The Mineral Nutrition of Wild Plants Revisited: A Re-evaluation of Processes and Patterns

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I. SUMMARY

This review considers four main topics in the nutritional ecology of wild plants: nutrient-limited plant growth, nutrient acquisition, nutrient use efficiency, and nutrient recycling through litter decomposition. Within each of these four areas, plants have evolved major adaptive strategies with respect to their nutritional ecology.

In most terrestrial ecosystems, plant growth is N-limited but P-limitation also occurs frequently. The type of limitation is determined by differences in biogeochemistry between N and P, by anthropogenic disturbances such as increased atmospheric N deposition and other forms of eutrophication, and by the effects of ecosystem management on N and P cycles. The foliar N : P mass ratio is a good indicator of the type of limitation: plant growth is N-limited at N : P ratios < 14, P-limited at N : P ratios > 16, and co-limited by N and P at intermediate values.

Variation in nutrient uptake capacity is, especially for immobile ions such as phosphate, determined more by biomass allocation patterns than by uptake kinetics. However, species from nutrient-poor habitats do not necessarily allocate more biomass to their roots than species from more fertile environments. These species may compensate for low biomass allocation to the roots by having a high specific root length (SRL: root length per unit root mass). The uptake of organic nitrogen compounds by both mycorrhizal and non-mycorrhizal plants is a novel aspect of the terrestrial N cycle. The ability of plants to use this 'short-cut' of the N cycle may be of great adaptive significance in nitrogen-poor habitats, because it gives some plants access to a nitrogen source of which other species are deprived.

Whole-plant nutrient use efficiency (NUE) is generally measured as productivity per unit nutrient uptake or loss. It is shown that in nutrient-poor environments selection is on traits that reduce nutrient losses rather than on traits conferring a high NUE *per se*. Low tissue nutrient concentrations and low tissue turnover rates, characteristic traits of evergreens, are the most important determinants of high nutrient retention in nutrient-poor environments. High nutrient resorption efficiency, however, is important in all species and does not differ consistently between species from nutrient-poor and nutrient-rich environments. Due to selection on the components of NUE rather than on NUE itself, there are no clear patterns in whole-plant NUE

when comparing species from environments differing in soil fertility. At the phenotypic level, however, NUE decreases with increasing soil fertility.

A theoretical and experimental analysis of the relation between leaf-level NUE and underlying leaf traits showed that, for woody species, leaf-level nitrogen use efficiency (NUE_N) is most strongly determined by variation in mature leaf N concentration. For herbaceous species, however, N resorption efficiency is the most important determinant of NUE_N. For phosphorus use efficiency (NUE_P), P resorption efficiency contributes most strongly to maximization of NUE_P in all growth-forms. This occurs because maximum P resorption efficiency is higher than maximum N resorption efficiency. In addition, at high resorption efficiencies (r) NUE is disproportionally increased by small increases of r. In all growth-forms, leaf lifespan is only a minor contributor to variation in both leaf-level NUE_N and NUE_P. This is not in agreement with the pattern at the whole-plant level. Evergreen species have higher leaf-level NUE_N and NUE_P than other growth-forms.

Litter decomposition is a key process in the nutrient cycles of most terrestrial ecosystems. At large geographical scales, litter decomposition is determined mainly by climatic factors. At a regional scale, however, litter chemistry is the most important determinant of litter decomposability. In most climatic regions, the leaf litter of evergreen shrubs and trees decomposes slower than that of deciduous shrubs and trees. This is due mainly to the low nutrient concentrations in evergreen leaves and the high concentrations of secondary compounds. This implies that the plant characteristics of evergreens do not only lead to high NUE, but also keep soil fertility low and thereby influence the competitive balance with deciduous species in their favour.

II. INTRODUCTION

The mineral nutrition of plants is a central topic of plant ecology. For decades, ecologists have investigated the various adaptations of plant species to different levels of nutrient availability in their natural habitat (e.g. Grime, 1979; Chapin, 1980; Grime *et al.*, 1997). The adaptations to low levels of soil fertility have received particular attention. In 1980, the well-known, and extensively cited paper 'The mineral nutrition of wild plants' was published in the *Annual Review of Ecology and Systematics* (Chapin, 1980). Since then, almost two decades have elapsed, and our ecological knowledge about most of the processes and patterns described in that paper has increased steadily. However, at present there is no paper in which the ideas and hypotheses put forward in that paper (which had a small factual basis) have been critically re-evaluated and subjected to rigorous statistical testing. Here, we review the advances that have been made in understanding the ecology of the mineral nutrition of wild plants from terrestrial ecosystems.

This review is based largely on an analysis of the extensive databases we have collected on various aspects of the mineral nutrition of wild plants. These databases are used to study (quantitatively and qualitatively) the inter-relations among various parameters related to mineral nutrition. We will do this both with respect to variation among growth-forms and to variation in soil nutrient availability. Thus, a substantial part of the review consists of a quantitative evaluation of various aspects of the mineral nutrition of perennials originating from habitats differing in soil fertility with special emphasis on the 'strategies' of different growth-forms and their ecological implications. We will approach the concept of strategies with regard to mineral nutrition by means of the nutrient use efficiency (NUE) of species (see Vitousek, 1982; Berendse and Aerts, 1987). This review focuses on N and P, because these nutrients are the main growth-limiting nutrients for plants in natural environments (Vitousek and Howarth, 1991; Koerselman and Meuleman, 1996; Verhoeven et al., 1996).

Our review is organized along three lines. First, we treat the issues of nutrient-limited plant growth and nutrient uptake, with special emphasis on the importance of the uptake of nutrients in organic form (both by mycorrhizal and by non-mycorrhizal plants) and the importance of symbiotic nitrogen fixation. In addition, we describe the influence of allocation patterns on mineral nutrient uptake. Next, we explore some of the nutritional aspects of leaf functioning and how nutrients are used for biomass production by the plant. We do that by studying the NUE of plants and the various components of NUE. Finally, we investigate the feedback of plant species to soil nutrient availability by reviewing patterns in litter decomposition and nutrient mineralization. The review concludes with a synthesis of the various aspects of the mineral nutrition of wild plants. To that end, we present a conceptual description of plant strategies with respect to mineral nutrition.

III. NUTRIENT-LIMITED PLANT GROWTH: WHICH NUTRIENT IS LIMITING?

A. Differential Limitation by N and P

By definition, mineral nutrients have specific and essential functions in plant metabolism: nitrogen is an important constituent of proteins and thus plays an essential role in all enzymatic activity, whereas phosphorus is involved in the energy transfer in the cell (adenosine triphosphate (ATP), reduced nicotinamide adenine dinucleotide phosphate (NADPH)) and, together with nitrogen, is an important structural element in nucleic acids (Marschner, 1995). Both elements are required for plant growth in relatively large quantities and are therefore classified as macronutrients. As potassium, the other macronutrient, limits plant growth only infrequently (Vitousek and Howarth, 1991; Koerselman and Meuleman, 1996), this element will not be discussed

here. Empirical data shown that a N : P mass ratio in leaves of about 10 is optimal for plant growth (Van den Driessche, 1974; Ingestad, 1979; Lajtha and Klein, 1988), although this ratio varies considerably among species. This suggests that plants should absorb (on a mass basis) about 10 times more N than P to promote balanced plant growth. Deviations from this ratio should, therefore, lead to N- or P-limited plant growth (see below). Nutrient limitation can be evaluated at the level of individual species or at the community level. It is important to distinguish between these levels, because in multispecies communities plant species may coexist that are differentially limited by N and P (DiTomasso and Aarssen, 1989; Koerselman and Meuleman, 1996), although the cause of differential nutrient limitation (N versus P) is not well understood.

At first sight, it seems surprising that plant growth in most non-tropical terrestrial ecosystems is N-limited (DiTomasso and Aarssen, 1989; Bridgham *et al.*, 1995; Shaver and Chapin, 1995; Wassen *et al.*, 1995) despite the wide-spread occurrence of biological N_2- fixation (Vitousek and Howarth, 1991). Vitousek and Howarth (1991) explain the relatively minor contribution of N_2-fixation to N supply in temperate terrestrial ecosystems by energetic constraints on the colonization or activity of nitrogen fixers or by limitation of N- fixers by another nutrient (phosphorus, molybdenum, iron) which would then represent the ultimate limiting factor to net primary production. Ecosystem N budget studies do indeed show that N_2- fixation is only a minor contributor to the total N supply for plant growth in late-successional ecosystems (Hemond, 1983; Morris, 1991; Koerselman and Verhoeven, 1992).

The reasons for differential nutrient limitation include differences in biogeochemistry between N and P (Vitousek and Howarth, 1991), anthro-pogenic disturbances such as increased atmospheric N deposition and other forms of eutrophication (e.g. Aerts *et al.*, 1992a), and effects of ecosystem management on N and P cycles (e.g. Koerselman and Verhoeven, 1992).

The biogeochemical cycles of N and P show many differences. First, they differ in their ultimate source. Nitrogen derives primarily from the atmosphere and phosphorus from rock weathering. As a result, nitrogen is nearly absent from new soils and does then limit Net Primary Production (NPP), whereas it gradually accumulates in the soil during later succession (Tilman, 1986; Vitousek *et al.*, 1987; Berendse, 1990). In contrast, the amount and availability of P decline during long-term soil development and eventually lead to extremely P-deficient soils, as in many tropical soils (Vitousek and Sanford, 1986), soils under Australian and South African–Mediterranean-type vege-tation (Specht and Rundel, 1990; Cowling, 1993), and glacial and aeolean sandy soils under north-west European heathlands (Aerts and Heil, 1993). These opposing trends suggest that during long-term ecosystem development, plant growth should shift from N to P limitation. Second, nitrogen (especially nitrate) is much more mobile in the soil, which promotes nitrogen leaching.

Moreover, nitrogen can easily move across ecosystem boundaries in gaseous form, especially in systems where substantial denitrification occurs or in terrestrial ecosystems with frequent fires. Depending on the magnitude of the N losses due to leaching, denitrification and fire, ecosystems may remain N-limited over long periods of time. Third, detrital N is mostly carbon-bonded whereas detrital P is mostly ester-bonded and often soluble. Due to the production of extracellular phosphatases, this phosphorus may quickly become available for plant uptake again (Hunt *et al.*, 1983; Howarth, 1988) whereas carbon-bonded N may be immobilized for a long time. This would promote N-limitation.

Differential nutrient limitation is caused not only by inherent differences in the biogeochemistry of N and P, but also by differences or changes in external inputs. Atmospheric nitrogen deposition is an important N input to many terrestrial ecosystems in north-west Europe and has a substantial impact on nutrient cycling in these ecosystems (Aerts and Heil, 1993). Human activities have now doubled the annual amount of N sequestered by terrestrial and aquatic ecosystems (Vitousek, 1994). Long-term exposure of ecosystems to high loads of atmospheric nitrogen will lead to an increase in the N : P mass ratio in plant tissues, and this may lead to changes from N-limited to P-limited plant growth (Aerts and Bobbink, 1999). This has been investigated in ombrotrophic raised bogs in Sweden, where strong temporal and spatial gradients in N deposition exist (Malmer, 1988, 1990; Aerts *et al.*, 1992a). These bogs, which are dominated by *Sphagnum* mosses, receive their mineral nutrients solely by atmospheric deposition and are therefore very suitable for monitoring the effects of N deposition on plant growth (Woodin and Lee, 1987; Malmer, 1988; Aerts *et al.*, 1992a). The increase of atmospheric N deposition in southern Sweden which has occurred during the past few decades has indeed resulted in strong increases in the N : P mass ratio in *Sphagnum* mosses (Malmer, 1990). Moreover, fertilization experiments by Aerts *et al.* (1992a) in *Sphagnum*-dominated bogs in Swedish Lapland (low N deposition) and in southern Sweden (high N deposition) showed that plant growth in the low N deposition area was N-limited, whereas in the high N deposition area it had become P-limited. Such a change of the primary element limitation on plant growth from N to P has also been observed in Dutch and Danish heathlands (Aerts and Berendse, 1988; Riis-Nielsen, 1997) and in mesotrophic fens in the Netherlands (Verhoeven and Schmitz, 1991).

Differential limitation by N and P may also be caused by ecosystem management. In north-western Europe, many species-rich fens are managed to preserve the high plant species diversity. The management usually consists of hay-making in summer and removal of the mown biomass (and the nutrients contained therein). Nutrient-budget studies of Dutch fens with a harvest regime have shown that this results in a substantial net P loss from these systems and a relatively small loss of N (Koerselman *et al.*, 1990). The overall

result is that plant growth in fens with a long history of mowing is P-limited, whereas it is N-limited in fens that are very infrequently mown or where mowing has started only recently (Verhoeven and Schmitz, 1991).

B. How to Detect N- or P-limited Plant Growth

It is common practice to study the nature of nutrient limitation in natural plant communities by factorial fertilizer experiments with the macronutrients N, P and K (Chapin et al., 1986b; Boeye et al., 1997). This is a straightforward method for studying nutrient limitation, but there are some associated problems. First, these experiments are time-consuming, laborious and impose some type of disturbance on the study site. Furthermore, due to specific site conditions, interpretation of the results may be difficult. For example, in chalk grasslands, most of the supplied P will be bound to calcium in the soil and will not be taken up by the vegetation. For this reason no growth response may be recorded after P addition, despite the fact that plant growth in such a community may be severely P-limited (Bobbink, 1991, 1992). Another example is provided by fertilization experiments by Shaver and Chapin (1995) in Alaskan tundra. Despite high N and P supply rates, recovery of the supplied N and P in plant biomass was extremely low. The authors suggested that immobilization in the upper moss layer and microbial immobilization played a major role in controlling the fertilizer response of vascular arctic tundra vegetation. Thus, chemical adsorption and microbial immobilization of the supplied nutrients may strongly interfere with the plant responses to nutrient additions.

Recently, Koerselman and Meuleman (1996) proposed to use the N : P mass ratio in plant tissues as an indicator of the type of nutrient limitation. Although this idea is certainly not new (see Redfield, 1958; Van den Driessche, 1974; Ingestad, 1979; Aerts et al., 1992a), a strong factual basis for this idea was provided. Koerselman and Meuleman (1996) collected data from 40 fertilization studies conducted in European wetland ecosystems (bogs, fens, wet heathlands, dune slacks, wet grasslands). They plotted the P-concentration against the N-concentration in above-ground bulk samples from the unfertilized controls of these experiments and indicated which type of limitation was found in the fertilization studies (Figure 1). The vegetation N : P ratio clearly discriminates between N- and P-limited sites. At N : P ratios > 16, the community biomass production was P-limited, whereas at N : P ratios < 14 there was N-limited plant growth in all but one study. At N : P ratios between 14 and 16, co-limitation by N and P occurred. In their analysis N concentrations varied more than 3-fold, whereas P concentrations varied more than 16-fold. Koerselman and Meuleman argued that this huge variation probably reflects differences in the supply ratio of N and P rather than differences in absolute N and P availability. Figure 1 also shows that there is no clear
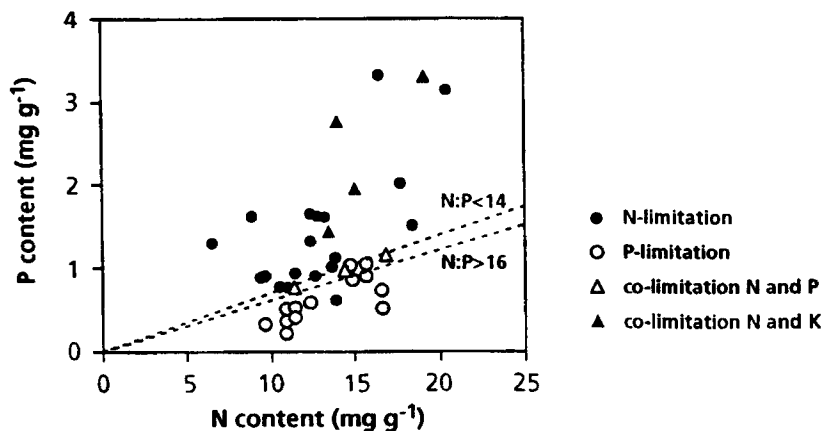
Fig. 1. Relationship between vegetation N and P content and the nature of nutrient limitation in 40 European wetlands (bogs, poor fens, rich fens, wet heathlands, wet grasslands and dune slacks). Data points are from studies in which fertilization experiments showed which type of nutrient limitation occurred. The nutrient contents shown were determined in unfertilized control plots. Dashed lines depict N : P mass ratios of 14 and 16, respectively. Redrawn from Koerselman and Meuleman (1996).

relationship between the nutrient concentration in plant tissue and the nature of nutrient limitation. For example, in wet grasslands nitrogen was limiting plant growth at relatively high concentrations of about 20 mg N g^{-1}, whereas it did not limit plant growth in wet heathlands and rich fens at concentrations of around only 10 mg N g^{-1}. Thus, in the data analysed by Koerselman and Meuleman (1996), it really is the ratio between N and P that controls plant growth, not the absolute concentration in plant tissue. However, in some cases very low concentrations of N and/or P may limit plant growth despite the fact that the N : P ratio may be favourable.

Use of the N : P ratio is a meaningful and easy first approach to the determination of nutrient limitation in plant species and plant communities. However, use of this parameter does not solve all problems involved in the determination of the type of nutrient limitation. The first problem with the analysis by Koerselman and Meuleman (1996) is that they apparently assume that the growth of plant species or vegetation is always limited by N and/or P. However, when both nutrients are in ample supply, the N : P mass ratio will still indicate a type of nutrient limitation, despite the fact that this is clearly not the case. A second point is that it is necessary to differentiate between nutrient limitation at the community level and limitation at the species level. Koerselman and Meuleman (1996) present a nice example in which it is shown that in several communities the N : P mass ratio of individual species is so different from that of the community as a whole that it must be concluded that

the growth of these species is controlled by an element that does not control community biomass production. This conclusion is supported by experimental data reviewed by DiTomasso and Aarssen (1989).

IV. NUTRIENT ACQUISITION

A. Root Uptake

The rate of nutrient acquisition by a plant is a function of the rate of uptake per gram of biomass, its total biomass, and the proportion of biomass allocated to nutrient-absorbing tissues. In this section we consider only the first of these factors. Allocation will be treated in the next section. Nutrient uptake is a complex process that involves (1) nutrient movement to the root surface, (2) the transport of nutrients from the root surface into the plant, (3) the capacity to form symbiotic linkages with mycorrhizal fungi or nitrogen-fixing bacteria and (4) modification of the soil environment to enhance nutrient supply. Each of these processes is strongly influenced by the physical relationship between roots and soil, making it difficult to determine which processes and traits actually control nutrient acquisition under natural conditions. We arbitrarily separate the plant effects on these processes in terms of physiological uptake by roots or leaves, rhizosphere effects, and mycorrhizal and N-fixing symbioses.

1. Patterns of Nutrient Uptake

Plants adapted to infertile soils typically have a high capacity (high V_{max}) to absorb mobile ions such as potassium (Veerkamp and Kuiper, 1982) but a relatively lower capacity to absorb immobile ions like phosphate (Chapin et al., 1986a; Raab et al., 1998). Presumably a low uptake capacity for immobile ions is not strongly disadvantageous in a low-nutrient environment because diffusion so strongly limits uptake in this situation that uptake capacity has little influence on nutrient uptake, and because mycorrhizal transfer may be more important than root uptake. Diffusion is less limiting to mobile ions, so there is selection for a high capacity to absorb these ions in plants adapted to infertile soils (Chapin, 1988).

Nitrogen differs from other nutrients in that it occurs as multiple forms in the soil: nitrate, ammonium and organic N. Most plants absorb any form of soluble nitrogen that is available in the soil, especially if acclimated to its presence (Atkin, 1996). However, since plants must synthesize different carrier proteins to absorb each N form, they differ in their relative preference for different N forms, depending on the relative supply of ions in the soil. For example, arctic and alpine plants, which experience high amino acid concentrations in soil and where N mineralization and nitrification are

strongly constrained by low temperature, preferentially absorb and grow on amino acids, whereas barley preferentially absorbs inorganic nitrogen (Chapin et al., 1993; Kielland, 1994; Raab et al., 1996). Spruce, which also grows on acid soils, preferentially absorbs ammonium over nitrate (Kronzucker et al., 1997), with untested capacity to absorb amino acids. Boreal forest herbs and shrubs also preferentially absorb glycine (an amino acid) over inorganic N in field experiments in Sweden, regardless of mycorrhizal status (Näsholm et al., 1998). In general, species from habitats with high nitrate availability (e.g. calcareous grasslands) preferentially absorb nitrate and have higher capacities to reduce nitrate than do species from low-nitrate habitats. Conversely, many plant species from habitats where ammonium is the dominant form of available nitrogen preferentially absorb ammonium relative to nitrate. Until recently, few studies have examined the capacity of plants to absorb organic N because it was assumed that microbes would outcompete plants for this N form. However, since N is typically transformed from insoluble organic N to soluble organic N to ammonium to nitrate, with some uptake of these forms by plants and/or microbes at each step, the supply rate in any soil must be in the order: soluble organic N $\geq$ ammonium-N $\geq$ nitrate-N (Eviner and Chapin, 1997). Thus the potential of plants to absorb soluble organic N may be much more important than previously appreciated (see section IV.B).

Plants can also tap organic P through production of phosphatases by roots. Phosphatase production is enhanced by a low P supply to the plants. The capacity to use organic P varies among species and also depends on soil conditions. It may range from almost zero to a capacity sufficient to explain most of the P acquisition by the plant (Kroehler and Linkins, 1991; Hübel and Beck, 1993). However, at present it is not clear whether this high potential uptake of organic P sources is also realized under field conditions.

2. Dependence on Nutrient Availability

Any factor that increases plant demand for a particular nutrient increases the plant's capacity to absorb that nutrient. Thus, high availability of light, warm temperature, and favourable moisture all lead to a high uptake capacity by a given genotype. With respect to nutrients, this adjustment in uptake capacity is specific to the nutrient that limits growth: nitrogen stress increases the potential to absorb nitrate or ammonium but decreases the potential to absorb other non-limiting nutrients, whereas phosphorus stress increases the capacity to absorb phosphate but reduces the capacity to absorb other ions (Lee, 1982) (Table 1). The situation with nitrate uptake is more complex than that of other ions, because plants must both absorb and assimilate nitrate (i.e. convert it to ammonium) before it becomes nutritionally useful. Plants exhibit a low constitutive level of nitrate uptake when grown in the complete

Table 1
Effect of environmental stresses on nutrient uptake rate (from Chapin, 1991).

Stress	Ion absorbed	Uptake rate by stressed plant (% of control)
Nitrogen	Ammonium	209
	Nitrate	206
	Phosphate	56
	Sulfate	56
Phosphorus	Phosphate	400
	Nitrate	35
	Sulfate	70
Sulfur	Sulfate	895
	Nitrate	69
	Phosphate	32
Water	Phosphate	13
Light	Nitrate	73

Values are for barley, except for water stress (tomato).

absence of nitrate; this uptake rate increases upon exposure to nitrate as a result of induction of synthesis of more carriers and of nitrate reductase (Huang et al., 1996).

Plants not only increase the maximum rate at which they acquire a nutrient under conditions of low supply but also reduce the leakage of nutrients out of the root, enabling them to acquire nutrients at lower external concentrations (Kronzucker et al., 1997). Efflux may actually be more important than influx in explaining differences in net nutrient uptake by plants (Kronzucker et al., 1997). Thus, plants are able to reduce external concentrations to lower levels under conditions of nutrient stress. This is consistent with Tilman's (1988) R* concept of competition, in which plants are presumed to compete effectively with their neighbours by reducing the concentration of a resource to concentrations lower than can be acquired by their neighbours. The capacity of plants to alter uptake capacity in response to growth at different nutrient levels is best developed in plants with high relative growth rate (Veerkamp and Kuiper, 1982; Chapin et al., 1986a), which is consistent with Grime's (1979) concept that rapidly growing plants have a high capacity to acquire nutrients.

B. Mycorrhizal Uptake

Most plants in both natural ecosystems and croplands are mycorrhizal and probably acquire a large proportion of their nutrients via mycorrhizas. However, a few plant species, especially those that predominate in disturbed

or fertile soils (e.g. Brassicaceae), do not form mycorrhizal associations (Allen, 1991; Smith and Read, 1997). Mycorrhizas are thought to acquire nutrients at a lower carbon cost than roots because of their smaller diameter and greater surface : volume ratio. Arbuscular mycorrhizas (AMs), which are generally associated with herbaceous plants or tropical trees, are critically important for the uptake of nutrients that diffuse slowly in soil, especially P, although mycorrhizas have also been implicated in absorption of NH_4^+ and other nutrients (Smith and Read, 1997). When mycorrhizal associations are experimentally suppressed in N-limited grasslands, plant production can become P-limited, suggesting that effective P uptake by mycorrhizas may be an important factor explaining the widespread N-limitation of temperate ecosystems (Grogan and Chapin, in press).

In recent years, it has become clear that the uptake of organic nitrogen compounds by both mycorrhizal and non-mycorrhizal plants is an important pathway in the terrestrial nitrogen cycle (Read, 1991; Chapin et al., 1993; Kielland, 1994; Northup et al., 1995; Turnbull et al., 1995). The ability of plants to use this 'short-cut' of the N cycle may be of great adaptive significance in nutrient-poor habitats, because it gives plants access to a nitrogen source of which other species are deprived. However, in temperate ecosystems the ability to take up organic N sources is restricted mainly to plants with ericoid mycorrhizas (EMs) and ectomycorrhizas (ECMs), and hardly occurs in species with arbuscular mycorrhizas (AMs) and in non-mycorrhizal plants (Smith and Read, 1997). The litter of EM plants usually has higher concentrations of secondary compounds than litter from AM and non-mycorrhizal plants, which may retard N mineralization and thus decrease the availability or inorganic N in the soil (Aerts, 1997b). It has been hypothesized that the use of differential nitrogen sources by the different mycorrhizal types may create positive feedbacks between plant species dominance, litter chemistry and mycorrhizal type. However, until now there has been hardly any field evidence for this hypothesis. Heathlands are very suitable ecosystems for investigating the ecological significance of differential uptake of organic and inorganic nitrogen sources. In nutrient-poor heathlands, ericoid species (in north-west Europe: *Erica tetralix, Calluna vulgaris* and *Empetrum nigrum*) predominate (Aerts and Heil, 1993). These ericoid mycorrhizal species have the ability to use organic N sources for their mineral nutrition, thus making them less dependent on mineralization of organic matter (Read, 1991). In these heathlands, the vegetation also contains grasses such as *Deschampsia flexuosa* and *Molinia caerulea* which have a high competitive ability only at high levels of nutrient availability. These species, with AMs, have no or only a very limited capacity to utilize organic N sources. This is a strong disadvantage under nutrient-poor conditions. This fascinating mechanism of species coexistence as a result of differential use of soil N sources may be disrupted as a result of increased

levels of atmospheric N deposition (Aerts and Bobbink, 1999). This results in both higher availability of inorganic N and in an increase in the ratio between inorganic and organic N in the soil. This may affect the degree of EM colonization, thus depriving the ericoid species of their relative advantage in nutrient-poor soils, and may increase the competitive ability of the grasses, because they can now utilize the inorganic N sources. Clearly, investigation of this type of species interaction may significantly contribute to our understanding of the regulation of species distribution over soil fertility gradients.

Plants reduce their degree of mycorrhizal infection under conditions of high nutrient supply (reviewed in Aerts and Bobbink, 1999), because under these circumstances plants can readily meet their nutrient requirements through direct uptake by roots without the additional carbon expenditure required to support mycorrhizal fungi. This explains why non-mycorrhizal genotypes grow more rapidly then mycorrhizal ones in fertile soils but grow quite slowly in low-P soils (Koide, 1991).

C. Leaf Uptake and Loss

Leaves, like roots, can both absorb and lose nutrients to solutions on the leaf surface, primarily by movement through the stomata (Sutton *et al.*, 1993). Therefore, uptake rates by leaves are greatest in species that have high stomatal conductance (generally rapidly growing species with a high Specific Leaf Area—leaf area per unit leaf mass). Environmental conditions that favour high stomatal conductance (e.g. high light and water supply) also favour high uptake rates by leaves (Sutton *et al.*, 1993). The effect of nitrogen status of leaves is variable among studies. Leaves with high N status have high stomatal conductance (promoting uptake) but also tend to lose NH_3 more readily through stomata (see below).

Leaves with high nutrient concentrations lose more nutrients than those with low tissue concentrations, in either gaseous form (NH_3) or as solutions. The susceptibility to leaching loss is greatest for monovalent cations (Na, K), less for divalent cations, and least for organically bound nutrients such as N and P (Tukey, 1970; Chapin and Moilanen, 1991). Nutrient loss by leaching is greatest when water first contacts a leaf (Tukey, 1970). N and P loss is most pronounced during autumn, when nutrients are mobilized by the senescence process. Deciduous and evergreen trees both lose approximately 15% of their annual above-ground nutrient return to the soil via leaching (Table 2). The higher rates of nutrient loss by deciduous species are balanced by the greater time during which evergreen leaves are available to be leached.

Nutrient absorption by leaves can be a net source of nutrients to plants when concentrations are high in rain water or when there are high concentrations of

Table 2
Nutrients leached from the canopy (throughfall) as a percentage of the total above-
ground nutrient return from plants to the soil for 12 deciduous and 12 evergreen
forests (from Chapin, 1991)

Nutrient	Throughfall (% of annual return)	
	Evergreen forests	Deciduous forests
N	14 ± 3	15 ± 3
P	15 ± 3	15 ± 3
K	59 ± 6	48 ± 4
Ca	27 ± 6	24 ± 5
Mg	33 ± 6	38 ± 5

Values are mean ± SD.

NH_3 in the air. The most dramatic examples of N uptake by leaves occur
downwind from industrial sources of NO_x or agricultural sources of volatilized
NH_3.

D. Symbiotic N Fixation

There is a vast literature on symbiotic N fixation, so only those patterns related
to plant nutrition will be summarized here. As with root uptake and mycor-
rhizal association, species differ in their capacity to acquire N by symbiotic
fixation, with this capacity restricted to eight families among vascular plants,
including Fabaceae (with about 3000 N-fixing species) and Betulaceae (e.g.
Alnus) (Lambers *et al.*, 1998). Among species with the capacity to fix N, there
are strong differences in the N fixation rate among genotypes of both the plant
and microbial symbiont. The N fixation rate is sensitive to plant nutrient
status. Under conditions of low N supply, symbiotically fixed N can account
for more than 75% of the nitrogen acquired by clover (Boller and Nösberger,
1987) and often accounts for half or more of plant nitrogen in other species
with N-fixing symbionts (Gault *et al.*, 1995; Vance, 1995; Sprent *et al.*, 1996;
Lambers *et al.*, 1998). N-fixing plants reduce the N fixation rate when grown
in soils with a high N supply, presumably to reduce the high energetic cost of
N fixation (Marschner, 1995). Conversely, soils that are low in P support low
fixation rates because of the important role of P in the energetics of N fixation.

E. Rhizosphere Effects

Plants strongly influence rates of N and P uptake from soil by modifying the
physical and chemical nature of the rhizosphere. Mass flow of soil solution to
the root caused by transpiration carries soluble N and P to the root surface,
where it is available for uptake. In crops, mass flow supplies an estimated

80% of total N delivery to the root but only 5% of P delivery, because of the greater mobility of N in soils (Lambers *et al.*, 1998). In infertile tundra soils, where the concentration of N and P in the soil solution are much lower, mass flow supplies less than 1% of N and P delivery to the root surface. Diffusion and transport by mycorrhizal fungi are the major mechanisms, other than mass flow, that move nutrients to the root surface.

When plants absorb an excess of cations over anions, as commonly occurs when N is absorbed as an organic acid or ammonium, roots secrete H^+ to maintain charge balance. The resulting decline in rhizosphere pH can reduce P availability in acidic soils (Marschner, 1995).

In organic soils, most soluble P is organic. Root surface phosphatases can account for most of the P acquired by plants in these soils (Kroehler and Linkins, 1991), as described above. Some plants also secrete organic acids which can increase P availability both by acidifying the rhizosphere (in calcareous soils) and by chelating cations that form insoluble phosphates. By solubilizing these compounds, chelates enhance P diffusion to the root surface. Iron phosphate is a common form of insoluble phosphate in acid soils, and plants typical of these soils secrete pisidic acid which chelates iron and solubilizes phosphate. Plants typical of calcareous soils produce citrate, which increases P availability by chelating calcium (Marschner, 1995). Secretion of these organic acids is greatest under P-limiting conditions (Johnson *et al.*, 1996).

Plants also strongly influence nutrient availability in the rhizosphere through the exudation of organic acids, carbohydrates and amino acids, which stimulate microbial activity. Root exudates appear to stimulate net N mineralization under relatively fertile conditions, where soil microbes are carbon-limited (Zak *et al.*, 1994; Hungate, 1998), but cause microbial immobilization of N in infertile soils (Diaz *et al.*, 1993). An additional mechanism by which exudation can enhance nutrient supply is through the stimulation of microbial grazers such as amoebae and nematodes, which feed on bacteria and excrete excess N; this N is then available for absorption by plants (Clarholm, 1985). Annual N uptake by vegetation is often twice the N mineralization estimated from incubation of soils in the absence of roots (Chapin *et al.*,1988). Much of this discrepancy could involve more rapid nutrient cycling that occurs in the rhizosphere, as fuelled by root exudation. Root exudation rates differ several-fold among species (V.T. Eviner, unpublished data), but the differences in exudation rates among plant growth forms and the nutritional controls on exudation are poorly known.

V. BIOMASS ALLOCATION IN RELATION TO NUTRIENT ACQUISITION

Because the bulk of the nutrients required for plant growth usually enters the plant by means of root and/or mycorrhizal uptake (section IV), the allocation of biomass to roots is an important determinant of nutrient acquisition. Studies on

the allocation of biomass began early in this century (e.g. Turner, 1922; Crist and Stout, 1929). Important progress was made with the classical papers by Brouwer (1962a,b) on the effect of light intensity and nutrient supply on the partitioning of biomass between shoots and roots. These papers were the basis for the 'functional equilibrium' concept. Since then, Brouwer's findings have been corroborated by numerous other studies (e.g. Chapin, 1980; Robinson and Rorison, 1983; Boot and Den Dubbelden, 1990; Boot and Mensink, 1990; Garnier, 1991; Aerts et al. 1991, 1992b). Allocation to the root system can be studied at the between-organ level (root weight ratio (RWR)—root mass as a fraction of total plant mass) or at the within-organ level (specific root length (SRL)—root length per unit root mass) (Trewavas, 1986). Moreover, root hair density is an important determinant of nutrient acquisition, particularly for nutrients with a low mobility in soil, such as phosphate (Clarkson, 1985; Hofer, 1991). Finally, root architecture is an important determinant of the efficiency of exploration and exploitation of mobile soil resources (Fitter, 1987, 1991).

An important question is whether there are inherent differences in biomass allocation patterns between species from nutrient-poor and nutrient-rich habitats. Studies on this topic are often complicated by the fact that allocation patterns are very plastic and are strongly influenced by light intensity and nutrient levels (Brouwer, 1962a,b; Robinson, 1986; Robinson and Rorison, 1988; Aerts and De Caluwe, 1989; Boot and Den Dubbelden, 1990; Olff et al., 1990, Olff, 1992). Therefore, the adaptive significance of allocation patterns has to be studied at several levels of resource availability. In this review, we will confine ourselves to the relation between allocation patterns and nutrient availability.

A. Patterns in Biomass Allocation

It has long been postulated that plants from infertile sites allocate more biomass to roots than do plants from more fertile sites (Grime, 1979; Chapin, 1980; Tilman, 1985, 1988; Tilman and Wedin, 1991). This contention was mostly based on relatively short-term studies (several weeks) in growth cabinets with juvenile plants grown at optimal levels of resource availability without inter-ference with other plants. For example, Poorter and Remkes (1990) and Poorter et al. (1990) studied relative growth rate (RGR—growth rate per unit plant mass) and allocation in 24 wild plant species and found that biomass allocation to the leaves (leaf weight ratio (LWR)) and the ratio between leaf area and leaf mass (specific leaf area (SLA)) were positively correlated with RGR. Moreover, differences in potential RGR were habitat related: fast-growing species are found in environments with high levels of resource availability, whereas slow-growing species occur in all kinds of adverse environments. These observations agree with the hypothesized higher root allocation of slow-growing species. Garnier (1991, 1992) showed that the trend of increasing RGR with increasing biomass allocation to leaves, as reported by Poorter and

Remkes (1990), only holds for dicotyledonous species and not for grasses. Monocotyledonous herbaceous species allocate relatively more biomass to the roots and less to leaves, compared with dicotyledonous herbaceous species with the same inherent RGR (Garnier, 1991). Van der Werf *et al.* (1993) also found that there were only minor interspecific differences in allocation patterns in a growth analysis among five monocotyledonous species from low- and high-productive habitats at high N, whereas at low N supply the fast-growing species allocated more biomass to their roots than did the slow-growing species. Thus, these growth cabinet studies indicate that allocation patterns are quite variable and depend strongly on the growth-form under consideration.

These growth analysis data, obtained from studies with juvenile plants under artificial conditions, cannot easily be extrapolated to field situations (Garnier and Freijsen, 1994). Field studies conducted by Berendse and Elberse (1989), Olff *et al.* (1990), Tilman and Cowan (1989), Gleeson and Tilman (1990) and Aerts (1993) showed that fast-growing species from nutrient-rich sites had higher biomass allocation to the roots than slow-growing species from nutrient-poor sites. This suggests that these species have a higher capacity for nutrient uptake. However, nutrient uptake is often better correlated with root length than with root mass (Fitter, 1991). Thus, species may compensate for low biomass allocation to the roots by having a high SRL. This has indeed been found in some studies with species from nutrient-poor sites (Aerts *et al.*, 1991; Elberse and Berendse, 1993). This strongly suggests that there are different evolutionary solutions to the allocation problem: plants may have a high nutrient uptake capacity as a result of high biomass allocation to the roots, or they may have high uptake capacity by having a lower root allocation but a higher SRL. These results are not consistent with theories of evolutionary trade-offs in allocation between shoot and root.

Nutrient uptake depends not only on specific absorption rate (SAR–uptake rate per gram of root), SRL and proportional allocation to roots, but also on plant biomass. At the level of the ecosystem, nutrient supply should be considered as an absolute resource (expressed, for example, as the amount of nutrients per unit of ground area). So nutrient acquisition depends on the absolute amount of nutrient-absorbing tissues (expressed, for example, as root mass or root length per unit of ground area). Root biomass depends on both the biomass of plants and the proportion of that biomass allocated to roots. This implies that allocation ratios are only poor indicators of resource capture. This is illustrated by a study with experimental populations of *Carex diandra, C. rostrata* and *C. lasiocarpa* (species from mesotrophic fens) and *C. acutiformis* (a species from eutrophic fens). It was found that percentage biomass allocation to below-ground parts (roots + rhizomes) was higher in the low-productive species (Aerts *et al.*, 1992b). However, because of the higher total biomass of the high-productive species at high N supply, their absolute below-ground tissue mass significantly exceeded that of the low-productive species. This implies that these high-productive species have a

lower RWR, but a higher root mass per unit of ground area, and can therefore acquire more nutrients.

From these results, we conclude that allocation patterns found in growth cabinet studies cannot be extrapolated directly to field situations, especially when species with different biomasses and/or different growth-forms are compared. Moreover, the adaptive significance of root biomass allocation patterns is probably less important than root morphology (i.e. SRL) in explaining species adaptations to habitats with different levels of nutrient availability.

B. Dependence on Nutrient Availability

The most frequently observed phenotypic response to suboptimal nitrogen supply is an increase in biomass allocation to the roots, especially in fast-growing species (e.g. Aerts and De Caluwe, 1989; Boot and Den Dubbelden, 1990; Shipley and Peters, 1990; Tilman and Wedin, 1991; Lambers and Poorter, 1992; Van der Werf *et al.*, 1993; Wilson and Tilman, 1995). This effect is observed both in growth cabinet and field studies. This raises the issue of the relative importance of phenotypic responses of root allocation compared with inherent interspecific differences. Olff (1992) studied the effects of light and nutrient availability on dry matter and N allocation in six successional grass species. He found that phenotypic responses to variation in light and nutrient supply were much larger than interspecific differences. This emphasizes once again the very plastic nature of resource allocation in plants.

Nutrient supply varies spatially as well as temporally (Campbell and Grime, 1989, 1992). Many species are capable of rapid root proliferation into nutrient-rich patches (De Jager, 1982; Crick and Grime, 1987; Eissenstat and Caldwell, 1987; Campbell *et al.*, 1991; Berntson *et al.*, 1995; Grime *et al.*, 1997). This high plasticity in the spatial arrangement of the root system may be of great adaptive significance in soils with strong spatial differences in nutrient availability.

Nutrient supply effects on SRL are variable. In some studies, SRL does not change with changes in nutrient supply (Fitter, 1991; Aerts *et al.*, 1992b). In other studies, SRL is higher under conditions of low nutrient availability (Fitter, 1985; Boot and Mensink, 1990; Hetrick *et al.*, 1991; Berntson *et al.*, 1995). This increases the uptake capacity of the root system.

Root hair formation also depends on nutrient availability. In agricultural plants root hair formation increased at low levels of phosphate and nitrate supply (Föhse and Jungk, 1983). Also in grass species an increased root hair length was observed in response to low nutrient supply, especially in slow-growing species (Boot and Mensink, 1990; Liljeroth *et al.*, 1990).

In conclusion, most plant species are very plastic in adjusting various aspects of root allocation to changes in mineral nutrient supply. Among herbaceous species, fast-growing species show a higher phenotypic plasticity than slow-growing species (Lambers and Poorter, 1992). This high degree of

plasticity contributes to an ability for high rates of resource acquisition in productive habitats and as such confers to the success of fast-growing species in these environments (Grime *et al.*, 1997). However, among broader comparisons of growth-forms there is no relationship between growth rate and plasticity of root : shoot ratio (Reynolds and D'Antonio, 1996). Often plasticity in some traits (e.g. root : shoot ratio) leads directly to low plasticity in other traits (e.g. nutrient concentration), so that it is unlikely that there is a general relationship between plasticity and relative growth rate.

VI. NUTRIENT STORAGE

A. The Concept of Storage

Storage constitutes the resources that build up in a plant and can be mobilized in the future to support biosynthesis. There are three general categories of storage (Chapin *et al.*, 1990):

(1) Accumulation is the increase in compounds that do not directly promote growth. Accumulation occurs when resource acquisition exceeds demands for growth and maintenance (Millard, 1988). Accumulation accounts for much of the short-term fluctuation in chemical composition of plants, for example the daily fluctuation of leaf carbohydrates or the nitrogen accumulation, also termed 'luxury consumption', that occurs following pulses of nitrogen availability.

(2) Reserve formation involves the metabolically regulated synthesis of storage compounds that might otherwise directly promote growth. Reserve formation directly competes for resources with growth and defence (Rappoport and Loomis, 1985). For example many plants divert nitrogen to storage organs in autumn, despite strong limitation of production by N supply (Shaver *et al.*, 1986).

(3) Recycling is the reutilization of compounds whose immediate physiological function contributes to growth or defence but which can subsequently be broken down to support future growth (Chapin *et al.*, 1990). Recycling of nutrients following leaf senescence allows reutilization of about half of the nitrogen and phosphorus originally contained in the leaf (section VII.B). These stored nutrients are then a nutrient source for new growth at a later time.

B. Variation among Growth-forms

Most plants depend strongly on storage, but the time-scale of this dependence and the type of storage differ among growth-forms. Annual plants invest most nutrients directly into growth with minimal reserve storage. At the initiation of reproduction, roots and leaves begin to senesce, with nutrients being recycled

from vegetative to reproductive tissues. Typically 50–90% of N and P but less than 5% of the carbon is recycled from vegetative to reproductive tissues (Chapin and Wardlaw, 1988). Annuals also show relatively modest short-term nutrient accumulation in response to pulses of nutrient supply, because their rapid growth enables pulses of growth to match pulses of supply (Chapin *et al.*, 1990).

Most perennial plants depend strongly on storage, but the type of storage differs among species. Biennials and species adapted to frequent disturbances develop large nutrient storage reserves, even under conditions of nutrient limitation. For example, during the first year of growth biennials such as *Arctium tomentosum* develop a taproot that stores nutrients and carbohydrates, but form only a rosette of leaves above ground (Heilmeier *et al.*, 1986; Heilmeier and Monson, 1994). These reserves in the taproot support rapid growth the following year. Similarly, many mediterranean shrubs develop large N and P reserves that can support regrowth after fire, despite strong nutrient limitation in these habitats; these storage reserves are typically best developed in 'sprouter' species with low RGR rather than in more rapidly growing 'seeder' species (Keeley and Zedler, 1978).

Evergreen species are thought to depend less on reserve storage than deciduous species, because much of the leaf senescence coincides with new growth, allowing direct recycling of nutrients from old to new leaves (Chapin and Shaver, 1989; Nambiar and Fife, 1991). Jonasson (1989) tested this hypothesis by removing old leaves of several evergreen species from different ecosystems but found that this had no effect on the nutrient pools in new leaves. This discrepancy demonstrates clearly that it is impossible to make conclusions about the importance of storage simply by comparing the patterns of nutrient loss from old tissues with nutrient gain in new tissues. Often the patterns of nutrient stores in below-ground parts and nutrient uptake are unknown and assumed to be unaffected. Clearly, experiments such as those of Jonasson (1989) are required to demonstrate the situations when storage is important.

C. Nutrient Dependency

Increased nutrient supply directly augments nutrient accumulation in all plants (i.e. the accumulation of nutrients in excess of immediate needs for growth) (Schulze *et al.*, 1985). This nutrient accumulation is most pronounced in plants that grow slowly, because these species typically have lower plasticity in their capacity to invest newly acquired nutrients in growth (Chapin *et al.*, 1990). Seasonal reserve storage is much more pronounced (and increases more strongly in response to nutrient addition) in perennial forbs, graminoids and deciduous shrubs than in evergreens (Chapin and Shaver, 1989).

VII. NUTRITIONAL ASPECTS OF LEAF TRAITS

In the coming sections we explore how various leaf traits (leaf nutrient concentration, nutrient resorption from senescing leaves, and leaf lifespan) vary among growth-forms and how they are affected by changes in mineral nutrient supply. Next, we explore how these leaf traits contribute to leaf-level nutrient use efficiency (NUE). In perennials, NUE is generally measured as productivity per unit nutrient uptake or loss (cf. Vitousek, 1982). A commonly used index for NUE is the inverse of litter nutrient concentrations.

The data used in these sections mainly originate from the database presented in Aerts (1996) with minor additions from the literature about leaf lifespan and related traits listed in Reich et al. (1992). The calculation of the NUE index of Vitousek (1982) requires data on both nutrient concentration in mature leaves and on nutrient resorption from senescing leaves. As a result, about 15% of the data of Aerts (1996) could not be used, because those data originated from papers in which only one of the two parameters was presented. Nevertheless, the data set used here is about five times as large as the 'NITROGEN' data set of Reich et al. (1992), and three times as large as the data set of Killingbeck (1996) on resorption efficiency, and therefore provides a strong basis for evaluating general patterns in leaf-level NUE and its underlying components.

A. Leaf Nutrient Concentrations

In a recent analysis of a wide array of plant traits, Grime et al. (1997) suggested that mineral nutrients should be considered as the fundamental currency of vegetation processes at scales ranging from the individual to ecosystems. They found a marked correlation between foliar concentrations of N, P, K, Ca and Mg, high concentrations of which coincided with the capacity for rapid growth in productive conditions and an inability to sustain yield under limiting supplies of nutrients. Thus, leaf nutrient concentrations are important determinants of the functioning of plant species in their habitat.

1. Variation among Growth-forms

Nitrogen concentrations in mature leaves of perennials show clear differences between growth-forms (Figure 2A). Evergreens have significantly lower N concentrations than forbs and graminoids, and deciduous species have the highest N concentrations. The large data set ($n = 77$) of Thompson et al. (1997) on N and P concentrations in temperate herbaceous species was not included in the analysis because it did not meet the criterion that leaf-level NUE could be calculated from the basic data. If those data had been included, then forbs and graminoids would have had the highest N and P concentrations in mature
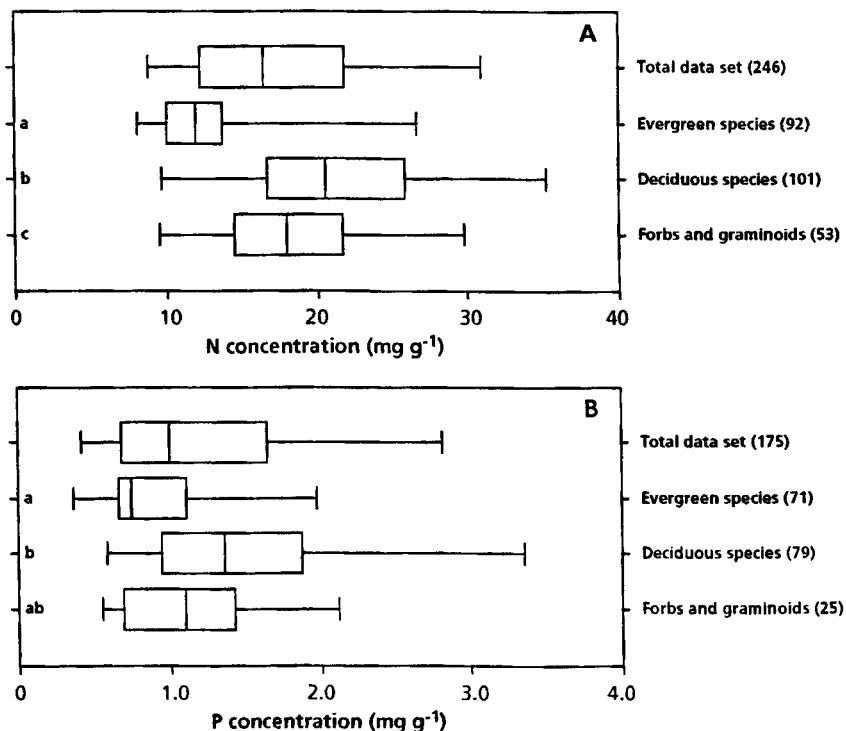
Fig. 2. Box plots showing the distribution of (A) leaf N and (B) leaf P concentrations. Results are presented for the entire data set, evergreen shrubs and trees, deciduous shrubs and trees, and forbs and graminoids. The middle line in each box indicates the geometric mean of the observed distribution, the left and right parts the 25th and 75th percentiles, and the left and right 'error bars' the 5th and 95th percentiles. Values in parentheses indicate number of observations. Different letters indicate statistical difference between growth-forms (Tukey test after analysis of variance, $P < 0.05$).

leaves. However, as is clearly shown in Figure 2, there is considerable overlap among the various growth-forms. Thus, growth-form comparisons within small subsets of the data may lead to another pattern. As the carbon assimilation of a leaf is linearly related to the nitrogen content of that leaf (Field, 1983; Hunt *et al.*, 1985; Hirose and Werger, 1987; Evans, 1989), this implies that the patterns of N concentration in mature leaves have clear consequences for the carbon gain of these growth-forms. Another ecological factor that might be correlated with variation in leaf N concentration is chemical defence against herbivory. According to the carbon-nutrient balance theory of Bryant *et al.* (1983), chemical defence against herbivory should be carbon based in nutrient-poor habitats and nitrogen based in more carbon-limited habitats. At present, it is not

clear how much of the nitrogen present in leaves should be considered as 'defence N'. Thus, it is not clear what the contribution is of N-based defence to the variation in leaf N concentrations as shown in Figure 2.

The pattern of phosphorus concentrations is more or less similar to that of N concentrations, but in general the variation is larger (Figure 2B). Phosphorus concentrations in leaves of evergreen species are lower than in deciduous species. Forbs and graminoids occupy an intermediate position (but see the comment above). As is the case with nitrogen, these patterns may have direct consequences for the rate of photosynthesis in the leaves. It has been shown that the rate of photosynthesis is dependent on the leaf P concentration (Herold, 1980) and that P deficiency inhibits photosynthesis (Terry and Ulrich, 1973). However, in most cases photosynthetic rate correlates more closely with N than with P concentration.

The larger variation in leaf P concentration compared with leaf N concentration was also observed by Fitter et al. (1998) for temperate and tropical plants. They found that leaf P concentration is not correlated simply with leaf N concentration, resulting in an even larger variation in leaf N : P ratios compared with the variation in concentrations of N and P (cf. section III). They concluded that leaf N concentrations are more closely regulated than leaf P concentrations and that, despite the widespread occurrence of mycorrhizal symbiosis, the variation in leaf P concentrations most likely reflects the variation in P availability in various habitats. The question that remains then is how plants respond to variation in leaf P concentration. Fitter et al. (1998) showed that leaf P concentration probably plays a crucial role in the regulation of resource allocation between vegetative and reproductive development.

2. Dependence on Nutrient Availability

Leaf nutrient concentrations as determined in field studies reflect both genotypic and phenotypic sources of variation. Nutrient availability has two different effects on leaf nutrient concentrations. First, it may increase concentrations within species, especially when another nutrient becomes limiting (e.g. Aerts, 1989a,b; Millard and Proe, 1993; Bowman, 1994). Second, it may also lead to changes in community species composition (e.g. Tilman and Cowan, 1989; Gleeson and Tilman, 1990; Tilman and Wedin, 1991; Verhoeven and Schmitz, 1991; Bobbink, 1992; Aerts and Bobbink, 1999), which may have important consequences for leaf nutrient concentrations at the community level. In general, nutrient-poor sites are dominated by slow-growing species with low leaf nutrient concentrations, notably evergreens (Monk, 1966; Aerts, 1995). At increasing levels of nutrient availability these species are replaced by forbs and graminoids and/or deciduous shrubs and trees (e.g. Aerts and Berendse, 1988), which have

higher leaf nutrient concentrations (Aerts, 1995). Both genetic differences and phenotypic responses of plants to nutrient supply contribute to the low N and P concentrations of evergreen species observed in the field (Figure 2) (Craine and Mack, 1998). Thus, increased nutrient availability leads to higher leaf nutrient concentrations at the community level due to both phenotypic responses and species replacements.

B. Nutrient Resorption from Senescing Leaves

Resorption of nutrients from senescing leaves is of great adaptive significance, because it enables plants to reuse these nutrients and thereby can lead to a higher nutrient retention (Chapin, 1980; Chabot and Hicks, 1982; Aerts, 1990). This process has important implications at both the population level (see section VIII) and the ecosystem level (sections X and XI). At the ecosystem level, nutrient resorption from senescing leaves has a profound influence on element cycling. The nutrients that are resorbed during senescence are directly available for further plant growth, which makes a species less dependent on current nutrient uptake. Nutrients that 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 available for plant uptake again. Compared with the resorption pathway, this dependency of plants on the decomposition pathway has the disadvantages that each plant must compete for the mineralized N with micro-organisms (Kaye and Hart, 1997) and with neighbouring plants, and that part of the nitrogen can be incorporated in stable soil organic N pools and become unavailable for plant uptake (Aerts, 1997a). However, low molecular organic N compounds can be taken up by mycorrhizal (Read, 1991) and non-mycorrhizal plants and provide a large part of the annual N requirement (Kielland, 1994).

A repeated suggestion of early studies based on comparison of a few plant species was that plants from nutrient-poor environments have a higher nutrient resorption efficiency than those from more nutrient-rich environments. Is this true?

1. Variation among Growth-forms

As evergreen shrubs and trees are the dominant growth-form in nutrient-poor environments, it seems reasonable to assume that they have higher resorption efficiency than other growth-forms. However, an analysis of the literature shows that there is no difference in N and P resorption between growth-forms (Figure 3A and B). In all growth-forms, median N and P resorption is somewhere around 50%. This implies that, although nutrient resorption is an important nutrient conservation mechanism at the species level, it apparently does not explain the distribution of growth-forms over habitats differing in soil
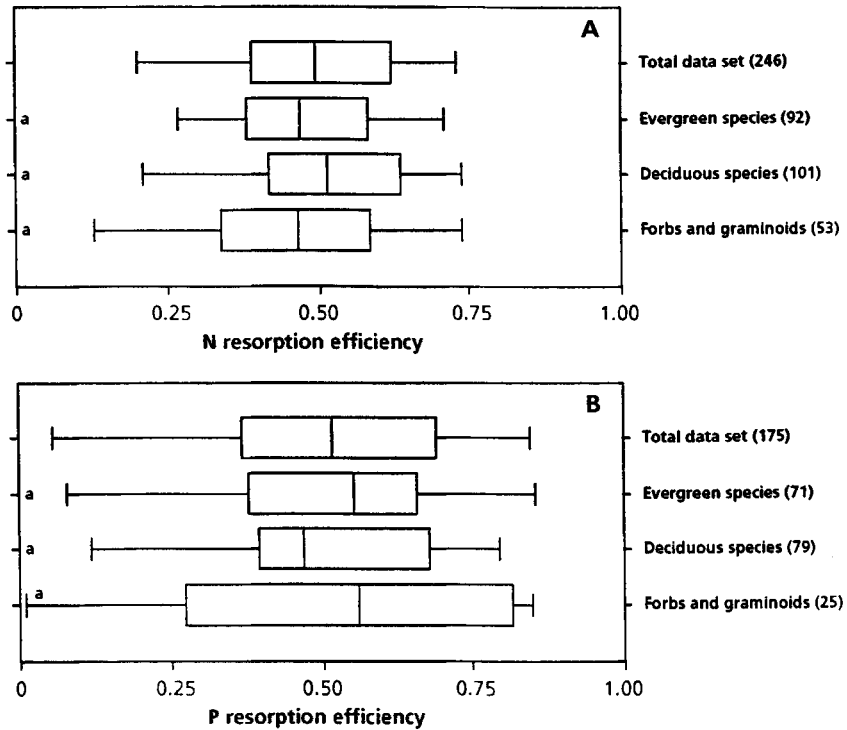
Fig. 3. Box plots showing the distribution of (A) N and (B) P resorption efficiency from senescing leaves. See Figure 2 for further explanation.

fertility (Chapin and Kedrowski, 1983; Aerts, 1996; Killingbeck, 1996). However, note that the variation in P resorption efficiency is much larger than that in N resorption efficiency. Moreover, maximum values of P resorption efficiency are higher than those for N and the minimum levels of P resorption are lower than those for N. These differences between N and P resorption efficiency have important consequences for leaf-level N and P use efficiency (section IX).

2. Nutritional Controls

Although the distribution of certain growth-forms is clearly related to soil fertility, this cannot be explained by differences in nutrient resorption efficiency (Aerts, 1996). This raises the question of whether there are consistent differences at the phenotypic level in nutrient resorption between high- and low-fertility conditions. The answer is negative: in an analysis of published

fertilization experiments covering 60 species (Aerts, 1996) there was no response of N resorption in 63% of the experiments analysed, whereas in 32% there was a decrease in N resorption in response to increased nutrient availability. Also, P resorption (37 species analysed) showed no response in 57% of cases, and in 35% P resorption decreased upon enhanced nutrient supply. Nutrient resorption in evergreen shrubs and trees showed especially low responsiveness to changed nutrient availability.

Thus, if there are nutritional controls on nutrient resorption efficiency at the phenotypic level, these must be less important than other factors that have yet to be identified. The most clear nutritional control on nutrient resorption is found when plants are grown at abnormally high nutrient concentrations, where nutrient resorption efficiency is low (Chapin and Moilanen, 1991). Under natural nutrient supplies there is no relationship between resorption efficiency and the lability of N- and P-containing chemical fractions in plants (Chapin and Kedrowski, 1983).

The lack of nutritional controls on nutrient resorption raises the question of which other factors control nutrient resorption. Several possible controls have been proposed, including the relative sink strength of plant organs (Nambiar and Fife, 1991), the rate of phloem transport (source–sink interactions) (Chapin and Moilanen, 1991) and soil moisture availability (Boerner, 1985; del Arco et al., 1991; Escudero et al., 1992; Pugnaire and Chapin, 1993). However, as Nambiar and Fife (1991) have emphasized, there is unlikely to be a single explanation for variation in nutrient resorption efficiency.

If there are indeed multiple controls over nutrient resorption efficiency, most resorption efficiencies observed in the field and reported in the literature are unlikely to be the maximum resorption efficiency of which a species is capable (Killingbeck, 1996). A second possible explanation for the large range in resorption efficiency reported in the literature could be that plants control the minimum N and P concentration of senesced leaves (resorption proficiency) rather than the proportion of nutrients withdrawn during senescence (resorption efficiency) (Killingbeck, 1996). Killingbeck (1996) has argued that resorption proficiency is the trait on which selection is most likely to have acted. We discuss the nutritional significance of resorption efficiency in section IX.

C. Leaf Lifespan

Although leaf lifespan is not a direct nutritional leaf trait, variation in leaf lifespan is of great importance for a wide variety of ecological processes, including those related to mineral nutrition. These issues have been considered extensively by Reich et al. (1992), so we will confine ourselves to a synthesis of the most relevant results for this review.

1. Variation among Growth-forms

By definition, leaf lifespan of sclerophyllous evergreen species is much longer than that of other growth-forms, which do not differ consistently in lifespan (Figure 4.) Reich *et al.* (1992) showed that long leaf lifespans, as found in evergreen species, are negatively correlated with the maximum rate of photosynthesis (both per unit leaf area and per unit leaf mass), the mass-based N concentration in the leaf, and the specific leaf area (SLA). They found that species with the longest leaf lifespan, the lowest SLA, the lowest leaf nitrogen concentration, and the lowest maximum rate of photosynthesis are either conifers in low-temperature, dry and/or nutrient-poor environments, or evergreen broad-leaf species inhabiting nutrient-poor environments. The low maximum rate of photosynthesis (per unit leaf mass or leaf area) of evergreens is significantly correlated with the low maximum RGR of seedlings of evergreens.

In addition to the earlier review, Reich *et al.* (1997) have demonstrated that similar interspecific relationships exist among leaf structure and function and plant growth in a wide variety of biomes, ranging from tropical and temperate forests to alpine tundra and desert. For a data set of 280 species they found that photosynthesis and respiration increase in similar proportion with decreasing leaf lifespan, increasing leaf N concentration and increasing SLA. The productivity of individual plants and of leaves in vegetation canopies also changes in constant proportion to leaf lifespan and SLA. This global-scale convergent evolution can provide a quantitative basis for evaluating interspecific and intraspecific species differences and for comparing among ecosystems and biomes.

From the analysis of Reich *et al.* (1992) it appeared that the largest variability in leaf trait occurs among species with short lifespans (< 1 year), and the lowest
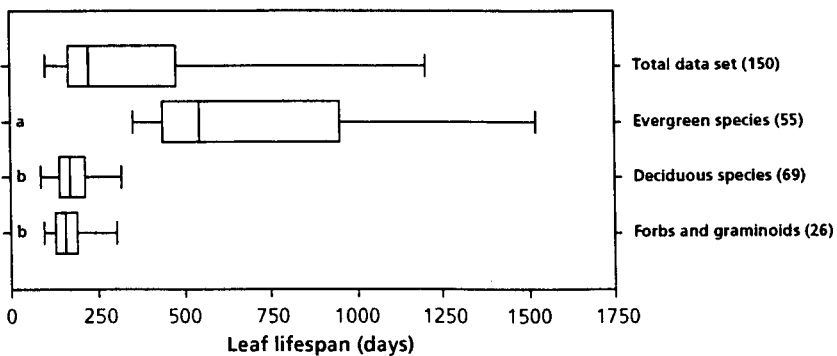

Fig. 4. Box plots showing the distribution of leaf lifespan. See Figure 2 for further explanation.

variability among species with leaf lifespans of more than 2 years. As a result, deciduous species with leaves that persist for 9–10 months are likely to share traits more closely with evergreen species that retain foliage for 2–3 years than with deciduous species that keep their leaves for 2–3 months. Similarly, the nutrient concentrations of senesced leaves differ strikingly between species with leaf longevities greater or lesser than 1.5 years (Craine and Mack, 1998). Thus, the tendency to 'lump' together all temperate evergreens with leaf lifetimes > 1 year and to compare them with deciduous plants with lifetimes of < 1 year may be misleading in certain instances.

2. Dependence on Nutrient Availability

At the community level, there is a clear relation between leaf lifespan and nutrient availability. Nutrient-poor communities are generally dominated by slow-growing (mostly) evergreen species with long leaf lifespans, whereas nutrient-rich communities are dominated by fast-growing deciduous species with high rates of leaf turnover.

The effect of increased nutrient availability on leaf lifespan at the phenotypic level is, however, rather variable. No effect was found by Aerts (1989a) with the evergreen shrub *Calluna vulgaris*, and by Reader (1980) with the evergreen shrubs *Kalmia polifolia* and *Ledum groenlandicum*. Similarly, in a study on leaf lifespan with four *Carex* species from the fens differing in nutrient availability Aerts and De Caluwe (1995) found that leaf lifespan was not significantly affected by enhanced N supply, except in *C. diandra*, where leaf lifespan decreased upon enhanced N supply. Decreasing leaf lifespan upon enhanced nutrient supply was also found by Reader (1980) with the evergreen shrub *Chamaedaphne calyculata*, by Aerts (1989a) with the evergreen shrub *Erica tetralix*, and by Shaver (1981, 1983) with the evergreen shrub *Ledum palustre*. Bazzaz and Harper (1977), on the other hand, found an increased leaf lifespan upon enhanced nutrient supply with the herb *Linum usitatissimum*. Apparently, the leaf longevity of individual species is not unambiguously controlled by nutrient availability.

VIII. NUTRIENT USE FOR BIOMASS PRODUCTION

A. Nutrient Use Efficiency (NUE)

The nutrients taken up by plants are generally used for the production of biomass. The relative amounts of nutrients taken up and the relative amounts of carbon fixation determine whether a species can persist in natural plant communities (Tilman, 1988; Aerts *et al.*, 1990; 1991; Huston, 1994). Due to its prime importance in the explanation of the distribution of plant species over environmental gradients, the interrelation between the carbon and nutrient

economy of plant species has become one of the major topics in plant ecology. This issue has been investigated with respect to both variation in resource use efficiency among species and the dependence of resource use efficiency on environmental circumstances, notably nutrient availability. Major progress has been achieved by studying the nutrient use efficiency (NUE) of plant species (e.g. Vitousek, 1982; Boerner, 1984; Pastor et al., 1984; Shaver and Melillo, 1984; Birk and Vitousek, 1986; Berendse and Aerts, 1987; Aerts, 1990; Shaver and Chapin, 1991; Escudero et al., 1992; Aerts and Van der Peijl, 1993; Bridgham et al., 1995). In perennials, NUE is generally measured as productivity per unit nutrient uptake or loss (cf. Vitousek, 1982). As such, this parameter integrates a wide variety of physiological processes, including the relation between the net carbon assimilation rate of plants and leaf nutrient content and the partitioning of nutrients between resorption and decomposition pathways (Aerts, 1997a). In the paragraphs below we refer to nitrogen use efficiency as NUE_N and to phosphorus efficiency as NUE_P.

High NUE is considered to be advantageous under conditions of low soil fertility, because it entails a high biomass production per unit of nutrient taken up. The problem with most indices of NUE is that they are ratios without a time dimension and therefore do not take into account the dynamic behaviour of plants in response to nutrient supply. Thus, these indices of NUE do not directly show why a high NUE is beneficial in low-nutrient habitats. This problem was addressed by Berendse and Aerts (1987), who postulated that selection in low-nutrient habitats is not necessarily on a high NUE but rather on plant traits that reduce nutrient losses (see Grime, 1979), whereas in high-nutrient habitats selection will be on characteristics that lead to a high rate of dry matter production. Moreover, they hypothesized that, as a result of evolutionary trade-offs, genotypically determined plant characteristics that lead to a high growth rate are inversely correlated with those that reduce nutrient losses. Thus, nutrient-poor habitats will be dominated by slow-growing species with low nutrient turnover rates, and nutrient-rich habitats by fast-growing species with high rates of nutrient turnover. Berendse and Aerts (1987) proposed to analyse the adaptive strategies of perennials with respect to nitrogen availability by distinguishing two components of NUE: the mean residence time of nitrogen in the plant (MRT) and the nitrogen productivity (A_{NP}). In this concept NUE (g biomass g^{-1} N) equals the product of MRT and A_{NP}, which in turn equals total productivity divided by the total loss of the growth-limiting nutrient in litter (both above and below ground). The mean residence time (MRT, years) measures how long a unit of nitrogen is present in the population. The nitrogen productivity (A_{NP}, g biomass g^{-1} N year^{-1}) is defined as annual productivity divided by the annual average of the amount of the growth-limiting nutrient present in the population.

Growth analysis with juvenile plants has shown that a high nitrogen productivity is strongly correlated with high leaf nitrogen concentrations

and a high specific leaf area (Ågren, 1985, 1988; Poorter and Remkes, 1990; Grime et al., 1997; Hunt and Cornelissen, 1997). The MRT of nutrients in the plant is determined by a variety of plant traits, such as tissue lifespan, tissue nutrient concentration and nutrient resorption efficiency from senescing tissues (Aerts, 1990). It is common knowledge that species from nutrient-poor habitats have low tissue turnover rates (e.g. Aerts, 1990; Escudero et al., 1992; Reich et al., 1992; Ryser and Lambers, 1995; Schläpfer and Ryser, 1996; Eckstein and Karlsson, 1997; Eissenstat and Yanai, 1997). Recently, it has been postulated that tissue density is a possible link between tissue lifespan, nutrient retention and growth rate. High maximum relative growth rate is correlated with low tissue density (Garnier and Laurent, 1994; Ryser and Lambers, 1995; Schläpfer and Ryser, 1996). Tissue lifespan might also be determined by tissue density, as the high amount of sclerified structures in tissues with a high density increases its resistance to environmental hazards and thus increases lifespan (Garnier and Laurent, 1994; Van Arendonk and Poorter, 1994). Thus, fast-growing species will have high resource acquisition capacity due to high areas of resource-absorbing surfaces, but due to low tissue density the lifespan of leaves and roots is short, leading to low nutrient retention. Slow-growing species, on the other hand, have a lower resource acquisition capacity, but the high tissue density leads to low tissue turnover rates and thus to a high nutrient retention.

Two recently developed models, which are based on the NUE concept of Berendse and Aerts (1987), show that a high MRT leads to clear advantages in low-nutrient habitats (Aerts and Van der Peijl, 1993; Berendse, 1994a). Both models explicitly assume that there is a trade-off between plant traits that lead to low nutrient loss rates and those that lead to a high dry matter production. In the model of Aerts and Van der Peijl (1993), two species are considered which have an equal NUE, but one species is nutrient conserving (high MRT) and has a low nitrogen productivity, whereas the other has a high nutrient turnover rate (low MRT) and a high nitrogen productivity. The model clearly demonstrates that the species with a high MRT attains a higher equilibrium biomass than that with the low MRT, but that the species with a high nitrogen productivity attains the equilibrium biomass at a faster rate (Figure 5). Thus, the model shows that: (1) a nutrient-conserving strategy leads to a direct advantage in nutrient-poor environments; (2) NUE alone is not a good predictor for the success of a species in nutrient-poor environments; and (3) high-productivity species initially have a higher net biomass increase than low-productivity species even in nutrient-poor environments. Using a similar approach, Berendse (1994a) also showed that under conditions of nutrient-limited growth species with low nutrient loss rates can outcompete species with high nutrient loss rates, even when these species have a higher competitive ability for nutrient uptake.
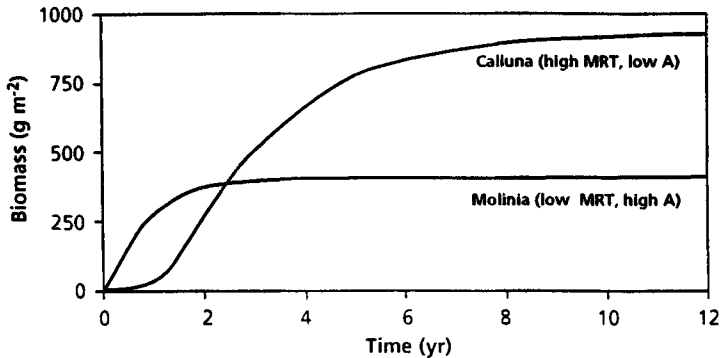
Fig. 5. Simulated long-term biomass dynamics of two species with an equal nutrient use efficiency (NUE), but which differ in their components of NUE. *Calluna vulgaris* has a high mean residence time of nutrients (MRT), but a low nitrogen productivity (A_{NP}), whereas *Molinia caerulea* has the opposite characteristics. Redrawn from Aerts and Van der Peijl (1993).

B. Patterns in NUE

Numerous recent studies on patterns in NUE have provided a basis for evaluating the ideas put forward in the previous sections. At the phenotypic level, NUE generally decreases with increasing soil fertility or fertilization (e.g. Pastor *et al.*, 1984; Birk and Vitousek, 1986; Chapin and Shaver, 1989; Aerts and De Caluwe, 1994; Bowman, 1994; Bridgham *et al.*, 1995; van Oorschot *et al.*, 1997), although at very low soil fertility levels NUE may also decrease (Bridgham *et al.*, 1995). However, species from high-fertility sites do not necessarily have lower NUE than species from low-fertility sites (Aerts, 1990; Son and Gower, 1991; Aerts and De Caluwe, 1994). This emphasizes that it is important to differentiate between phenotypic and genotypic responses of NUE to changes in soil fertility. In addition, many of these patterns are based on study of a single organ (e.g. leaves) or on above-ground parts only, which may be misleading.

A proper evaluation of NUE requires data at the whole-plant level, because patterns of above-ground NUE are not necessarily similar to whole-plant NUE (Aerts, 1990). Unfortunately, few whole-plant field studies have been conducted owing to the difficulty of measuring below-ground nutrient dynamics in natural ecosystems. Therefore, we will consider interspecific differences in NUE at three levels: whole plant, above ground, and leaves (see Reich *et al.*, 1992).

1. Whole-plant NUE

To our knowledge, the only field study on whole-plant NUE was performed by Aerts (1990). In that study, which was performed with species from

nutrient-poor and nutrient-rich heathlands, it was found that the nutrient-conserving ericaceous species *Erica tetralix* and *Calluna vulgaris* (dominant in nutrient-poor heathlands) had a high MRT and a low A_{NP}, whereas the high-productivity grass *Molinia caerulea* (dominant in nutrient-rich heathlands) had a low MRT and a high A_{NP} (Aerts, 1990). The NUE of these species was equal. However, when only above-ground NUE was considered, the grass species had a much higher NUE than the ericaceous species.

2. Above-ground NUE

Contrary to general ecological belief, there are no clear patterns in above-ground NUE at the interspecific level. Gray (1983) studied NUE of the ever-green shrub *Ceanothus megacarpus* in Californian chaparral and the drought-deciduous shrubs *Salvia leucophylla* and *Artemisia californica* in coastal sage. NUE was higher in the evergreen species for all major elements. This was due mainly to a higher nutrient retention compared with the coastal sage. However, Aerts (1990) reported lower above-ground NUE for two erica-ceous shrubs compared with a co-occurring grass species. A similar pattern was observed by Son and Gower (1991) in a study of evergreen and deciduous plantation trees.

   An interesting case of species-specific patterns in N and P use efficiency in response to fertilization was reported by Bowman (1994). In two alpine tundra communities differing in nutrient limitation, the N-limited dry meadow had a higher N use efficiency, whereas the N–P co-limited wet meadow had a higher P use efficiency. Fertilization with N, P or N + P reduced the NUE of the supplied nutrients at the community level. A large part of this change was mediated through changes in species and growth-form composition in response to enhanced nutrient supply.

   Eckstein and Karlsson (1997) studied above-ground growth and NUE of 14 plant species in subarctic Sweden. These 14 wild species represented four life-forms (woody evergreen, woody deciduous, graminoid and herb) and were growing in two contrasting habitats: a nutrient-rich meadow birch forest and a nutrient-poor bog. Their data showed that above-ground NUE was not affected by habitat, life-form or species. However, they did find an inverse relation between MRT and A_{NP}, as predicted by Berendse and Aerts (1987): species dominant in the low-nutrient bog (woody evergreens) had the highest MRT and the lowest A_{NP}, whereas species dominant in the more nutrient-rich forest (herbs and graminoids) were characterized by a low MRT and a high A_{NP}. Deciduous woody species occupied an intermediate position (Figure 6). Their results, as well as the community level patterns observed by Bridgham *et al.* (1995), indicate that NUE varies within rather narrow limits (by a factor of less than 3) compared to its components (variation by a factor 10 or more). This strongly supports the hypotheses of
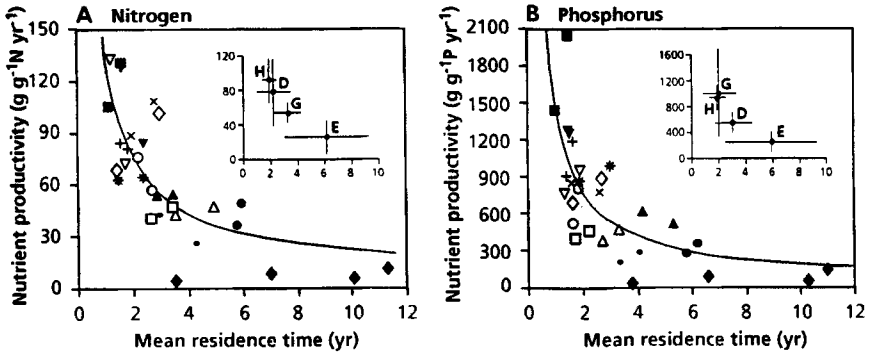
Fig. 6. Relationship between above-ground nutrient mean residence time (MRT) and nutrient productivity (A_{NP}) for 14 species from subarctic Sweden. Regression statistics: (A) $r^2 = 0.60$, $P < 0.001$ for nitrogen (B) $r^2 = 0.54$, $P < 0.001$ for phosphorus. The inset figures indicate the mean ± SD of MRT and A_{NP} for the respective growth-forms: D, deciduous shrubs; E, evergreen shrubs; G, graminoids; H, herbs. Redrawn from Eckstein and Karlsson (1997).

Berendse and Aerts (1987) which state that selection in nutrient-poor habitats is not necessarily on a high NUE, but rather on a high nutrient retention and that, as a result of evolutionary trade-offs, there is an inverse relation between nutrient retention and nutrient productivity.

These hypotheses are further supported by a re-analysis of the large data set that Vitousek (1982) used in his seminal paper on NUE of forest ecosystems (Knops et al., 1997). In contrast with Vitousek's original hypothesis that the amount of nutrients in litterfall increases with increasing soil fertility, Knops and co-workers found that the relationship between the fertility of ecosystems and the amount of nutrients in the litterfall was inconclusive. They concluded that there is no indication of higher NUE in nutrient-poor ecosystems. Rather, they suggested that there might be a more general relationship between the mean residence time of nutrients or nutrient productivity and ecosystem fertility.

3. Leaf-level NUE

In contrast with data on whole-plant and above-ground NUE, the data on leaf-level NUE are very abundant. This makes it possible to investigate the relative contribution of various leaf traits (leaf nutrient concentrations, nutrient resorption from senescing leaves, and leaf lifespan) to leaf-level NUE in different growth-forms. Given the large variation in, for example, leaf lifespan between evergreen and deciduous species (Reich et al., 1992; Aerts, 1995), it is likely that growth-forms will differ in determinants of leaf-level NUE. These issues will be treated in the next section.

IX. PATTERNS IN LEAF-LEVEL NUTRIENT USE EFFICIENCY AND ITS COMPONENTS

A. Leaf Traits and their Contribution to Leaf-level NUE: Theoretical Considerations

Leaf-level nutrient use efficiency expresses how much biomass is produced by a leaf during the retention time of a unit of nutrient that has been taken up (Small, 1972; Reich *et al.* 1992). However, it should be noticed that this organ-level efficiency ignores the carbon that is fixed by the leaf and supports production or respiration elsewhere in the plant. First, we explore theoretically how various leaf traits may contribute to NUE. We will illustrate this for nitrogen, but a similar reasoning can be developed for phosphorus.

Small (1972) developed a simple approach for calculating an index of NUE for perennial species. The mean residence time (MRT, years) of a unit of N in the leaf was estimated according to the formula:

$$MRT = \text{leaf lifespan} * 1/(1-r) \tag{1}$$

where r is the nutrient resorption efficiency (fraction of the total leaf nutrient pool that is resorbed during senescence: $0 < r < 1$) and leaf lifespan is expressed in years.

Based on the rate of net photosynthesis of individual leaves on a dry mass basis (A_{mass}, mmol CO_2 g^{-1} h^{-1}) and the N content of the mature leaf ([N], mg N g^{-1}) the NUE index of Small (1972), which he named 'Potential photosynthate g^{-1} N', can then be calculated as:

$$NUE = A_{mass} * MRT/[N] \tag{2}$$

which equals

$$NUE = (A_{mass} * \text{leaf lifespan} * 1/(1-r))/[N] \tag{3}$$

This formula does not, of course, yield a direct estimate of the amount of biomass that is produced during the retention time of a unit of nutrient. To calculate this, information must be available for the conversion efficiency of photosynthate into biomass of the plant species under study. Moreover, Small assumed that A_{mass} does not change during the lifespan of a leaf, that no self-shading occurs during canopy development, and that there is no leaf mass loss during senescence. Despite these simplifying assumptions, the approach of Small (1972) clearly shows which parameters are important as determinants of leaf-level NUE and how they are related to NUE. In addition, the conversion efficiency of photosynthate into biomass is nearly constant for all plant parts and species (Chapin, 1989; Poorter, 1994). In the remainder of this review, we

will concentrate on a discussion of the importance of leaf lifespan, resorption efficiency and leaf N concentrations as determinants of NUE. Unfortunately, there are hardly any literature sources in which data on both A_{mass}, leaf lifespan, nutrient resorption efficiency and N concentrations are provided. There is, however, a substantial amount of data on both leaf lifespan, r and [N]. Moreover, A_{mass} and leaf N concentrations are highly correlated ($r^2 = 0.74$–0.85; Reich et al., 1992), which might obscure possible direct relationships between these two parameters and NUE. As a result, the analysis will be restricted to the three parameters mentioned above.

Thus, the relation between NUE and leaf traits can be described by the following equation for NUE:

$$NUE = (1/[N]) * (1/(1-r)) * lifespan * c \qquad (4)$$

in which c is a constant which takes A_{mass} and the conversion efficiency into account.

Thus, leaf lifespan shows a linear relation with NUE, but both [N] and r are inversely related to NUE. This equation shows that NUE approaches infinity when [N] approaches zero, and/or r approaches 1, and/or leaf lifespan approaches infinity. These are, of course, biologically unrealistic situations, but they indicate which values the underlying leaf traits of NUE should approach in order to maximize NUE. The response of NUE to changes in the underlying leaf traits can conveniently be studied by partial differentiation of NUE with respect to these traits. This partial derivative shows how NUE changes per unit change of the trait under consideration.

1. Nutrient Concentration

Partial differentiation of NUE with respect to the leaf N concentration yields:

$$d(NUE)/d([N]) = (-1/[N]^2) * (1/(1-r)) * lifespan * c \qquad (5)$$

Equation (5) shows that the greatest change in NUE per unit change in [N] takes place at low N concentrations. The minus sign indicates that NUE decreases with increasing N concentration. These implications are illustrated graphically in Figure 7.

2. Resorption Efficiency

Partial differentiation of NUE with respect to resorption efficiency yields a different type of relationship:

$$d(NUE)/d(r) = (1/(1-r)^2) * (1/[N]) * lifespan * c \; (0 < r < 1) \qquad (6)$$
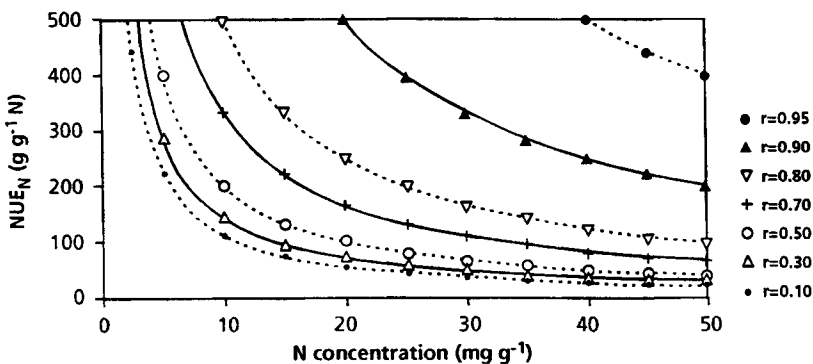
Fig. 7. Theoretical values of leaf-level nitrogen use efficiency (NUE$_N$) as a function of N concentration in mature leaves. Isoclines of N resorption efficiency (*r*) are shown.

In this case, the greatest changes in NUE per unit change in *r* are obtained at high values of *r* (Figure 8). NUE increases with increasing resorption efficiency.

3. Leaf Lifespan

When NUE is partially differentiated with respect to leaf lifespan, the following equation is obtained:

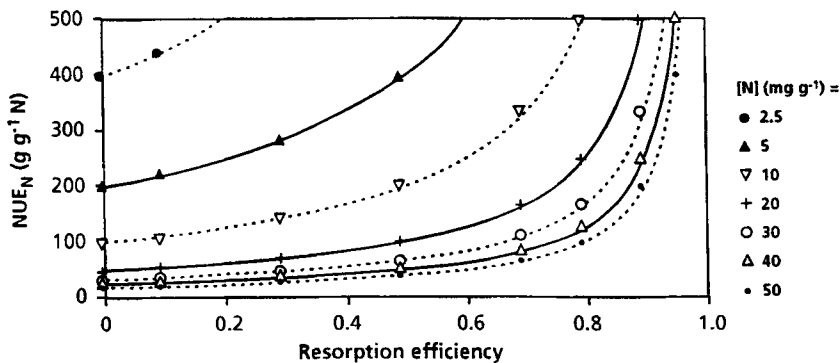$$d(\text{NUE})/d(\text{lifespan}) = (1/[\text{N}]) * (1/(1-r)) * c \tag{7}$$

Fig. 8. Theoretical values of leaf-level nitrogen use efficiency (NUE$_N$) as a function of N resorption efficiency (*r*). Isoclines of N concentration in mature leaves are shown.

Equation (4) shows that NUE increases with increasing leaf lifespan, but equation (7) shows that changes in NUE per unit change in leaf lifespan are independent of the actual value of leaf lifespan (Figure 9).

These equations and their graphic illustrations show that the largest changes in NUE per unit change in the leaf trait under consideration are obtained when N resorption efficiency increases above values of about 0.75 and/or when leaf N concentrations decrease below values of about 15 mg N g^{-1}. For leaf lifespan, the change in NUE per unit change in lifespan is independent of the actual value of the leaf lifespan. These results imply that maximization of leaf-level NUE requires natural selection to favour traits that lead to N resorption efficiencies higher than 0.75 and leaf N concentrations lower than 15 mg N g^{-1}. For phosphorus, for which the concentrations are about a factor 10 lower, these values are 0.75 and 1.5 mg P g^{-1}, respectively (data not illustrated graphically). In the coming paragraphs, we explore whether and how these findings are realized in plant species belonging to different growth-forms.

B. Actual Patterns in Leaf-level Nutrient Use Efficiency and the Relation with Underlying Leaf Traits

Vitousek (1982) and Birk and Vitousek (1986) have proposed a more simple index of NUE, the inverse of leaf litter N concentration:

$$NUE = 1/([N] * (1-r))\qquad(8)$$

This index is similar to that of Small (1972) and has the advantages that only two parameters are needed for its calculation and that it gives a direct estimate
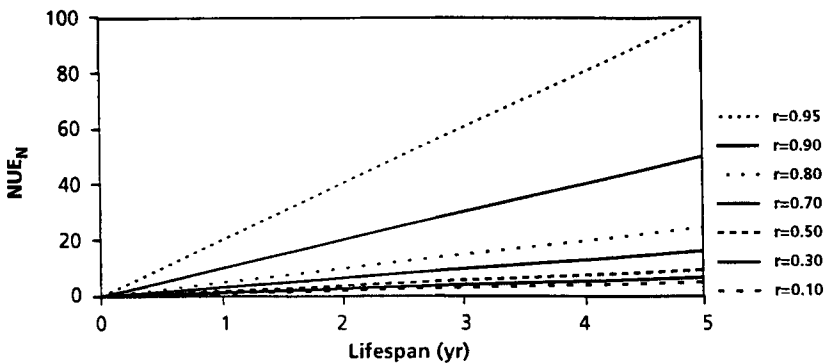

Fig. 9. Theoretical values of leaf-level nitrogen use efficiency (NUE_N) as a function of leaf lifespan. Isoclines of N resorption efficiency (r) are shown. Note that NUE values are on a relative scale (see text for explanation).

of the amount of biomass produced per unit of N taken up. Therefore, this index will be used for the calculation of NUE.

1. Nitrogen Use Efficiency

Leaf-level nitrogen use efficiency of evergreens is higher than that of the other growth-forms. However, there is considerable overlap (Figure 10). This implies that, within small subsets of this large data set, the differences between growth-forms may deviate from the patterns presented here.

We used path analyses to unravel the contribution of various leaf traits to NUE_N. When the entire data set was considered, leaf N concentration showed the highest (negative) correlation with NUE_N (Figure 11A). Moreover, a large part of the correlation of leaf lifespan with NUE_N was due to an indirect effect of leaf N concentration on leaf lifespan. A similar picture emerged when evergreen shrubs and trees were considered (Figure 11B). In this growth-form, leaf
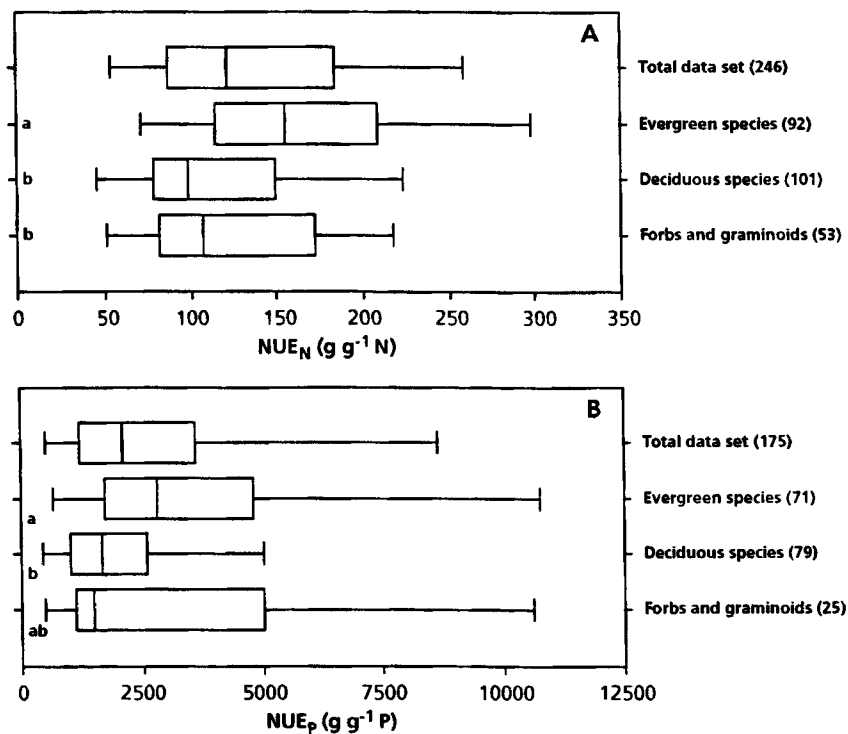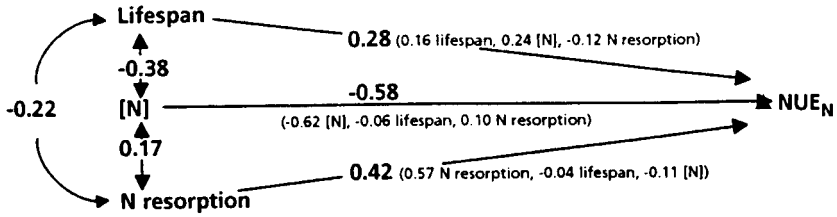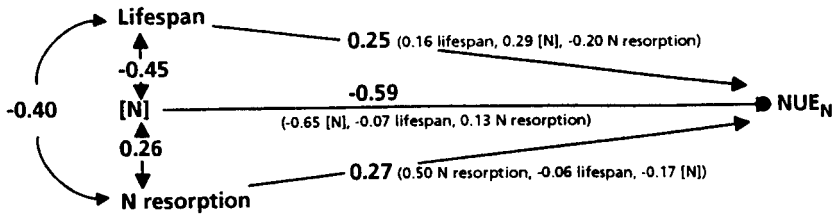

Fig. 10. Box plots showing the distribution of nitrogen use efficiency (NUE_N) and phosphorus use efficiency (NUE_P). See Figure 2 for further explanation.

(A) Total data set (n=148)

Lifespan

0.28 (0.16 lifespan, 0.24 [N], -0.12 N resorption)

-0.38

-0.22   [N] ──────────── -0.58 ──────────── NUE$_N$

(-0.62 [N], -0.06 lifespan, 0.10 N resorption)

0.17

N resorption   0.42 (0.57 N resorption, -0.04 lifespan, -0.11 [N])

(B) Evergreen species (n=54)

Lifespan

0.25 (0.16 lifespan, 0.29 [N], -0.20 N resorption)

-0.45

-0.40   [N] ──────────── -0.59 ──────────── NUE$_N$

(-0.65 [N], -0.07 lifespan, 0.13 N resorption)

0.26

N resorption   0.27 (0.50 N resorption, -0.06 lifespan, -0.17 [N])

(C) Deciduous species (n=68)

Lifespan

-0.65 (-0.34 lifespan, -0.31 [N])

0.50

[N] ──────────── -0.79 ──────────── NUE$_N$

(-0.62 [N], -0.17 lifespan)

0.62

N resorption

(D) Forbs and graminoids (n=26)

[N]

-0.43

NUE$_N$

0.81

N resorption
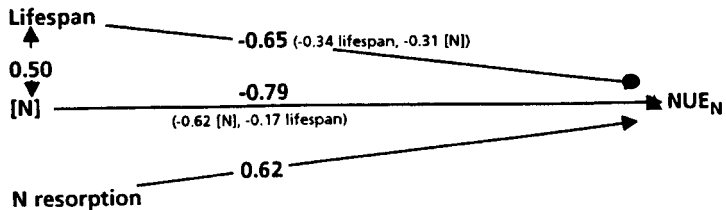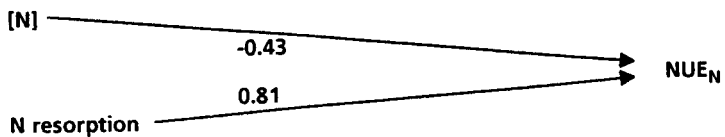
Fig. 11. Path diagrams describing the structure of the relationship between leaf-level nitrogen use efficiency (NUE$_N$) and various leaf characteristics for (A) the total data set, (B) evergreen woody species, (C) deciduous woody species and (D) forbs and graminoids. Numbers in bold type show the Pearson correlation coefficients among the variables, whereas values in parentheses partition the Pearson correlation coefficients between NUE$_N$ and the predictor variables into direct and indirect (i.e. attributable to indirect relationships with the other predictor variables) effects.

N concentration has an overriding effect on NUE_N, both directly and indirectly through effects on both other leaf traits. For deciduous shrubs and trees, N resorption efficiency from senescing leaves is more important as a determinant of NUE_N than in the evergreens (Figure 11C). However, in the deciduous shrubs and trees, leaf lifespan shows a negative correlation with NUE_N. Thus, within this growth-form a short leaf lifespan is associated with higher NUE_N. This is probably due to the fact that leaf lifespan is positively correlated with leaf N concentration. In the other growth-form with short-lived leaves, the forbs and graminoids, N resorption efficiency is the most important determinant of NUE_N (Figure 11D). In these herbaceous species, there is no significant effect of leaf lifespan on NUE_N. Thus, variation in the NUE_N of evergreen and deciduous shrubs and trees is determined mainly by variation in N concentration in mature leaves. In forbs and graminoids, however, N resorption efficiency is the most important predictor of variation in NUE_N. For all growth-forms, leaf lifespan is only of minor importance in explaining variation in NUE_N.

Theoretical analysis indicated that NUE_N shows the greatest increase per unit change in N concentration at values of N below 15 mg g^{-1} (equation (5); Figure 7) and also that the greatest increase per unit change in resorption efficiency was obtained at values of r above 0.75 (equation (6); Figure 8). This raises the question of how plants in real life maximize NUE_N and whether there are differences among growth-forms. To investigate this, we plotted the N concentration in mature leaves against N resorption efficiency from senescing leaves, and have indicated various NUE_N isoclines (Figure 12). This figure shows a number of interesting
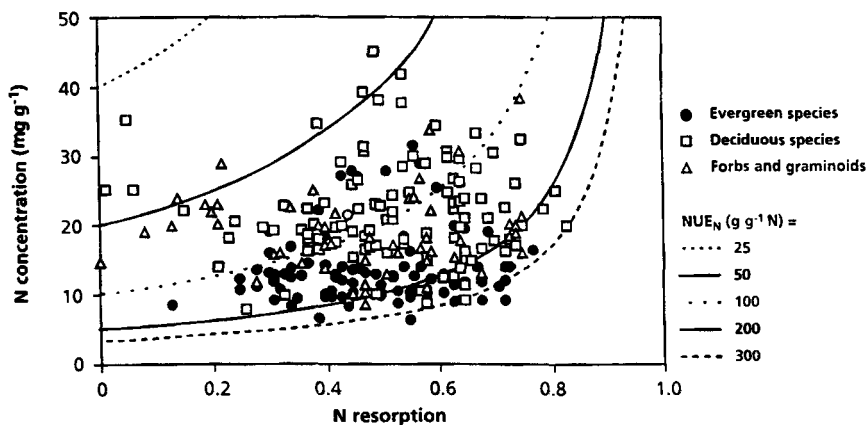

Fig. 12. N concentration in mature leaves as a function of N resorption from senescing leaves of species from various ecosystems ($n = 249$). Various NUE_N isoclines are shown. The relation between N concentration and N resorption was not significant.

phenomena. First, it appears that leaf-level NUE_N has a maximum value of about 300 g g^{-1} N (see Figure 10), which corresponds to a minimum N concentration in leaf litter of about 3 mg g^{-1}. Second, of the 47 cases where NUE_N exceeded 200 g g^{-1} N, in only four cases was the resorption efficiency greater than 0.75, whereas in 36 cases the N concentration in mature leaves was lower than 15 mg g^{-1}. Third, in 13 of 18 cases where NUE_N was greater than 250 g g^{-1} N, the species were evergreen shrubs and trees. From these observations, and from the relations presented in Figures 7–11, it can be concluded that plant species maximize their NUE_N more by the synthesis of leaves with low N concentrations than by having leaves with high N resorption efficiency and/or long lifespans. The species with the highest values of NUE_N are mainly evergreen shrubs and trees.

2. Phosphorus Use Efficiency

In evergreen shrubs and trees leaf-level phosphorus use efficiency was higher than in deciduous shrubs and trees, whereas the NUE_P of forbs and graminoids did not differ significantly from that of the other growth-forms (Figure 10). As was the case with NUE_N, there is large variation in NUE_P within growth-forms.

The path analyses showed that P resorption from senescing leaves was the most important determinant of leaf-level NUE_P (Figure 13). In evergreen species, it was the only determinant of NUE_P. This contrasts with the pattern for NUE_N, in which N concentration in mature leaves was the most important determinant of NUE_N. In general, the correlation between leaf traits and NUE_P was higher than that between leaf traits and NUE_N (see Figures 11 and 13). As was the case with NUE_N, leaf lifespan showed only a weak correlation (both directly and indirectly) with NUE_P.

According to the theoretical analysis, the greatest increase of NUE_P per unit change in P concentration would occur at P concentrations lower than 1.5 mg g^{-1} and/or at P resorption efficiencies higher than 0.75. An analysis similar to that for NUE_N (Figure 12) showed an interesting pattern. In contrast with the pattern for NUE_N, NUE_P was most apparently maximized due to very high P resorption efficiencies (Figure 14), with a maximum value of 0.98 in *Pinus strobus* (Small, 1972). This agrees with the findings of the path analyses. Apparently, P resorption efficiencies can be higher than N resorption effiencies. This has also been noted by Walbridge (1991), DeLucia and Schlesinger (1995) and Aerts (1996). This suggests that leaf P fractions are more readily broken up or retranslocatable than N fractions. The maximum value of NUE_P is about 15 000 g g^{-1} P, which corresponds to a minimum P concentration in senesced leaves of 0.07 mg g^{-1}. This extremely low P concentration is achieved mainly by the very high maximum P resorption efficiency (cf. equation (4)).
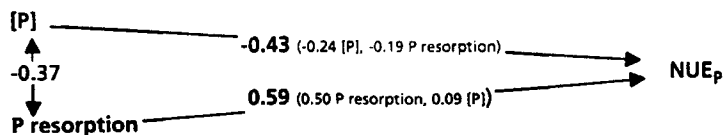
(A)   Total data set (n=101)

[P] ――――――
▲   **-0.43** (-0.24 [P], -0.19 P resorption)
-0.37   **NUE$_p$**
▼   **0.59** (0.50 P resorption, 0.09 [P])
P resorption ――――――

(B)   Evergreen species (n=37)

P resorption ――――― **0.82** ――――――――――――→ NUE$_p$

(C)   Deciduous species (n=46)

Lifespan ――
▲   **0.80** (0.36 lifespan, 0.21 [P], 0.23 P resorption)
-0.35
0.33   [P] ―――――――― **-0.95**   → **NUE$_p$**
▲   (-0.61 [P], -0.13 lifespan, -0.21 P resorption)
-0.30
▼   **0.99** (0.70 P resorption, 0.11 lifespan, 0.18 [P])
P resorption

(D)   Forbs and graminoids (n=17)

[P] ――――――
-0.62
NUE$_p$
0.86
P resorption ――――
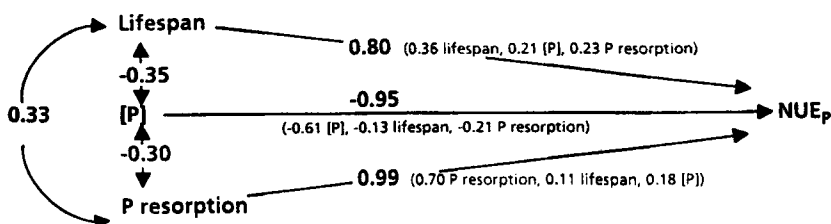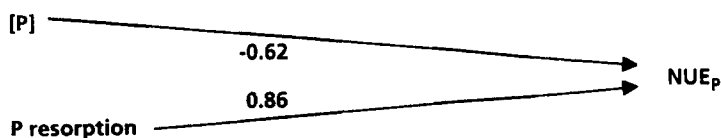
Fig. 13. Path diagrams describing the structure of the relationship between leaf-level phosphorus use efficiency (NUE$_p$) and various leaf characteristics for (A) the total data set, (B) evergreen woody species, (C) deciduous woody species and (D) forbs and graminoids. For further explanation see Figure 11.

C. Physiological Constraints on Maximization of Leaf-level NUE

It can be concluded that for woody species leaf-level nitrogen use efficiency is most strongly determined by variation in mature leaf N concentration. For herbaceous species, however, N resorption efficiency is the most important determinant of nitrogen use efficiency. For phosphorus use efficiency, P resorption efficiency contributes most strongly to maximization of NUE$_p$ in all

Fig. 14. P concentration in mature leaves as a function of P resorption from senescing leaves of species from various ecosystems ($n = 175$). Various NUE_p isoclines are shown. $[P] = 2.059 - 0.0145$ PRESORPTION; $r^2 = 0.14$, $P < 0.01$.
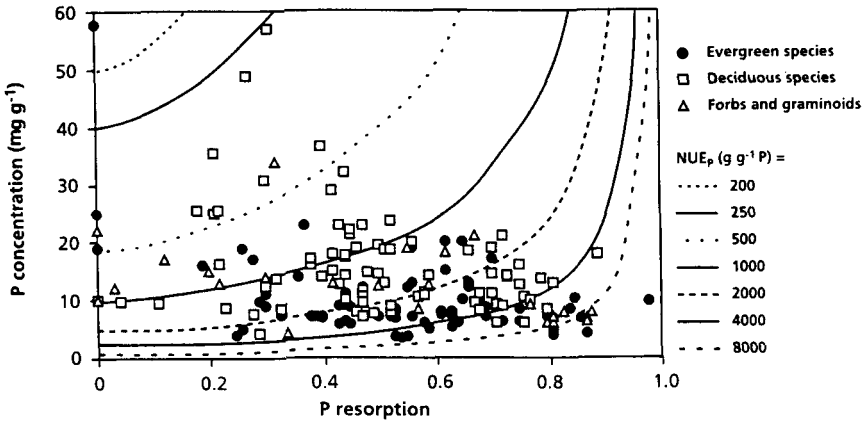
growth-forms. It appears that, for all growth-forms, leaf lifespan is only a minor contributor to variation in both NUE_N and NUE_p.

An intriguing question arising from these findings is why N resorption does not contribute strongly to maximization of NUE_N, whereas P resorption does this very strongly. The most likely explanation is that N resorption has an upper limit of about 0.80, whereas P resorption has an upper limit of about 0.90 (see Walbridge, 1991; Aerts, 1996; Killingbeck, 1996). It is clearly shown that above resorption efficiencies of 0.75 NUE shows a strongly disproportional increase, owing to the inversely quadratic nature of the partial derivative of NUE against r (see equation (6)). Thus, this relatively small difference in maximum resorption efficiencies has disproportionate consequences for maximization of NUE. From our analysis it appears that the minimum level to which the N concentration can be reduced in senesced leaves is about 3 mg N g^{-1}; for P this is about 0.07 mg P g^{-1}. These concentrations appear to be the biochemical lower limits for N and P in senesced leaves and are similar to the values (3 mg N g^{-1} and 0.1 mg P g^{-1}) reported by Killingbeck (1996).

At first sight, it may seem strange that leaf lifespan is not the most important contributor to maximization of NUE, because lifespan data vary more than 20-fold (Figure 4), whereas both nutrient resorption efficiencies and nutrient concentrations vary much less (Figures 4 and 5). The weak relation between NUE_N and leaf lifespan was also found by Reich *et al.* (1992) in the analysis of their 'NITROGEN' data set ($r^2 = 0.27$). For nitrogen, the path analysis provides some clues to the solution of this problem. It is obvious that

most of the variation in leaf lifespan is present within the evergreens (Figure 4). In this growth-form, there is a strong negative correlation between leaf lifespan and the N concentration of the leaf (see Reich *et al.*, 1992) and N resorption efficiency (Figure 11). Thus, evergreen species with long leaf lifespans have low N concentrations in mature leaves and low N resorption efficiency. As a result of this pattern, and because of the different response of NUE to changes in leaf lifespan on the one hand and nutrient concentration and nutrient resorption efficiency on the other (see equations 4–7; Figures 7–9), leaf N concentration is the most important contributor to NUE_N in evergreen species. For the growth-forms with short-lived leaves (< 1 year), leaf lifespan is negatively related to NUE_N (deciduous shrubs and trees) or does not show a relation with NUE_N (forbs and graminoids). For phosphorus, this explanation does not hold. An important reason is that P resorption efficiency shows in all growth forms a very large variation (Figure 3B) and has very high maximum values. Thus, variation in P resorption efficiency can contribute more to maximization of NUE_P than leaf lifespan (see equations (7) and (8)).

D. Ecological Consequences

The theoretical analysis and the analysis of actual patterns in NUE and its underlying components made clear that in perennials NUE_N is maximised by the synthesis of low-nitrogen leaves. This is most apparent in evergreen shrubs and trees, species that are confined mainly to nutrient-poor sites (Monk, 1966; Aerts, 1995). However, this strategy has some important ecological consequences. First, the penalty for having leaves with low N concentrations is a low carbon assimilation rate and thus a low growth rate (Chapin, 1980; Hirose and Werger, 1987; Reich *et al.*, 1992). As a result, evergreen species show a low responsiveness to environmental changes, in terms of both biomass increase and reproductive output (Chapin *et al.*, 1983; Aerts, 1995). This low responsiveness of evergreens to environmental change is probably due to the trade-off between plant traits that reduce nutrient losses and those that lead to high rates of dry matter production (Aerts, 1990; Shaver and Chapin, 1991; Reich *et al.*, 1992; Grime *et al.*, 1997). This implies that changes in nutrient availability may lead to a decrease of the relative abundance of evergreen species. Such a decrease has been observed in heathlands in north-west Europe after anthropogenic increases of atmospheric nitrogen deposition (Aerts and Heil, 1993).

Compared with the evergreens, the deciduous shrubs and trees and the forbs and graminoids have higher leaf N concentrations, comparable N resorption efficiency, higher litter N concentrations, much shorter leaf lifespans, and lower values of NUE_N (Figures 4–6, 10). Furthermore, these growth-forms are characterized by another type of relationship between NUE_N and the underlying leaf traits (Figure 11). In these growth-forms, and especially in the forbs

and graminoids, NUE_N depends more on resorption efficiency than in the evergreens. In addition, these growth-forms have a higher SLA than evergreens (Reich et al., 1991, 1992; Reich, 1993). This suite of leaf traits (high N concentrations, high SLA and high leaf turnover rates) is the main determinant of a high potential productivity of plants and makes these growth-forms more plastic in their response to environmental changes (Poorter and Remkes, 1990; Poorter et al., 1990; Reich et al., 1992; Grime et al., 1997; Hunt and Cornelissen, 1997). As a result, species with these traits dominate the more fertile habitats and replace evergreen species when nutrient availability in a particular habitat is increased (Aerts and Berendse, 1988; Aerts et al., 1990, 1991; Fox, 1992; Jonasson, 1992; Havström et al., 1993; Wookey et al., 1993; Parsons et al., 1994, 1995; Aerts and Bobbink, 1999).

The ecological consequences of traits leading to high NUE_P (mainly high P resorption efficiency) are of a different nature. High P resorption efficiency leads to very low P concentrations in litter, which may affect the decomposability of that litter (Aerts and De Caluwe, 1997). This suggests that NUE and leaf litter decomposability are strongly interrelated, as discussed in sections X and XI.

X. LITTER DECOMPOSITION

Decomposition of plant litter is a key process in the nutrient cycle of terrestrial ecosystems (Meentemeyer, 1978; Vitousek, 1982; Van Vuuren et al., 1993; Vitousek et al., 1994; Aerts and De Caluwe, 1997). Litter decomposition rates are controlled by environmental conditions, by the chemical composition of the litter and by soil organisms (Swift et al. 1979; Blair et al. 1990; Beare et al. 1992). Mineralization of nutrients contained in litter is often referred to a three-stage process: first, nutrients in soluble form are leached from the litter; second, nutrient immobilization occurs; and, finally, net nutrient mineralization from the litter takes place, thereby making nutrients available for plant uptake again.

A. Nutrient Leaching from Senesced Leaves

There is a marked difference between the leachability of different ions: K and Mg are very mobile and easily leached from fresh litter, whereas N, P and Ca show a much lower rate of leaching (Swift et al., 1979). Although many authors have emphasized the importance of nutrient leaching from fresh litter, there are relatively few quantitative estimates of this process.

Most authors estimate how much N and P are leached from senesced leaves by expressing it as a percentage of the initial N and P content of those leaves (Table 3). From these data it is clear that nutrient leaching is extremely variable.

Table 3
Potential N and P leaching from senescing leaves, expressed as a percentage of initial
leaf N and P pool in senesced leaves, as reported in different studies

Reference	Species	N leaching (%)	P leaching (%)
Morton (1977)	*Molinia caerulea* in England	0	0
Chapin and Kedrowski (1983)	Four deciduous and evergreen trees in Alaska	0.1–0.3	0.04–0.6
Boerner (1984)	Four deciduous tree species in Ohio	0–8	0–10
Ganzert and Pfadenhauer (1986)	*Schoenus ferrugineus* in Germany	0	0
Pastor *et al.* (1987)	*Schizachyrium scoparium* in Minnesota	4–57*	N.D.
Chapin and Moilanen (1991)	*Betula papyrifera* in Alaska	31	31
Ibrahima *et al.* (1995)	Seven evergreen and deciduous Mediterranean species	0–15†	N.D.
Aerts and De Caluwe (1997)	Four *Carex* species in fens in the Netherlands	8–12	3–14

*Four levels of N supply; positive relation between initial N content and N leaching.
†In four species 0%, in three other 9–15%.
N.D., not determined.

Site fertility effects on leaching have been investigated by several authors. Boerner (1984) studied N leaching in relation to site fertility in four deciduous tree species. He found lower N and P leaching at low-fertility sites in 10 of 16 cases. Pastor *et al.* (1987) found no consistent effect of fertilization on initial N content of leaf litter of *Schizachyrium scoparium*, but they did find a strong positive correlation between N leaching and initial N content of the leaves. Aerts and De Caluwe (1997) studied nutrient supply effects on N and P leaching from senesced leaves of four *Carex* species. They found that potential N leaching from field litter differed among species and amounted to values between 8% and 12% of the initial N content of the leaves. However, there was no consistent difference between N leaching of field litter and of litter produced under high-fertility growth conditions. Potential P leaching from field litter varied between 3% and 14%, and was strongly increased when plants were grown under high P conditions. In that case, a maximum value of 65% was observed in *Carex lasiocarpa*. Rustad

(1994) also found such high P leaching from tree leaf litter from a red spruce ecosystem in Maine, USA, which had initial C : P ratios similar to those in the experimental litters from the study of Aerts and De Caluwe (1997). These data indicate that litter with high N and P concentrations generally shows relatively higher N and P leaching losses than low-nutrient litter.

B. Climatological and Chemical Controls on Litter Decomposition

There are three main levels of litter decomposition control which operate in the following order: climate > litter chemistry > soil organisms (Swift *et al.*, 1979; Lavelle *et al.*, 1993). Climate has a direct effect on litter decomposition due to the effects of temperature and moisture. However, as a result of the climatic control of soil formation and nutrient cycling (Vitousek and Sanford, 1986; Lavelle *et al.*, 1993), climate must also have an indirect effect through the climatic impact on litter chemistry (Swift and Anderson, 1989).

Aerts (1997b) analysed the effects of climate and litter chemistry on first-year leaf litter decomposition using literature data from 44 locations, ranging from cool temperate sites to humid tropical sites. Actual evapotranspiration (AET) was used as an index for the climatic control of decomposition, and litter chemistry was characterized by N and P concentrations, C : N and C : P ratios, lignin concentrations, and lignin : N and lignin : P ratios. The decomposability of the litter was expressed by the decomposition constants (k values) which are based on the single exponential decay model proposed by Olson (1963):

$$W_t = W_0 \, e^{-kt} \tag{9}$$

in which W_t and W_0 are litter masses at time t and time 0; k is the decomposition constant (year^{-1}) and t is time (years).

At a global scale, climate (expressed as AET) is the best predictor for the decomposition constants of the litter (Figure 15), whereas litter chemistry parameters have much lower predictive values (Table 4). This is in agreement with work of Berg *et al.* (1993) who studied litter decomposition of *Pinus* species using 39 experimental sites spanning climatic regions from subarctic to subtropical and Mediterranean sites. Also in their experimental study, climate (expressed as AET) exerted the strongest influence on litter decomposition over broad geographical scales, whereas litter chemistry was important at local scales only. Using path analysis, Aerts (1997b) showed that the climatic control on litter decomposability is mediated partly through an indirect effect of climate on litter chemistry. This is due to the fact that climate determines to a large extent the distribution of soil types. Indirectly, the soil type may influence decomposition via the composition of the decomposer
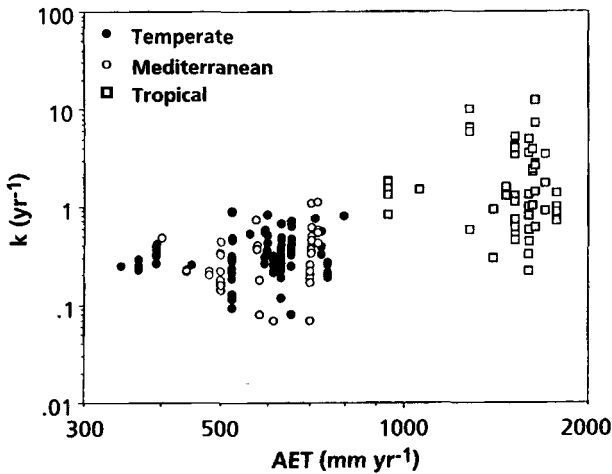
Fig. 15. Relationship between first-year leaf-litter decomposition constants (k) and actual evapotranspiration (AET) for temperate, Mediterranean and tropical sites. Redrawn from Aerts (1997b).

community and the resource quality of the plant litter input (Swift and Anderson, 1989). Vitousek and Sanford (1986) found that, in comparison with rates in temperate forests, N mineralization rates and nitrification rates are high on fertile tropical lowland soils. These results are consistent with the high N concentrations in litter from tropical plant species (Aerts, 1997b) and rapid circulation of N in vegetation in most lowland tropical sites (except on spodosols).

Within a particular climatic region, however, litter chemistry parameters exert the strongest control on litter decomposability, especially in the tropics (Table 4). In general, litters from the tropical sites have higher N concentrations and lower lignin : N ratios than litters from other climatic regions, which results in a higher decomposability of the litter. In both the tropics and the Mediterranean region, the lignin : N ratio is the best chemical predictor of litter decomposability. In the temperate region, however, there appeared to be no good chemical predictor of decomposability. This is in contrast to the findings of many field studies conducted in the temperate zone, in which limited sets of species were studied within a particular site (e.g. Melillo *et al.*, 1982; Meentemeyer and Berg, 1986; Blair, 1988; Taylor *et al.*, 1991). In these studies, a relationship was found between litter decomposability and litter chemistry. A possible explanation for this discrepancy might be that within a specific site there is a match between the local climate, soil characteristics, soil fauna and litter chemistry. As a result, the microbial activity is closely related to the resource quality, but in a way that is specific for the site. When data from

Table 4

Summary of significant regressions of decomposition constants (k: year^{-1}) against actual evapotranspiration (AET: mm year^{-1}) and various litter chemistry parameters (percentage concentrations) in different climatic regions (from Aerts, 1997b)

Parameter	d.f.	Regression (k)	r^2	P
All climatic zones				
AET	192	$0.000057 \, (AET)^{1.371}$	0.46	< 0.0001
C : N ratio	62	$20.184 \, (CNRATIO)^{-0.966}$	0.26	< 0.0001
N concentration	187	$0.555 \, (NCONC)^{0.888}$	0.24	< 0.0001
Lignin : N ratio	130	$4.612 \, (LIGNIN/N)^{-0.718}$	0.24	< 0.0001
P concentration	133	$1.601 \, (PCONC)^{0.369}$	0.10	< 0.0001
C : P ratio	57	$4.345 \, (CPRATIO)^{-0.350}$	0.06	< 0.05
Lignin : P ratio	94	$0.993 \, (LIGNIN/P)^{-0.133}$	0.04	< 0.05
Temperate zone				
N concentration	89	$0.895 \, (NCONC)^{0.174}$	0.05	< 0.05
Mediterranean zone				
Lignin : N ratio	29	$3.165 \, (LIGNIN/N)^{-0.714}$	0.24	< 0.005
C : N ratio	23	$7.830 \, (CNRATIO)^{-0.781}$	0.16	< 0.05
AET	37	$0.00041 \, (AET)^{1.024}$	0.08	< 0.05
N concentration	37	$0.901 \, (NCONC)^{0.546}$	0.08	< 0.05
Tropical zone				
Lignin : N ratio	34	$20.26 \, (LIGNIN/N)^{-0.907}$	0.57	< 0.0001
Lignin : P ratio	28	$26.99 \, (LIGNIN/P)^{-0.525}$	0.44	< 0.0001
C : P ratio	16	$3231 \, (CPRATIO)^{-1.175}$	0.39	< 0.005
C : N ratio	16	$19.82 \, (CNRATIO)^{-0.729}$	0.26	< 0.05
Lignin concentration	34	$24.07 \, (LIGNIN)^{-0.957}$	0.26	< 0.001
N concentration	57	$1.291 \, (NCONC)^{0.744}$	0.24	< 0.0001
P concentration	51	$5.590 \, (PCONC)^{0.534}$	0.23	< 0.0001

many sites are combined and litter decomposition is related to litter chemistry, as in the analysis of Aerts (1997b), the variation at the intermediate level (local climate, soil characteristics, soil fauna) is ignored. As a result, the relationship between litter decomposition and litter chemistry can be masked by this unaccounted for variation.

C. Variation in Litter Decomposition among Growth-forms

Leaves of evergreens usually contain higher concentrations (on a mass basis) of lignin and other secondary compounds than leaves of deciduous species (Chapin, 1989; Aerts and Heil, 1993; Van Vuuren et al., 1993). These high amounts of secondary compounds in leaves of low-productivity species are usually explained as a defence mechanism against herbivory (Coley et al., 1985; Grime et al., 1996) or as structural components that enable evergreen leaves to withstand unfavourable conditions in the non-growing season

(Poorter and Bergkotte, 1992). This may have serious implications for the decomposability of those leaves (Aerts, 1995). This effect can be reinforced by the lower N concentrations in the leaves of evergreens compared with leaves from other growth-forms (Figure 2). The rate of litter decomposition is in many cases negatively correlated with the lignin concentration or the lignin : N ratio, and positively correlated with the N concentration (Aerts, 1997b). This suggests that the leaf decomposition rate of evergreen species is lower than that of deciduous species. We investigated this hypothesis by a reanalysis of the leaf litter decomposition data from Aerts (1997b). As litter decomposition is controlled most strongly by climate (see above), the data for each climatic region were analysed separately. In both temperate and tropical regions leaf litter decomposition rates of evergreen shrubs and trees and of forbs and graminoids are significantly lower than those of deciduous shrubs and trees (Table 5). In the Mediterranean region, however, there was no difference in leaf litter decomposability between evergreen and deciduous species. A possible reason might be that slow-growing deciduous species, as found in this region, also contain high concentrations of (hemi)cellulose, insoluble sugars and lignin (Niemann et al., 1992; Poorter and Bergkotte, 1992), which may lead to low decomposition rates.

A low decomposability of plant litter in low-nutrient environments is less detrimental to evergreen than to deciduous species (Hobbie, 1992; Chapin, 1993; Van Breemen, 1993; Berendse, 1994b). Using a simulation model in which nutrient cycling and plant competition between an evergreen and a deciduous species were included, Berendse (1994b) demonstrated that the plant traits of evergreens (long tissue lifespans, low nutrient concentrations and low litter decomposition rates) can be favourable under nutrient-limited growth conditions. Low litter decomposability and the resulting low rate of nutrient release from that litter, as observed in evergreen species, leads to longer dominance of the evergreen species. This implies that the plant characteristics of evergreens do not only lead to high NUE, but also keep soil fertility

Table 5
First-year decomposition constants (k: year^{-1}) for leaf litter in different climatic zones, according to growth-form.

Zone	Evergreen species	Deciduous species	Forbs and graminoids
Temperate	0.31 ± 0.09 (33)	0.45 ± 0.20* (32)	0.29 ± 0.11 (22)
Mediterranean	0.37 ± 0.26 (20)	0.40 ± 0.24 (13)	N.D.
Tropical	1.37 ± 1.16 (21)	3.20 ± 1.45* (10)	1.66 ± 2.10 (13)

Values are mean ± SD with number of observations shown in parentheses.
*P < 0.05 versus other two growth-forms in that zone.

low and thereby influence the competitive balance with deciduous species in their favour (see Hobbie, 1992; Van Breemen, 1993).

XI. TRADE-OFF BETWEEN NUTRIENT USE EFFICIENCY AND LITTER DECOMPOSABILITY?

In section IX it was shown that high nutrient resorption contributes to high NUE but leads to low litter nutrient concentrations, and vice versa. This has direct implications for litter decomposition rates and nutrient release, because decomposition and nutrient release from litter are often positively related to the nutrient concentrations in the litter and negatively related to the C : nutrient ratio or the lignin : nutrient ratio (Coulson and Butterfield, 1978; Taylor *et al.*, 1989; Table 4). These observations suggest that there may be a trade-off between leaf-level NUE and litter decomposability. Aerts (1997a) investigated this hypothesis by a reanalysis of the data presented in section X.B. This analysis shows that there is indeed a trade-off between both NUE_N and NUE_P and litter decomposability: first-year decomposition constants are negatively related to NUE_N and NUE_P (Figure 16). However, the percentage of variance explained by the regression models is relatively low (24% for NUE_N, 10% for NUE_P). This is due mainly to the fact that in many low-productivity species both NUE and k are low (Figure 16), i.e. the rate of decomposition is low even if the N or P concentration of the litter is relatively high.

Owing to the strong climatic control on litter decomposition rates, part of the large scatter might be explained by the different climatic origin of the data points. However, a reanalysis of the data for each climatic zone separately did not result in an improved relationship between k values and NUE (data not shown). This was also the case when a separation was made between growth-forms (data not shown). A more likely explanation for the relatively weak relationship between NUE and litter decomposability lies in the secondary chemistry of the species considered. The chemistry of secondary compounds in plants is directly related to both the growth rate of plant species and to the decomposability of litter. Although both aspects have received considerable attention over the past few years, only a few attempts have been made to search for a casual connection between them (see Grime *et al.*, 1996; Cornelissen and Thompson, 1997). In general, low productivity species have higher amounts of secondary compounds than high-productivity species (Ellis, 1972; Bryant *et al.*, 1983; Niemann *et al.*, 1992; Poorter and Bergkotte, 1992).

These differences in secondary chemistry have a profound effect on the productivity of plant species per unit N in the plant and thereby on their NUE. On a daily basis, low-productivity species produce less biomass per unit N in the plant than high-productivity species (Lambers and Poorter, 1992). This difference is partly compensated by the longer lifespan of plant tissues in low-productivity species, but it may still lead to equal or lower plant-level NUE
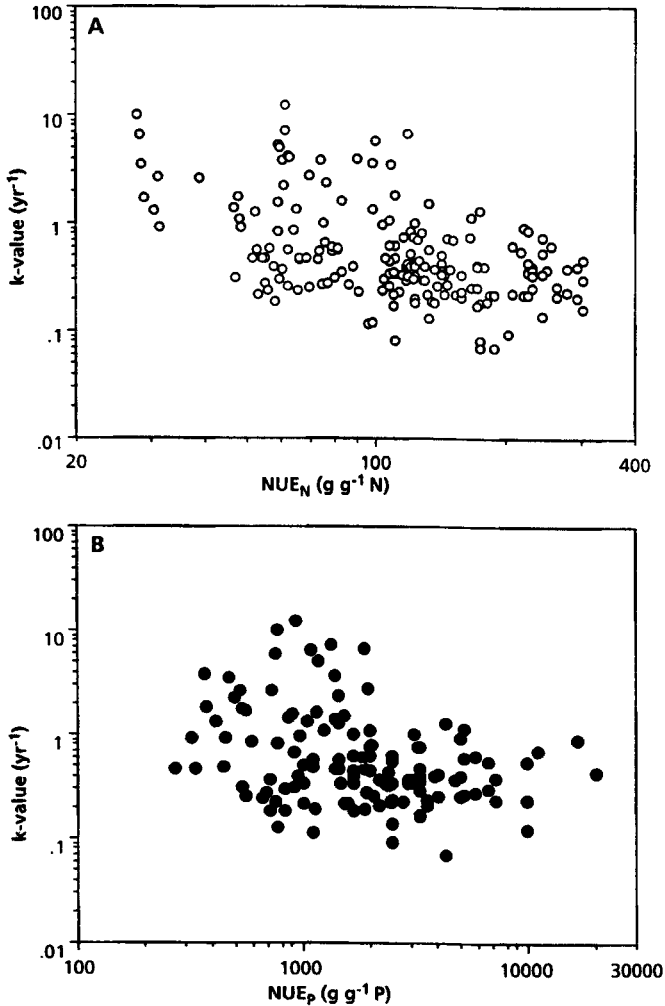
Fig. 16. Relationship between first-year leaf-litter decomposition constants (k) and
(A) leaf-level nitrogen use efficiency (NUE_N) and (B) phosphorus use efficiency
(NUE_P). Data were obtained from Aerts (1997b). Regression models: $k = 33.11$
$(NUE_N)^{-0.888}$, $r^2 = 0.24$, $187 = $ d.f., $P < 0.0001$; $k = 8.69$ $(NUE_P)^{-0.368}$, $r^2 = 0.10$, $133 = $
d.f., $P < 0.001$. (A) is redrawn from Aerts (1997a).

compared with that in high-productivity species (Aerts, 1990, 1995; Son and
Gower, 1991). Moreover, high concentrations of phenolics in leaves, as
observed in low-productivity species growing at infertile sites (Ellis, 1972;
Haukioja *et al.*, 1985; Nicolai, 1988), may lead to precipitation of proteins

before protein hydrolysis, which reduces nutrient resorption (Chapin and Kedrowski, 1983) and thereby NUE. Thus, low-productivity species do not necessarily have a high NUE (see Aerts, 1990, 1995; Son and Gower, 1991).

The secondary chemistry also affects litter decomposability. Litter decay is in many cases negatively related to the lignin concentration or the lignin : nutrient ratio of the litter (Berg, 1984; Van Vuuren et al., 1993; Aerts, 1997b; Aerts and De Caluwe, 1997). Also the phenolics : nutrient ratio may have a strongly retarding effect on litter decay (Thomas Asakawa, 1993; Constantinides and Fownes, 1994; Aerts and De Caluwe, 1997).

These observations show that, in addition to their significant role in defence against herbivory, the presence of secondary compounds in plants may lead both to low NUE and to low litter decomposability, and alter the hypothesized trade-off between NUE and litter decomposability. This may explain the large number of data points in Figure 16 in which values of both NUE and k are low. This combination of low productivity (and thus low litter production), low NUE and low litter decomposability may lead to a low rate of ecosystem N cycling (Chapin, 1993; Van Breemen, 1993). This may prevent the invasion of highly competitive species that are dependent on high N availability (Aerts and Van der Peijl, 1993; Berendse, 1994a,b). However, the decomposition data presented here refer to first-year mass loss and not to net N mineralization from the litter. Especially during the initial stages of decomposition, considerable N immobilization may occur (Blair, 1988; Aerts and De Caluwe, 1997). Moreover, element dynamics in decomposing litter may differ between the early and late stages of decomposition (Rustad, 1994).

XII. CONCLUSIONS: PLANT STRATEGIES

In this review, we have distinguished four main topics in the nutritional ecology of plants: nutrient-limited plant growth, nutrient acquisition, nutrient use efficiency, and nutrient recycling through litter decomposition. Within each of these areas, plants have evolved sets of adaptive traits ('strategies') with respect to their nutritional ecology. Species from nutrient-poor habitats often have the ability to take up organic nitrogen sources, they have a root allocation pattern directed towards the acquisition of nutrients that diffuse slowly to the roots, and they possess traits that lead to high nutrient retention such as tissues with slow turnover rates, low concentrations of mineral nutrients and high concentrations of secondary compounds, which serve amongst others as a defence against herbivory. All these traits lead to a low growth rate and/or to a low potential of resource capture. High nutrient resorption efficiency, however, is important in all species and does not differ consistently between species from nutrient-poor and nutrient-rich environments. Species from nutrient-rich habitats have traits that lead to rapid growth and quick capture of both above- and below-ground resources. The fact that this differentiation

does occur between species from habitats differing in soil fertility strongly suggests that there is a trade-off between their respective traits. This trade-off is adequately described by the NUE model of Berendse and Aerts (1987) in which two components of NUE are distinguished: the mean residence time (MRT) of nitrogen which reflects the 'nutrient retention strategy', and nitrogen productivity (A_{NP}) which reflects the 'rapid growth strategy'. Because of selection on the components of NUE rather than on NUE itself, there are no clear patterns in whole-plant NUE when comparing species from environments differing in soil fertility. At the phenotypic level, however, NUE decreases with increasing soil fertility.

Our analysis shows that the underlying leaf traits associated with high leaf-level NUE differ both among growth forms and among the nutrients under consideration. For woody species, leaf-level nitrogen use efficiency (NUE_N) is most strongly determined by variation in mature leaf N concentration. For herbaceous species, however, N resorption efficiency is the most important determinant of NUE_N. For phosphorus use efficiency (NUE_P), the situation is different: P resorption efficiency contributes most strongly to maximization of NUE_P in all growth-forms. This is due to the fact that maximum P resorption efficiency is higher than maximum N resorption efficiency and that at high resorption efficiencies (r) NUE is disproportionally increased by small increases of r. It appears that, for all growth-forms, leaf lifespan is only a minor contributor to variation in both leaf-level NUE_N and NUE_P. This is not in agreement with the pattern at the whole-plant level. Evergreen species have higher leaf-level NUE_N and NUE_P than other growth-forms.

It is important to note that the traits associated with competitive dominance in habitats differing in soil fertility may also have effects on ecosystem nutrient cycling. In nutrient-poor environments, species produce relatively small amounts of litter due to low productivity and long lifespans of the various tissues. This litter generally has low nutrient concentrations and high concentrations of secondary compounds such as lignin and phenolics. Thus, species from nutrient-poor environments produce litter that decomposes slowly and from which only low amounts of nutrients are released. The opposite holds for species from fertile environments. Owing to their high productivity and high tissue turnover rates, they produce relatively large amounts of litter. Moreover, this litter contains relatively high concentrations of mineral nutrients and low concentrations of secondary compounds. As a result, this litter decomposes relatively quickly and releases high amounts of nutrients. Thus, in nutrient-poor ecosystems the combination of low productivity (and thus low litter production) and low litter decomposability may lead to a low rate of ecosystem nutrient cycling. This may prevent the invasion of highly competitive species which are dependent on high nutrient availability. On the other hand, the traits of species from fertile environments lead to a high rate of ecosystem nutrient cycling and this excludes slow-growing and

nutrient-conserving species from these habitats. From these patterns, it can be concluded that the strategies of species from nutrient-poor and nutrient-rich habitats promote long-term ecosystem stability. This is an important evolutionary consequence of these strategies, although it is questionable whether long-term ecosystem stability is prone to natural selection.

Within the nutritional ecology of plants, several major issues still have to be resolved. A fascinating issue is how the differential uptake of inorganic and organic N sources contributes to plant coexistence and how this is related to ecosystem nitrogen cycling and ecosystem stability. A major gap in our knowledge of patterns in NUE along soil fertility gradients is that there are hardly any data on whole-plant NUE in natural ecosystems. Moreover, we still do not know which factors control nutrient resorption from senescing tissues, how this is related to the dynamics of secondary compounds in senescing tissues, and how these processes are reflected in litter decomposition and nutrient release from litter. Moreover, the fact that both mycorrhizal and non-mycorrhizal plants are capable of taking up various organic N compounds requires that studies of plant nutrition in natural ecosystems focus more on the dynamics of these compounds in the soil.

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