption measured as*
Graminoids					
Shaver & Melillo (1984)	NP fertilization	*Carex lacustris*	N,P	Decrease	Concentration^A
		Calamagrostis canadensis	N,P	Decrease	Concentration^A
		Typha latifolia	N,P	Decrease	Concentration^A
Aerts & De Caluwe (1989)	NPK fertilization	*Molinia caerulea*	N,P	None	Concentration^A
Jaramillo & Detling (1992)	Simulated urine patches	*Agropyron smithii*	N	Decrease	Concentration^M
		Bouteloua gracilis	N	Decrease	Concentration^M
Aerts & De Caluwe (1994)	N fertilization	*Carex diandra*	N	Decrease	Concentration^A
		Carex rostrata	N	Decrease	Concentration^A
		Carex lasiocarpa	N	Decrease	Concentration^A
		Carex acutiformis	N	Decrease	Concentration^A
Bowman *et al.* (1995)	N fertilization	*Kobresia myosuroides*	N	None	Concentration^M
		Calamagrostis purpurascans	N	None	Concentration^M
		Carex rupestris	N	None	Concentration^M
		Deschampsia caespitosa	N	None	Concentration^M

*Concentration^A: based on changes in nutrient concentration per unit leaf area; Concentration^M: based on changes in nutrient concentration per unit leaf mass; Pool: based on changes in foliar nutrient pools.

†'None' also includes nonsignificant trends; ‡No clear statistics provided; §Ferns are included in the category Forbs.