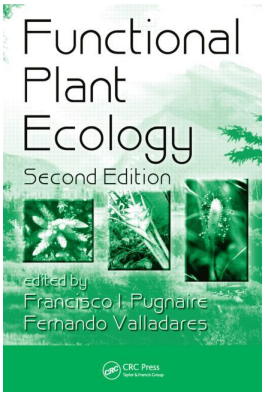

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Acquisition, Use, and Loss of Nutrients

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8 Acquisition, Use, and Loss of Nutrients

Frank Berendse, Hans de Kroon, and Wim G. Braakhekke

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INTRODUCTION

In many natural environments, nutrient supply is one of the most important factors that affect the productivity and the species composition of plant communities (Kruijne et al. 1967, Elberse et al. 1983, Pastor et al. 1984, Tilman 1984). In many grassland, heathland, wetland and forest communities increased fertilizer gifts and increased nitrogen inputs through atmospheric deposition have caused not only dramatic changes in species composition, but also important losses of plant species diversity (Aerts and Berendse 1988, Berendse et al. 1992). To understand the changes in plant communities that occur after an increase in nutrient supply, it is essential to understand how plant species are adapted to environments with different nutrient availabilities. The relation between nutrient supply and long-term success of a plant individual in a natural ecosystem is determined by three important components of plant functioning:

1. the acquisition of nutrients in soils that are always more or less heterogeneous;
2. the use of absorbed nutrients for carbon assimilation and other plant functions;
3. the loss of nutrients determining the length of the time period that nutrients can be used.

In this chapter, we subsequently consider these three aspects and finally attempt to integrate them to conclude how plant species cope with nutrient-poor and nutrient-rich environments. We focus on plants growing in their natural habitat. Such plant individuals experience a heterogeneous substrate, they have to compete for soil resources and light with other plants, and they frequently lose large quantities of nutrients through abscission, disturbances, and herbivory.

NUTRIENT UPTAKE KINETICS: BASIC PRINCIPLES

Nutrient uptake is determined by both supply and demand at the root surface. Nutrients arrive at the root surface by the mass flow of water toward the root, which is driven by transpiration. Plants deplete the soil solution near the roots, when the nutrient uptake rate exceeds the rate at which nutrients arrive. By doing so they create concentration gradients around the roots that trigger diffusion of nutrients toward the root surface, which adds to the supply by mass flow. When the depletion at the root surface proceeds, uptake must come in pace with the supply rate. When the supply by mass flow exceeds the demand, nutrients (and other solutes) can either be excluded, accumulating near the root, or enter the root and accumulate in the plant to concentrations that may eventually become deleterious (Marschner 1995, Fitter and Hay 2002).

Depletion and accumulation at the root surface can occur simultaneously for different elements. Table 8.1 gives an indication of the relation between the demand of the major nutrients and their supply by mass flow. The listed concentrations in plant biomass are considered to be sufficient for adequate growth (Epstein 1965). There is a close relation between biomass production, nutrient demand, and water uptake. Based on the amount of water transpired during the production of a unit biomass (transpiration coefficient), we can calculate the nutrient concentration in the soil solution that would satisfy the nutrient demands as listed in the first column by means of mass flow alone. Actual concentrations in the soil solution of an average agricultural soil illustrate that mass flow rates of S, Mg, and Ca amply exceed the demand, whereas mass flow of P falls entirely short of the demanded rate of supply. In agricultural soils, mass flow rates of N and K are usually sufficient, but in most natural soils, concentrations of N, P, and K are much lower, so that the supply by mass flow alone is insufficient to satisfy the demand. Consequently, diffusion must play an important role in the supply of these nutrients to plants growing on natural soils. This calls for a root system that has the ability to take up nutrients selectively against a concentration gradient.

Selective uptake and transport through cell membranes is an energy-demanding process. Passive, nonselective uptake without energy expenses is only possible where nutrients do not have to pass a cell membrane on their way to the vascular cylinder of the root. Passive uptake can revert into efflux when the concentration in the soil solution falls below the concentration inside the root. Passive cation uptake through cell membranes can also proceed against a

TABLE 8.1
Average Nutrient Concentrations in Plant Biomass (Epstein 1965), Concentrations in Soil Solution Required to Satisfy the Demand by Mass Flow, Assuming the Transpiration Coefficient is 0.3 dm^{-3} g^{-1} d.wt., and Actual Concentrations in the Soil Solution in an Arable Field

	Element Concentration in Plant Biomass (mmol kg^{-1} d.wt.)	Sufficient Concentration in Mass Flow (mM)	Actual Concentration in Bulk Soil Solution (mM)
N	1000	3.33	3.1
K	250	0.83	0.5
Ca	125	0.42	1.7
Mg	80	0.27	0.5
P	60	0.20	0.002
S	30	0.10	0.6

Source: After Peters, M. in *Schriftenreihe des Institutes für Pflanzenernährung und Bodenkunde*, H.P. Blume, ed., Universität Kiel, Kiel, 1990.

concentration gradient, because cells can create an electrochemical gradient by actively pumping out protons across the membrane. Anions, on the other hand, have to be transported actively through cell membranes by means of carrier enzymes.

Passive uptake without energy expenses would be sufficient for nutrients that are required in low quantities and occur in relatively high concentrations in the soil solution, if it were not for the closed structure of the root. Since passive uptake is not selective and cannot be regulated, plants that rely too much on passive uptake can easily be overloaded with nutrients and toxic ions when concentrations in the soil solution are high. This makes it understandable why plant roots possess an endodermis that prevents passive nutrient transport (see Chapter 5, this volume). Solutes can enter the root via the apoplastic pathway between the cortex cells, but no further than the endodermis with its bands of Caspari. Solutes that are transported by mass flow to and into the root at a higher rate than the active uptake rate by rhizodermal, cortex, or endodermis cells accumulate between the cortex cells and at the root surface. This leads to diffusion in the direction opposite to the water flow, away from the root, back into the soil. Most nutrients enter the root across a cell membrane somewhere in the cortex by means of active transport and continue their way inside along the symplastic pathway, from one cell to another via intercellular cytoplasma connections (plasmodesmata), to pass through the endodermis and finally enter the vascular cylinder (Marschner 1995). A small fraction of the nutrients can circumvent the endodermis at the root tip where the bands of Caspari are not yet formed, and at places where the endodermis is pierced by lateral roots, torn, or damaged otherwise.

Active uptake against a concentration gradient, by means of an energy-demanding process, is the predominant uptake process for the major nutrients N, P, and K. The uptake rate depends on the nutrient concentration at the root surface. Usually an asymptotic relation is found between the concentration in a nutrient solution and the uptake rate, when measured in short-term experiments with excised roots from plants that have been deprived of nutrients for a few weeks. The uptake as a function of the concentration in the surrounding solution is generally described by:

$$V = V_{\max} \frac{C_l}{C_l + K_m},$$

in which V is the gross uptake rate (μmol g^{-1} fw h^{-1}), $V_{\max}$ is the maximum uptake rate, C_l is the nutrient concentration in the soil solution at the root surface (mM), and K_m is the Michaelis constant, which is the value of C_l where V is half $V_{\max}$. The Michaelis–Menten equation is typical for the kinetics of enzymatic processes and reflects the fact that the carrier enzymes in the cell membranes become saturated with increasing nutrient concentration. K_m^{-1} expresses the affinity of the carriers for the substrate ion (i.e., the slope of the curve in the origin, which is measured by $V_{\max}/K_m$). Although different nutrient ions are transported by different carriers, the selectivity of the carriers is not perfect. Different nutrients may compete for the same carriers, so that K_m may be increased by the presence of other ions with the same electrical charge.

The maximum uptake rate ($V_{\max}$) is realized when the concentration (C_l) is so high that all carrier enzymes are continuously occupied with a substrate ion. $V_{\max}$ depends on the density and the activity of carriers in the cell membranes. It depends also on the internal nutrient status of the plant, because the activity of the carriers can be suppressed by high nutrient concentrations in the root (compare $V_{\max}$ under deprived and well-fed conditions, Figure 8.1). This negative-feedback control operates when plants are growing under nutrient-rich conditions. It can reduce $V_{\max}$ to less than 20% of its value in a deprived plant (Loneragan and Asher 1967) and prevents accumulation of too high nutrient concentrations in the root. On the other hand, it has been found that plants growing under nutrient poor conditions can

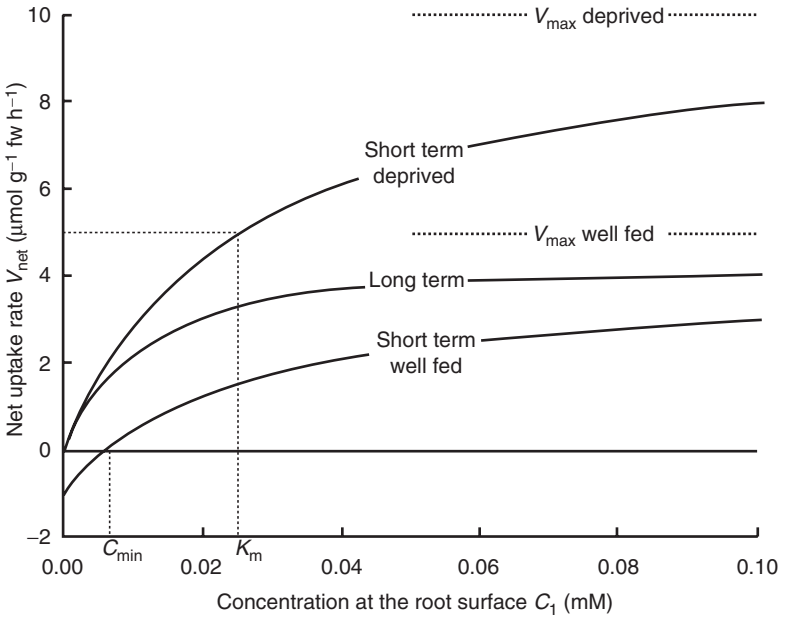

FIGURE 8.1 Relation between external nutrient concentration at the root surface (C_l) and net nutrient uptake rate ($V_{net} = V - E$). The upper curve represents the short-term uptake by excised roots from previously deprived plants ($V_{max} = 10$, $K_m = 0.025$, efflux $= 0$). The lower curve represents short-term uptake by excised roots of previously well-fed plants ($V_{max} = 5$, $K_m = 0.025$, efflux $= 1$). C_{min} is the concentration at which $V_{net} = 0$. The curve marked long term represents nutrient uptake by whole plants grown for several weeks on nutrient solutions with constant concentration, so that V_{max} and efflux are in steady state with the internal nutrient concentration and C_l.

temporarily increase V_{max} when the concentration in the soil is increased (Lefebvre and Glass 1982, Jackson et al. 1990).

Consequently, roots of a well-fed plant are operating far below their maximum uptake capacity. When the soil becomes depleted and the nutrient concentration in the plant starts to drop, the negative-feedback control on V_{max} is relaxed, so that V_{max} increases, which compensates for the decrease in supply rate. The responses of V_{max} to changes in internal and external nutrient concentrations allow a plant to regulate its nutrient uptake and rapidly use temporarily high nutrient concentrations that may occur locally in a predominantly poor soil. Under rich conditions, it allows a plant to maintain its overall uptake rate even when a large part of the root system is removed.

Besides uptake, efflux of nutrients may occur. When active uptake takes place, nutrient concentrations inside the root are usually higher than those outside the root. Since roots are not perfectly closed, leakage of nutrients can reduce the net uptake rate (V_{net}). When nutrient influx and efflux occur simultaneously, the plant can only decrease the nutrient concentration in the soil solution until it reaches a minimum concentration (C_{min}) at which influx and efflux are equal. At values of C_l lower than C_{min}, the efflux is larger than the gross influx, so that the net influx is negative and the roots lose nutrients to the solution until C_l equals C_{min} (Figure 8.1).

Like V_{max}, C_{min} is not a constant. Under nutrient poor conditions, when nutrient concentrations inside the root are low, the efflux is also low. Together with the release of the feedback control on V_{max}, this results in very low values of C_{min} under nutrient-poor conditions (Figure 8.1). It is unclear at present whether the K_m value is also able to respond to changes in internal or ambient nutrient concentrations (Marschner 1995). The reported

changes in uptake kinetics of roots in response to localized nutrients (e.g., Drew and Saker 1975, Jackson et al. 1990) may be due to changes in V_{max} or efflux rate alone. In most plant species, the value of K_m for N, P, and K is so low that the concentration of these nutrients at the root surface can become virtually zero, for example, 0.35 μM for NO_3^- (Freijsen et al. 1989), 1 μM for K^+ (Drew et al. 1984), and less than 0.01 μM for $H_2PO_4^-$ (Breeze et al. 1984).

NUTRIENT ACQUISITION IN SOILS

The description of active nutrient uptake given earlier applies mainly to uptake by single roots in a well-mixed nutrient solution. However, the relation between uptake and concentration in the soil solution is of little consequence for the overall nutrient uptake by a whole plant growing in a poor soil. In soils, uptake of N, P, and K is almost always limited by the rate of transport toward the root surface and not by the capacity of the uptake mechanism. Concentrations of these nutrients in the soil solution are often so low, and the uptake is so efficient that all available nutrients near the root surface can be taken up within a few minutes. When nutrient uptake is not immediately compensated by nutrient transport from the bulk soil toward the root surface, the nutrient concentrations at the root surface fall and the uptake rate decreases. Even in nutrient solutions, where transport rates (TRs) are high, depletion at the root surface may reduce nutrient uptake rates, as appears from the stimulating effect of stirring (Freijsen et al. 1989). The importance of nutrient transport to the root in nutrient-poor soils is illustrated by the following analysis of the balance between nutrient supply and uptake at the root surface (Nye and Tinker 1977).

As explained earlier, nutrient uptake is determined by the concentration at the root surface (C_l), which, in its turn, is the resultant of nutrient transport to the root and the net nutrient uptake rate (V_{net}). The transport rate is the sum of the mass flow rate and the diffusion rate (DR). The mass flow rate is the product of water flow (V_w) and nutrient concentration in the bulk of the soil solution (C_b). The diffusion rate is the product of the concentration gradient toward the root surface (dC/dx) and the effective diffusion coefficient (D_e). The effective diffusion constant, in turn, depends on the moisture content of the soil, the tortuosity of the diffusion pathway, and the buffer power of the soil, which accounts for the degree to which nutrient transport is impeded by interaction with soil particles. Phosphate is strongly adsorbed to soil particles, which leads to low values of C_b resulting in low rates of mass flow and diffusion. At the other end of the spectrum, nitrate is much more mobile, because adsorption is negligible. Potassium takes an intermediate position.

The net uptake rate (V_{net}) is calculated as the gross uptake rate (V), minus the efflux rate (E). This leads to the following equations:

$$TR = V_w\ C_b + D_e \frac{dC}{dx},$$

$$V_{net} = \left[V_{max} \frac{C_l}{C_l + K_m} \right] - E.$$

When the transport rate equals the net uptake rate, a dynamic equilibrium develops (with equilibrium concentration and uptake rate C_l* and V_{net}*). When C_l is lower than C_l*, the transport rate is higher than the net uptake rate, so that C_l increases until it reaches C_l* (cf. Figure 8.2). When C_l is higher than C_l*, the transport rate is lower than the net uptake rate, so that C_l decreases until it reaches C_l*. At a short term (hours), the equilibrium concentration (C_l*) and the corresponding equilibrium uptake rate (V_{net}*) are stable. When uptake proceeds for a few days, the equilibrium shifts gradually to lower C_l values, because the depletion zone grows, the diffusion gradient becomes less steep, and the transport rate decreases. Around thin roots, depletion proceeds slower than around thick roots, because of the radial geometry

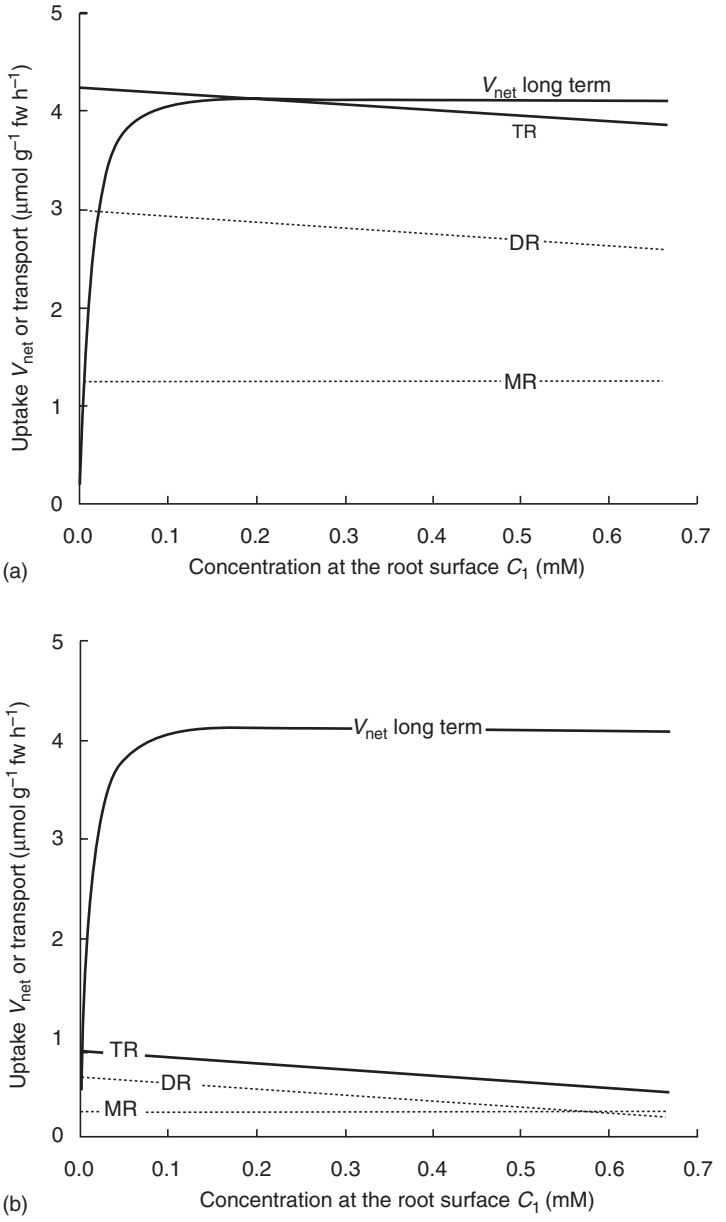

FIGURE 8.2 Net uptake rate (V_{net}) and nutrient transport rate to the root surface (TR) as a function of the nutrient concentration at the root surface (C_l). The diffusion rate (DR), the mass flow rate (MR), and their sum (TR) at (a) high ($C_b = 5$) and (b) low concentrations ($C_b = 0.3$) in the bulk soil. In either case, the equilibrium concentration (C_1*) and equilibrium uptake rate (V_{net}*) are found at the intersection of the lines V_{net} and TR. The parameter values used are hypothetical, keeping midway between NO_3^- and K^+. V_{net} is identical to the long-term uptake in Figure 8.1.

of roots. The amount of soil per unit root surface present within the same distance from the root surface is larger (and contains more nutrients) when the root diameter is smaller.

The depletion zone around the root continues to grow until the transport rate becomes so low that it equals the rate at which nutrients are released from the soil within the depletion zone by means of dissolution, desorption, or mineralization. Immobile nutrients, like

phosphate, are released slowly and have narrow depletion zones, low uptake rates, and low C_l*. Eventually, when the nutrients adsorbed to soil particles are depleted up or when mineralization is interrupted due to low temperatures, the release rate falls and uptake stops.

To maximize uptake, plants can reduce the distance over which nutrients are transported through the soil, by increasing the density of their root system. Plants can realize higher root densities by increased allocation of carbon to their rooting system but also by reduced root diameters which leads to an increased root length and root surface per unit of root biomass. Root hairs are important in this respect, because they are thin and require little investment of biomass per unit of soil explored. However, their vulnerability and short life span make them less profitable when the bulk of the soil is already depleted, so that a plant has to "sit and wait" for nutrients that are released from the solid phase. In such nutrient-poor situations many plant species are living in symbiosis with fungi that form mycorrhizas. Such associations strongly increase the total surface area by which nutrients can be taken up. Fungal hyphae have much smaller diameters than roots (see Chapter 5, this volume).

Silberbush and Barber (1984) have studied the effect of changes in plant and soil characteristics on the equilibrium uptake rate of plants growing in soil. Figure 8.2 illustrates their results. The equilibrium uptake rate (V_{net}*) and nutrient concentration (C_l*) at the root surface are given by the intersection of the lines TR and V_{net}. When nutrient concentrations in the soil are high (Figure 8.2a, with $C_b = 5$), C_l* is situated at the horizontal part of the uptake curve. In this case, the equilibrium uptake rate V_{net}* is determined largely by the maximum uptake capacity of the roots (V_{max}) and not by the affinity of the uptake mechanism (K_m), nor by the mass flow or diffusion rate. Consequently, we may expect that natural selection on rich soils will favor plants with a high maximum uptake capacity (V_{max}).

When nutrient concentrations in the bulk soil are low (Figure 8.2b, with $C_b = 0.3$), C_l* is situated at the ascending part of the uptake curve. Here, V_{net}* is mainly determined by the effective diffusion coefficient D_e and by C_b, which determine the slope of the line that represents the diffusion rate and the intercept with the horizontal axis, respectively. In this case, the value of V_{net}* is relatively insensitive to changes in the kinetic parameters that rule the uptake process (K_m and V_{max}). Consequently, we may expect that natural selection of plants on poor soils will not lead to increased affinity or capacity of the nutrient uptake mechanism, but to properties that reduce the transport limitation, bringing the root surface closer to the nutrients (i.e., by fine and dense root systems and mycorrhizal associations). By increasing the root surface per unit plant biomass, a plant can sustain adequate growth rates with lower nutrient uptake rates per unit root surface and thus with lower nutrient concentrations at the root surface than competitors with a smaller root system.

The nutrient concentration in the bulk of the soil solution (C_b) can differ dramatically from the concentration at the root surface (C_l), implying that C_b is not a good indicator of nutrient availability. When the nutrient pool in the bulk of the soil solution is depleted, the nutrient supply to the root depends on the rate at which available forms of the nutrient are released from the organic and the mineral substrates. Plants can increase the release rate of nutrients by lowering the concentration in the soil solution or by affecting the chemical conditions or the microbial activity in the rhizosphere. Some species can use chemical forms or physical states (solid, dissolved, adsorbed, or occluded) of a nutrient that other species cannot use. Nitrogen, for example, can be taken up by most species only as NO_3^- and NH_4^+, but some species can also take up amino acids and other dissolved organic molecules that contain nitrogen (Kielland 1994, Northup et al. 1995, Schimel and Chapin 1996, Leadley et al. 1997). Some species can mobilize iron in calcareous soils by lowering the pH or by exudating chelating or reducing substances (Römheld and Marschner 1986). Phosphorus can be taken up by most species only as $H_2PO_4^-$, but some species are able to mobilize solid calcium phosphate by changing the chemical conditions in the rhizosphere, for example, by lowering pH, exudation of organic acids, or lowering the Ca concentration in the soil solution (Hoffland 1992). The ability to

mobilize insoluble nutrients by altering the chemical conditions in the rhizosphere can be enhanced by forming dense clusters of lateral roots that intensify the rhizosphere effects. These morphological adaptations are called proteoid roots, after the *Proteaceae* family, but they occur also in species of other taxa (e.g., *Lupine*). An excellent review of the ability of plant species to use alternative nutrient sources is given by Marschner (1995).

Many plant species from nutrient-poor soils have special adaptations that enable them to use nutrients from other sources than the soil solution. The most widespread of these are associations with mycorrhizal fungi and symbiosis with N-fixing bacteria such as *Rhizobium* and *Frankia*. Mycorrhizal fungi are able to decompose dead organic material and to transport the mineralized nutrients to the plant root (see Chapter 5, this volume). Recently, Jongmans et al. (1997) suggested that mycorrhizal fungi are also able to penetrate rocky materials and to absorb P, Mg, Ca, and K from minerals by the excretion of organic acids and to transport these nutrients to connected roots. More peculiar adaptations that occur mainly in extremely nutrient-poor ecosystems are parasitism on other plants (e.g., *Rhinanthus*, *Pedicularis*) and carnivory (e.g., *Drosera, Pinguicula, Utricularia*).

UPTAKE OF ORGANIC NITROGEN COMPOUNDS

A few decades ago, it was assumed that most plant species absorbed nitrogen as nitrate and ammonium except for species with ecto- or ericoid mycorrhizal associations (Read 1991). It was long considered that the mineralization of organic nitrogen to ammonium and its subsequent oxidation were the major bottlenecks restricting the nitrogen supply to plants (Chapin 1995). However, these ideas were strongly disturbed by the observation that measured rates of net microbial production of inorganic nitrogen were often less than half the observed rates of nitrogen acquisition by plants (Fisk and Schmidt 1995, Kaye and Hart 1997). In the 1990s, it became clear that quite a few species can absorb amino acids from solution and can easily survive when no other nitrogen forms are supplied (Chapin et al. 1993, Kielland 1994). Schimel and Chapin (1996) showed that two tundra sedges, *Eriophorum vaginatum* and *Carex aquatilis*, which were unlikely to have any of these mycorrhizal associations, nevertheless absorbed amino acids (glycine and aspartate) under field conditions. The amino acids that they provided to the plants were labeled with ^{15}N and ^{13}C to test whether complete amino acids were taken up or that ammonium that was derived from decomposing amino acid molecules was absorbed. The authors did not detect any of the ^{13}C in the produced plant tissues and they attributed this failure to respiration of the labeled C atoms. Glycine and aspartate can be easily converted into glycolysis or TCA cycle intermediates and subsequently respired. Näsholm et al. (1998) solved this problem by ^{15}N and dual ^{13}C labeling of the glycine molecule. Here both C atoms were labeled instead of only the carbon in the carboxyl group, preventing that all ^{13}C were rapidly respired after decarboxylation. Their measurements in a boreal forest showed that at least 91%, 64%, and 42% of the nitrogen from the absorbed glycine was taken up as intact glycine molecules in the dwarfshrub *Vaccinium myrtillus*, the grass *Deschampsia flexuosa*, and the trees *Pinus sylvestris* and *Picea abies*, respectively. These results showed unambiguously that these different species, irrespective of their completely different mycorrhizal associations, can bypass nitrogen mineralization. The dwarfshrubs and trees have ericoid and ectomycorrhizal associations and were expected to absorb organic nitrogen. But it was surprising that the arbusco-mycorrhizal grass species also appeared to be able to absorb amino acids. A recent review (Aerts and Chapin 2000) mentioned that "the ability to take up organic N sources . . . hardly occurs in species with arbuscular mycorrhizas." But it seems that the ability to absorb dissolved organic nitrogen compounds is much more widespread among plant species than we earlier believed (Schmidt and Stewart 1997, Lipson et al. 1999, Persson et al. 2003). Nevertheless, the quantitative significance of the uptake of dissolved organic nitrogen as compared with the uptake of ammonium and nitrate is still to be assessed.

ROOT FORAGING IN HETEROGENEOUS ENVIRONMENTS

So far we have examined nutrient uptake and transport in a homogenous substrate. However, nutrient availability in soils may vary dramatically beyond the zone of influence of the roots themselves. Soil patches of different quality are created at various scales by abiotic factors (soil type differences, soil depth, microtopography) as well as by biotic factors such as treefalls and stemflow in forests (Gibson 1988a,b, Hook et al. 1991, Lechowicz and Bell 1991, Farley and Fitter 1999). In arid environments, organic matter accumulates in the vicinity of isolated trees, shrubs, and persistent turf grasses creating islands of fertility in a nutrient-deprived matrix (Jackson and Caldwell 1993, Alpert and Mooney 1996, Ryel et al. 1996, Schlesinger et al. 1996). Consequently, from the point of view of the plant individual, in many habitats the spatial distribution of water and nutrients is profoundly heterogeneous from scales as small as a few centimeters, to tens of meters and more. How effectively can plants capture the resources in such a heterogeneous world? What fraction of the growth achieved at a homogeneous supply of soil resources can be realized when similar amounts of resources are patchily distributed? Do species from habitats of different resource status have different foraging abilities?

Especially for the less-mobile ions such as phosphate, pockets of nutrients may only be captured by the plant if roots expand their surface area into the richer patch (Hutchings and de Kroon 1994, Robinson 1994, 1996). This foraging behavior may be very effective, as is perhaps best illustrated with the classical study by Drew and coworkers with barley (*Hordeum vulgare*). Single root axes of barley were grown into three compartments in which the concentration of nutrients could be controlled separately. High nitrate concentration in a given compartment promoted the formation of more first- and second-order laterals per unit of primary root length within that compartment and greater lateral root extension (Drew et al. 1973). When one-third of the entire root system received a nutrient-rich solution, total lateral root length per unit of length of the primary axis was 10 times higher, and the total root biomass 6 times higher, in the high-nutrient compartment than those in the low-nutrient compartments. Later in the experiment, when the lateral roots had grown out, whole-plant relative growth rate (RGR) under localized supply of nutrients approached the RGR of control plants growing under homogeneous nutrient supply (Drew and Saker 1975). When phosphate was supplied to 2 cm of the main root axis—a fraction amounting to only a few percent of its total length—whole-plant RGR was more than 80% of its value in control plants in which the whole root system received phosphate. When applied to 4 cm of the main root axis, the RGR was similar to that of controls. The higher local nutrient uptake from small pockets of nutrients to which part of the root system was exposed was not only due to an enlargement of the local root surface area. In addition, phosphate absorption rates per unit of root length increased in the enriched compartment, compared with both other parts of the root system in treated plants and the root system of control plants (Drew and Saker 1975).

The enhanced formation of roots in nutrient hotspots is now referred to as root proliferation, selective root placement, or root foraging precision (de Kroon and Mommer 2006). Local conditions determine where lateral root growth and uptake is promoted (Drew et al. 1973, Drew and Saker 1975), but the magnitude of the local response depends on the conditions experienced by the rest of the root system and the entire plant. An experiment by Drew (1975) illustrates this well. He subjected roots of barley plants to either a uniform or localized nutrient supply. Part of the root system given a high phosphate supply produced more and longer lateral roots when the rest of the root system was receiving low phosphate rather than high phosphate (Figure 8.3). This suggests that the local morphological response is stronger when phosphate is more limiting to the plant. Broadly similar effects were produced when the nitrate and ammonium supply to different sections of the root system was varied (Drew 1975). However, effects were less clear for nitrate (Drew et al. 1973,

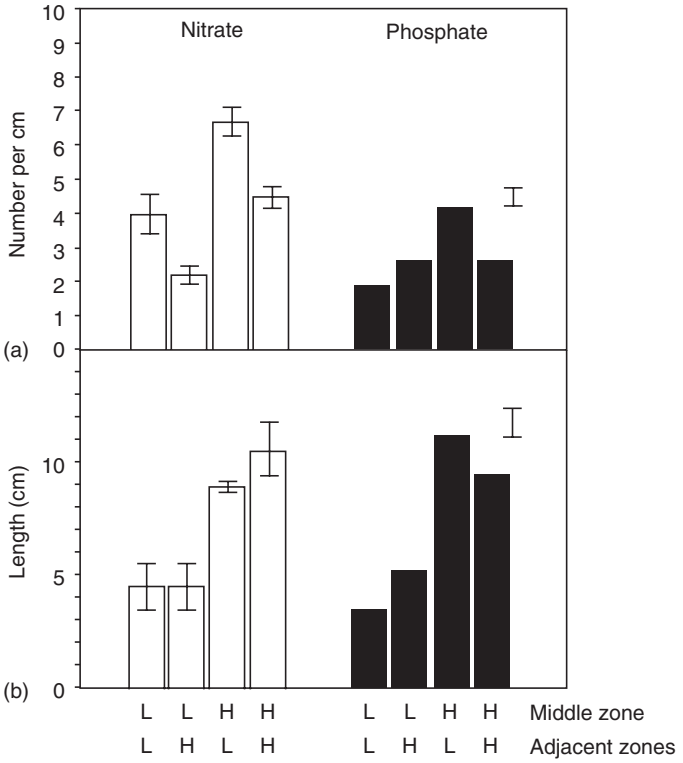

FIGURE 8.3 Effects of nitrate and phosphate supply on (a) the number of lateral roots per cm of main root axis and (b) the lengths of individual lateral roots in barley. Main root axes were divided into three zones and nutrients were supplied independently to each of these zones. Data given are those for the first-order laterals that developed in the middle zone. This zone experiences either a low (L) or a high (H) concentration of nitrate or phosphate. Adjacent rooting zones also grew in either a high- or low-nutrient solution. In the nitrate experiment, plants were grown hydroponically; in the phosphate experiment, they were grown in sand. Nitrate data are given as mean $\pm$SE, phosphate as means with separate bars showing the LSD at the 5% level. (After Drew, M.C., Saker, L.R., and Ashley, T.W., *J. Exp. Bot.*, 24, 1189, 1973; Drew, M.C., *New Phytol.*, 75, 479, 1975; adapted from Hutchings, M.J. and de Kroon, H., *Adv. Ecol. Res.*, 25, 159, 1994. Courtesy Academic Press. With permission.)

see Figure 8.3). In most studies in which nutrients were supplied heterogeneously, root growth was suppressed in the part of the root volume that experiences low nutrient supply (Robinson 1994).

The merits of the ability to forage for patchily distributed nutrients can perhaps best be illustrated by comparing the biomass production of plants grown on homogeneous and heterogeneous substrates each with the same overall nutrient availability. Fransen et al. (1998) created such treatments by mixing poor riverine sand with black humus-rich soil either homogeneously or by concentrating most of the black soil in a small column within the pot. Five grass species were grown individually in each of these treatments. Their roots readily reached and penetrated the enriched column but the responses were significant only for the three species characteristic of relatively nutrient-rich habitats. Combined for all species, whole-plant nutrient accumulation and biomass at the end of the experiment was significantly higher in the heterogeneous treatment than that in the homogeneous treatment. These results indicate that plant species may profit and grow faster at a heterogeneous distribution of soil nutrients, rather than slower. In this experiment with bunchgrasses the growth stimulus in the

heterogeneous treatment compared with the homogeneous treatment was small. Clonal species that spread horizontally have the ability to take up nutrients locally and produce most of the biomass beyond the nutrient-rich patch. For such species, a several-fold increase in biomass production may occur if the distribution of nutrients is not homogeneous, but concentrated in small hotspots (Birch and Hutchings 1994, Hutchings and Wijesinghe 1997, Wijesinghe and Hutchings 1997).

To what extent these results on root foraging ability in heterogeneous soils are generally valid? In a recent meta-analysis covering the results of over 100 species, Kembel and Cahill (2005) showed that the responses are very variable, confirming earlier overviews (Robinson 1994, Hodge 2004). Species varied from little or no root proliferation at all, distributing their roots equally over the rich and poor parts of the soil, up to the very plastic responses as observed for barley in Drew's experiments. Species may also differ markedly in the time between nutrient application and response. For example, when exposed to nutrient enrichment, roots of the cold desert species *Agropyron desertorum* showed a fourfold increase in the RGR of root length within one day, whereas *Artemisia tridentata* and especially *Pseudoroegneria spicata* responded less vigorously (Jackson and Caldwell 1989). In the latter species, extension growth was not affected until several weeks after nutrient application.

For one of the three datasets analyzed, Kembel and Cahill (2005) found support for the notion of Grime et al. (1986) that plant species with a higher RGR place their roots more selectively in heterogeneous soils. When in a given experiment, plants of different growth rates are harvested after a fixed period of time, as is usually the case, the degree of selective root placement is indeed positively correlated to growth rate (Fransen et al. 1999, Aanderud et al. 2003). This correlation has its origin in the modular nature of the root system (*sensu* de Kroon et al. 2005), in which roots respond locally to the nutrient concentrations that they experience. Species with larger RGRs in terms of plant biomass are likely to also have larger root RGRs (more lateral root formation and higher root extension rates) in the richer microsites. However, when corrected for growth rate differences, the degree of selective root placement is the same for slow-growing and fast-growing species (Fransen et al. 1999, Aanderud et al. 2003).

However, it should be realized that species with higher root proliferation in enriched patches do not necessarily obtain more nutrients from heterogeneous soil than species with less root proliferation, unlike the results of Drew and Saker (1975) and Fransen et al. (1998) suggest. For their larger datasets, Kembel and Cahill (2005) found no significant correlation between the response to nutrient heterogeneity in terms of biomass production and the precision by which the roots were placed in the nutrient-richer patches. Some of these variable results may be explained by slow response of root proliferation that may come too late relative to nutrient release in the patches (Robinson 1996, Van Vuuren et al. 1996), suggesting a much more prominent role of enhanced maximum uptake capacity (i.e., physiological plasticity) for the acquisition of finite nutrient patches. The gain in biomass in heterogeneous versus homogeneous soils also becomes smaller when the experiments last longer because patches deplete and the precision of root placement reduces (Kembel and Cahill 2005). This makes sense because when all soil nutrients are taken up, no differences in biomass production are to be expected between homogeneous and heterogeneous soils if in both treatments the same total amount of nutrients is supplied. Despite these methodological caveats, our current understanding is that the root proliferation in enriched microsites is less important for nutrient acquisition in heterogeneous soils than previously thought (de Kroon and Mommer 2006), except when plants are in competition (Hodge et al. 1999, de Kroon et al. 2003; but see Fransen et al. 2001).

To evaluate the ecological significance of selective root placement, its benefits must be compared with its costs. The immediate benefits may be limited but if the costs of wrong placement are small, selective root placement may still be profitable. Jansen et al. (2006)

recently demonstrated for the herb *Rumex palustris* that the costs of placing roots at the wrong location may indeed be small. They created homogeneous and heterogeneous soils in pots with a dripping system and *R. palustris* roots developed rapidly and selectively in the nutrient hotspot supplied in one quadrant of the pot. Midway the experiment, in some of the pots, the nutrient supply pattern was changed from homogeneous to heterogeneous and vice versa, or the hotspot was replaced to another location at the opposite side of the pot. By analyzing the root RGRs in different quadrants, Jansen et al. (2006) were able to show that root growth responded immediately to the shifts in local nutrient supply. An increase in root biomass in response to an increase in nutrient supply was achieved faster than a decrease in root biomass when the nutrient supply was decreased. However, as significant root biomass was built up in the first part of the experiment the shifts in actual root placement were slow, and the plants in the switch treatments were confronted with most of their roots located in the quadrant with low nutrient supply in the second part of the experiment. Surprisingly, costs of this wrong placement were absent. Plants for which the nutrient patches were switched had similar total nutrient uptake and growth as those for which the homogeneous or heterogeneous supply of nutrients was unchanged. Jansen et al. (2006) explained this lack of costs by redistribution of stored nutrients to new biomass, reducing the demand on new nutrient uptake, and by high physiological plasticity, that is, elevated uptake kinetics especially of the young roots that rapidly developed in new nutrient patches after the switch. These results suggest that plants may have a remarkable flexibility to relocate their root placement pattern even if immediate returns are small.

The costs of selective root placement may be much higher on the long term when patches gradually deplete and if new patches do not appear. Fransen and de Kroon (2001) grew isolated plants of the fast-growing grass *Holcus lanatus* and the slow-growing grass *Nardus stricta* for two growing seasons in homogeneous poor and rich soil, and in a heterogeneous treatment consisting of a poor half and rich half. In the first few months after the start of the experiment *Holcus*, but not *Nardus*, proliferated its roots rapidly in the richer patch of the heterogeneous soil, as quantified by minirhizotron observations. This proliferation paralleled elevated growth of *Holcus* in the heterogeneous soils relative to the homogeneously poor and rich treatments. However, already in the course of the first growing season, the growth of *Holcus* started to decline and by the end of the second year its biomass in heterogeneous soil was almost as low as that in homogeneous poor soil. For *Nardus*, by contrast, biomass production in heterogeneous soils over the 2 years increased relative to the homogeneous controls. Fransen and de Kroon (2001) concluded that the fast-growing *Holcus* overproduced roots in the nutrient-rich microsite resulting in significant costs in the long term when nutrients deplete and roots die off. Under conditions of nutrient depletion, *Nardus* with hardly any selective root placement and much longer root life spans has larger long-term returns.

The data available to date suggest that slow-growing species from resource-poor versus fast-growing species from resource-rich habitats differ only little in root foraging abilities, although the higher growth rate itself give the species an advantage, especially in a competitive setting. Both morphological and physiological plasticities are important attributes. In extremely nutrient-poor habitats such as nutrient-poor tundra, where patches if they appear rapidly deplete, the ability of roots to survive periods of resource depletion seems to be of greater significance than high levels of morphological plasticity. The maintenance of a large viable root mass, despite long periods of low nutrient availability, and the ability to commence absorption of nutrients rapidly when conditions permit enable species to acquire nutrient pulses of short duration (Crick and Grime 1987, Campbell and Grime 1989, Kachi and Rorison 1990). The high carbon costs of maintaining viable roots (Eissenstat and Yanai 1997) may not be a great problem in these habitats because carbon is not the limiting resource. In very productive environments, however, carbon costs of root maintenance may

be significant and roots generally have a shorter life span than species from less productive habitats (see Section "Allocation and Use of Absorbed Nutrients"). Rapid growth, high nutrient uptake rates, and a high turnover of roots may result in a more fugitive root behavior in these habitats. Enriched microsites are rapidly exploited after which the root system shifts its investments toward more profitable parts of the soil volume. This behavior is only profitable if such nutrient hotspots regularly reappear. The costs of switching foraging behavior continuously toward new patches may be limited, but the long-term costs of selective root placement is significant if patches deplete without getting replaced.

ALLOCATION AND USE OF ABSORBED NUTRIENTS

The acquisition of nutrients, their transport within the plant from the roots to the other organs, and their subsequent incorporation into organic compounds require a major carbon expense of the plant (Chapin et al. 1987, Farrar and Jones 2003). Vice versa, the assimilation of carbon requires nutrients, but especially N, in significant quantities. C_3 plants invest approximately 75% of their N in chloroplasts of which a major part is used in photosynthesis. About one-third of this chloroplast N is built into rubisco, the primary CO_2-fixing enzyme (Chapin et al. 1987). As a result, the photosynthetic capacity (the maximum rate of carbon assimilation) is highly positively correlated with leaf nitrogen concentration (Field and Mooney 1986, Evans 1989). The photosynthetic rate per unit of leaf nitrogen is referred to as the photosynthetic nitrogen use efficiency (PNUE) (Lambers and Poorter 1992, Fitter 1997). Beyond a critical level, photosynthesis does not increase further with increasing nitrogen concentration and may even decline. In such situations, other resources, such as light and water, may limit photosynthesis.

Although an important part of the assimilated N is allocated to the photosynthetic system, the plant requires N also for a whole variety of other plant functions (Lambers and Poorter 1992). The relationship between nitrogen concentration in the whole plant and RGR may be different for different plant species depending on—among other factors—the fraction of nitrogen that is allocated to the photosynthetic machinery. Such differences may be caused by variation in allocation to plant organs, such as leaves, roots, and stems, but also by differences in the allocation to the various organelles and compounds within the leaf. Some rapidly growing species such as *Lolium perenne* allocate an extremely large part of the leaf nitrogen to rubisco, whereas in other species part of the leaf nitrogen is used for the synthesis of defensive compounds or incorporated in supporting tissues. Ingestad (1979) characterized the relationship between RGR and whole-plant nitrogen concentration by the nitrogen productivity (A), defined as the rate of dry matter production per unit of nitrogen in the plant (g d.wt. g^{-1} N day^{-1}). Figure 8.4 gives the relationships between RGR and nitrogen concentration in the plant for three tree species, which appear to be linear with a virtually zero intercept over a broad range of nitrogen concentrations. The slopes of the regression lines represent the nitrogen productivities of each species. All three species increase their growth at higher internal nitrogen concentrations, but the faster-growing species make a more efficient use of the nitrogen that is present in the plant. Figure 8.4 also shows that the faster-growing species not only has a higher growth rate than the slower-growing species at higher nitrogen concentrations, but also at low concentrations. The difference in nitrogen productivity between the three species is probably caused by differences in allocation to the photosynthetic process, but may be explained as well by differences in costs of biosynthesis of plant tissues.

Whole-plant growth is optimized if all resources are equally limiting (Bloom et al. 1985). As a rule, new biomass is allocated to the plant organs that acquire the most strongly limiting resource. If nutrients are in short supply, there are several ways in which nutrient shortage in the plant may be avoided. More carbon may be invested in root biomass so that a larger soil volume can be explored and the competitive ability for soil nutrients is increased. Tilman

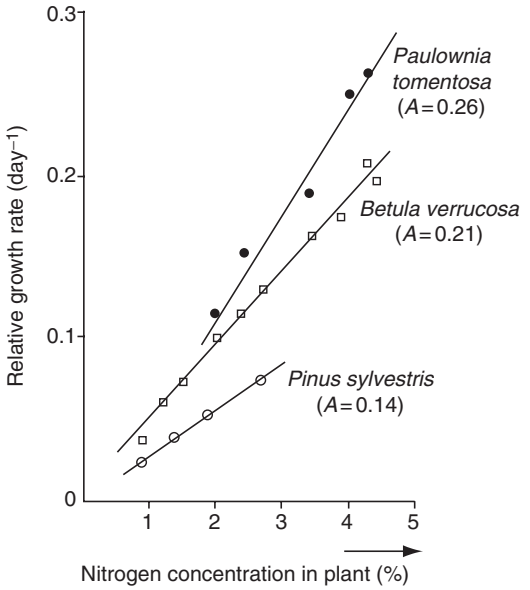

FIGURE 8.4 The relative growth rate of seedlings of three tree species versus nitrogen concentration in the total plant. The values of the nitrogen productivity A (g d.wt. g^{-1} N h^{-1}) are given by the regression coefficients of the presented lines. (After Ingestad, T., *Physiol. Plant.*, 45, 149, 1979; Hui-jun, J. and Ingestad, T., *Physiol. Plant.*, 45, 149, 1984; Ingestad, T. and Kähr, M., *Physiol. Plant.*, 65, 109, 1985; from Berendse, F. and Elberse, W.Th., *Perspectives on Plant Competition*, J.B. Grace and D. Tilman, eds, Academic Press, New York, 1990. With permission.)

(1988) suggested that increased allocation to root biomass would be one of the most important adaptations of plants to nutrient-poor soils. It has been known for a long time that the phenotypic response of all plant species to reduced nitrogen or water supply is an increased carbon and nitrogen allocation to roots (Brouwer 1962), but comparisons of species adapted to nutrient-rich and nutrient-poor sites do not confirm Tilman's hypothesis. Grass species adapted to nutrient-poor soils generally invest less or equal amounts of biomass in belowground parts than species characteristic of more fertile sites (Elberse and Berendse 1993). In a recent review of studies on plasticity in root weight ratio, Reynolds and D'Antonio (1996) showed that species from nutrient-poor and nutrient-rich habitats exhibit a similar increased root allocation in response to nitrogen shortage. The most important difference between species of nutrient-poor and nutrient-rich sites is that the roots of the former seem to have smaller diameters leading to an increased root length per unit root weight (Elberse and Berendse 1993, Fitter 1997).

The efficiency of nutrient utilization for growth also depends on other functions to which nutrients are allocated by the plant, such as support, defense, reproduction, and storage (Chapin et al. 1990). Allocation to supporting structures (such as woody tissue), chemical compounds for defense, or reproductive organs may curtail the growth rate of plants (Bazzaz et al. 1987). Plant species with a particularly high allocation to one or more of these functions, or plants in their reproductive phase, have low growth rates and low nitrogen productivity. Growth is also curtailed if a significant proportion of the resources is allocated to storage, that is, reserve formation that involves the metabolically regulated compartmentation or synthesis of storage compounds (Chapin et al. 1990, see Chapter 5, this volume). Although reserve formation directly competes for resources with growth, resources may accumulate because resource supply exceeds the demands for growth and other functions during a certain

period. This accumulation is commonly referred to as luxury consumption (Chapin 1980) and should be distinguished from reserve formation (Chapin et al. 1990). Luxury consumption allows the slower-growing species to absorb nutrients in excess of immediate growth requirements during nutrient flushes. The reserves built up in this way may be used to support growth in periods of nutrient depletion.

Classical plant ecophysiology often depicts the growth of plants in natural environments simply as resulting from soil nutrient uptake and carbon assimilation. However, in many perennial plant species, growth strongly depends on amounts of nutrients and carbon that have been stored during preceding growing periods (see de Kroon and Bobbink 1997). In the alpine forb species *Bistorta bistortoides*, stored N reserves in the rhizomes accounted for 60% of the N allocation to the shoot during the growing season (Jaeger and Monson 1992). In this species N storage was largely accommodated by increased concentrations of amino acids (Lipson et al. 1996). Resources stored in perennial plant organs may support the aboveground biomass production of plants to a considerable degree, as illustrated by the study of Jonasson and Chapin (1985) with the sedge *E. vaginatum*. In extremely nutrient-poor tundra, they compared the growth of tillers (with attached belowground stems and roots) in bags without access to soil nutrients with the growth of unbagged tillers. They found that the bagged tillers accumulated as much leaf biomass during one growing season as the unbagged plants. Nutrients were transported from the belowground stems to the leaves during the first 2 months after snow melt. After senescence at the end of the growing season, nutrient contents in the belowground stems of the bagged tillers were only slightly lower than those in the unbagged ones.

LOSSES OF NUTRIENTS THROUGH ABSCISSION AND HERBIVORY

It is clear that the growth of a perennial plant individual is not only determined by the amount of nutrients that it acquires, but also by the amounts of stored nutrients that can be reused. In environments where nutrients limit plant growth, the long-term dynamics of perennial plant populations is largely determined by the balance between the uptake and the loss of nutrients. Losses of nutrients may occur in various ways: abscission of leaves and flowers, root death, mortality due to disturbance, nutrient capture by herbivores, leaching from leaves, seed or pollen production, and exudation from roots.

One of the most important pathways by which plants lose nutrients is the seasonal abscission of leaves, roots, and other organs. Several studies show that there is a huge variation in life spans of leaves among vascular plant species. Escudero et al. (1992) found that the life spans of leaves of tree and shrub species in the Pyrenees varied by a few orders of magnitude from a few months to more than 4 years. A similar large variation (from a few months to 10 years) was reported in a survey of several studies of leaf life spans (Reich et al. 1992). Nutrient losses due to leaf abscission are quantitatively significant, but are reduced by active retranslocation of nutrients in the period preceding abscission. Measurements of nutrient withdrawal should take into account that not only is the nutrient content reduced but that also the dry weight per leaf can decline because of respiration or retranslocation of carbohydrates, implying that nutrient withdrawal should be measured on a whole-leaf basis. In arctic ecosystems, 20%–80% of N and 20%–90% of P in leaves was withdrawn before abscission, whereas there did not seem to be important differences in percentage withdrawal between graminoids, forbs, and deciduous and evergreen dwarfshurbs (Chapin et al. 1975, Jonasson 1983, Chapin 1989, Chapin and Shaver 1989). Morton (1977) studied the decline in nutrient concentrations in leaves of the deciduous grass *Molinia caerulea* during abscission at the end of the growing season. He compared open plots with plots that during fall and winter were covered with a transparent roof, preventing leaching of nutrients by rain. The reduction in N and P concentrations in dying leaves was measured to be about 75% and occurred both

in the open and the covered plots, but the decline in concentrations (ca. 90%) of K, Ca, and Mg took place only in the plots without cover. He concluded that the reduction in the N and P content of leaves occurred through active withdrawal from senescing leaves, but that the reduction in K, Ca, and Mg took place through leaching from the leaves to the soil.

Much less data are available about root life spans. Eissenstat and Yanai (1997) showed in their review that the time periods after which 50% mortality has occurred vary between 14 and 340 days, which correspond with life spans of 20–490 days (assuming a negative exponential decline in the number of living roots). Between-species comparisons are difficult because the life spans vary strongly among root cohorts produced in different seasons and most studies did not compare species at the same site. In a garden experiment we followed individual roots of 14 grassland species from birth to death using minirhizotrons. Average root life spans varied from 41 days in *Rumex obtusifolius* which occurs in very fertile habitats to 381 days in *Succisa pratensis* which is characteristic of nutrient-poor sites (Berendse, unpublished results). It is not yet clear whether nutrient losses due to root death can be significantly reduced through nutrient withdrawal preceding abscission. A few studies showed that nutrient resorption from dying roots is minimal (Nambiar 1986, Dubach and Russelle 1994), so that nutrient losses by root turnover might be very significant.

In addition to nutrient losses through seasonal abscission, an important pathway of nutrient loss occurs due to herbivory by a broad variety of organisms such as grazing mammals, phytophagous insects, parasitic fungi, and root nematodes. The quantities of nutrients that the plant loses because of the activities of herbivores aboveground and belowground have rarely been measured, but can probably be rather important. We simulated grazing through mammals by clipping plants with 8 week intervals at 5 cm above soil surface. We measured that at low levels of soil fertility the tall grass species *Arrhenatherum elatius* lost 57% of the total amount of nitrogen taken up, whereas the short grass *Festuca rubra* lost 24% (Berendse et al. 1992). These losses increased to more than 90% at higher soil nutrient levels.

The data presented strongly suggest that there is a wide variation in biomass and nutrient turnover among plant species depending on the life spans of plant organs, but they do not supply information about the quantitative significance of whole-plant nutrient loss rates as compared with nutrient supply rates. Especially, for plants growing in their natural environment such data are extremely difficult to collect. In the 1980s we carried out a comparative field study in which we attempted to quantify whole-plant nutrient losses and nutrient uptake in populations of the ericaceous dwarfshrub *Erica tetralix* and the perennial, deciduous grass *M. caerulea*. In recent decades, in many wet heathlands in Europe *E. tetralix* has been replaced by *M. caerulea*. In competition experiments in containers (Berendse and Aerts 1984) and in field fertilization experiments (Aerts and Berendse 1988, Aerts et al. 1990) we measured that at increased levels of nutrient supply *Molinia* is able to outcompete *Erica*, whereas *Erica* remains the dominant species under nutrient-poor conditions.

We measured nitrogen losses from populations of *Molinia* and *Erica* plants in adjacent sites for 2 years. Total losses of nitrogen from *Molinia* plants varied between 60% and 100% per year of the total amount of nitrogen present in the plants at the end of the growing season. We calculated the lower turnover rate assuming that 50% of the nitrogen in roots was withdrawn preceding abscission, whereas the higher figure was calculated assuming that no retranslocation took place. It is clear that losses of up to 100% have important consequences for the success of a population in an environment where nitrogen limits plant growth. Nitrogen losses from *Erica* were much smaller (ca. 30%). This seems to be an important adaptation to the nutrient-poor habitats that are dominated by this species. In Table 8.2, we compare the total N losses during 1982 with the N mineralization measured in the upper 10 cm of the soil during this year. The measured N mineralization is about equal to the total N supply rate. Almost all organic nitrogen is present in the upper 10 cm of the soil and the N input through atmospheric deposition is almost completely immobilized by the nutrient-poor

TABLE 8.2
The Relative Nitrogen Requirement, the Total (Aboveground and Belowground) Biomass at the End of the Growing Season and the Annual Nitrogen Loss from the Plant in Adjacent Populations of *Erica* and *Molinia* and the Annual N Mineralization on These Sites in 1982

	Erica	*Molinia*
Relative nitrogen requirement (mg N g^{-1} biomass $year^{-1}$)	2.3–3.4	7.4–11.7
Total biomass (g biomass m^{-2})	1270	919
Total N losses (g N m^{-2} $year^{-1}$)	2.9–4.3	6.8–10.8
N mineralization (g N m^{-2} $year^{-1}$)	11.5	10.1

litter layer, but is remineralized during the later phases of decomposition. In *Molinia*, the losses of N from the plant appear to be of the same order of magnitude as the rate of N supply to the plant, but in *Erica* N losses are less than 50% of the N that can be taken up.

If a plant loses a large part of the nutrients in its biomass annually, it must absorb more nutrients to maintain its biomass than a plant that is more economical with its acquired nutrients. To measure the nutrient uptake that plant species need in their natural environment, the concept of the relative nutrient requirement was introduced (Berendse et al. 1987). The relative nutrient requirement (L) is defined as the amount of nutrients that a plant population loses per unit of time and per unit of biomass. This amount of nutrients should be taken up again to maintain or replace each unit biomass during a given time period (mg N g^{-1} biomass $year^{-1}$). In the study referred to earlier, we measured that the relative nitrogen requirement was 2.3–3.4 mg N g^{-1} biomass $year^{-1}$ in *Erica* as compared with 7.4–11.7 mg N g^{-1} biomass $year^{-1}$ in *Molinia* depending on the assumption about N withdrawal from dying roots (Table 8.1). Apparently, *Erica* required much less nitrogen to be taken up to maintain its biomass than *Molinia* did. *Erica* plants appeared to require much less nitrogen because of the longer life spans of their leaves, stems and roots and not because of a higher retranslocation efficiency. The withdrawal of nitrogen from dying leaves in *Molinia* is even higher than that in *Erica*.

The differences between these two species seem to reflect a general pattern. Escudero et al. (1992) found that the life span of leaves of tree and shrub species in the Pyrenees was strongly correlated with the variation in soil fertility. Plant species dominant on infertile soils had leaves that lived longer than species that were abundant on more fertile soils. This positive correlation was not found between soil fertility and the fraction of N and P that was withdrawn from dying leaves. Recently, we carried out an experiment in which 14 plant species of Dutch grassland and heathland communities were grown in monocultures in experimental plots (Berendse, unpublished results). Here the direct effects of different soil characteristics were excluded. We found a significant inverse relationship between average leaf life span, as measured in these plots, and the nutrient index of each species which ranks the average soil fertility of the habitat in which the species involved is most frequently found (Figure 8.5).

ADAPTATION OF PLANTS TO NUTRIENT-POOR AND NUTRIENT-RICH ENVIRONMENTS

Plant species can increase their success in nutrient-poor habitats along three different lines. Firstly, they can maximize the acquisition of nutrients by increasing their competitive ability for soil nutrients or by exploring nutrient sources that are not available to competing plant

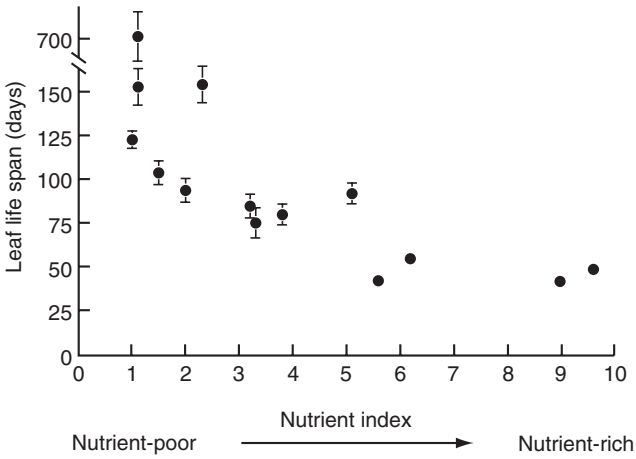

FIGURE 8.5 The average leaf life spans of 14 grassland and heathland species versus their nutrient index. Life spans were measured in plants growing in experimental plots under identical conditions. Measurements were carried out in 10 plants of each species by following marked leaves with 2 week intervals. The nutrient index is a descriptive parameter that ranks the average soil fertility of the habitats in which the species involved is most frequently found. Bars give standard errors of the mean. (From Berendse, unpublished results.)

populations. The affinity of the uptake system of most plants is sufficiently high to decrease the nutrient concentration at the root surface to practically zero. Further improvement of the uptake capacity is of little use. Uptake kinetics does not differ systematically between species from rich and poor soils. The competitive ability for soil nutrients can be increased by investing more carbon in fine root biomass or by changes in root morphology that increase root length or root surface area per unit biomass (by reduced root diameter or increased root hair density), so that a greater fraction of the available nutrients can be absorbed relative to competing plant species. In previous sections, we showed that, in general, plant species of nutrient-poor habitats do not invest more biomass in roots, but that some species of nutrient-poor habitats realize an increased absorbing root surface by producing thinner roots. In addition, species of nutrient-poor habitats do not seem to forage more effectively for patchily distributed nutrients, as compared with species from more productive habitats. However, many plant species of poor soils can explore additional organic nutrient sources by intimate associations with mycorrhizal fungi, and some genera (e.g., *Drosera*, *Pinguicula*, *Utricularia*) can even acquire and use living animal proteins. Deep-rooting species (such as forbs or trees) may absorb nutrients from deeper soil layers that are not available to competing species with a shallow rooting pattern.

The second line along which plant species may be adapted to nutrient-poor sites is by changes in the efficiency with which the nutrients that are present in the plant are used for carbon assimilation and subsequent growth. Different nutrients can be used for different plant functions affecting growth (e.g., N is mainly invested in rubisco, whereas K is required for stomata functioning). The parameter that measures this efficiency is the nutrient productivity A, as introduced in Section "Allocation and Use of Absorbed Nutrients". One would expect a strong selection in favor of an increased nutrient productivity in species adapted to nutrient-poor soils, but generally species of nutrient-poor habitats have lower nutrient productivities than species adapted to more fertile sites (e.g., Hui-jun and Ingestad 1984, Ingestad and Kähr 1985).

The third line of adaptation is increasing the length of the time period during which nutrients can be used. The length of this time period can be expanded by increased life spans

of leaves, roots, and other organs. Life spans can be increased by investing in supporting tissues and in defensive compounds that reduce the risks of herbivory. The residence time of nutrients in the plant can also be increased by retranslocation of a large part of the nutrients in dying plant parts, but we showed earlier that the fraction of nutrients retranslocated from leaves before abscission is not clearly correlated with the soil fertility of the habitat in which the species occurs most frequently (Escudero et al. 1992). The earlier introduced relative nutrient requirement or relative nutrient loss rate measures nutrient losses per unit of biomass, but can also be expressed per unit of nutrient in the plant (Ln; g N g^{-1} N $year^{-1}$). Under steady-state conditions where nutrient losses are equal to nutrient uptake the inverse of this parameter (Ln^{-1}) measures the mean residence time of nutrients in the plant.

For a further analysis of the adaptation of plants to nutrient-poor substrates it is helpful to combine the instantaneous efficiency of nutrient utilization or nutrient productivity (A) with the mean residence time (Ln^{-1}) to the overall nutrient use efficiency (NUE) which measures the amount of biomass that can be produced per unit of nutrient taken up (g biomass produced/g nutrient absorbed):

$$\text{NUE} = \frac{A}{\text{Ln}}.$$

One would expect that the NUE would be higher in species of nutrient-poor habitats as compared with species from more fertile sites. Berendse and Aerts (1987) calculated this parameter for adjacent field populations of *Erica* and *Molinia* using the amount of biomass and the amount of nutrients in the plant as present at the end of the growing season (Table 8.3). It is striking that there is only a relatively small difference in NUE between the two species, but that the NUE values are composed of entirely different combinations of A and Ln^{-1}. *Erica* has a low N loss rate combined with a low N productivity, whereas *Molinia* has a much larger loss rate, but also a higher instantaneous utilization efficiency A. Apparently, the same overall NUE can be realized by various combinations of plant properties. These data suggest that especially the components A and Ln^{-1} are relevant in the adaptation of plant species to habitats with different nutrient supplies, rather than the NUE itself. Later, we consider the differences in growth rate between these two species in relation to their different nutrient loss rates.

The dwarfshrub *Erica* is able to maintain itself as the dominant species on nutrient-poor sites because it is much more economical with the nutrients that it has absorbed than the perennial grass species. But this difference does not explain why *Molinia* outcompetes *Erica*

TABLE 8.3
Nitrogen Productivity (A; g biomass g^{-1} N $year^{-1}$), Mean Residence Time (Ln^{-1}; year), and Nitrogen Use Efficiency (NUE; g biomass g^{-1} N) as Calculated for *Erica* and *Molinia*

	Erica	*Molinia*
A	24	94
Ln^{-1}	4.3	1.4
NUE	103	132

Source: Berendse, F. and Aerts, R., *Funct. Ecol.*, 1, 293, 1987.

after an increase in nutrient supply. In a field experiment with different nutrient supply rates, the potential growth rate of the grass *Molinia* was found to be much higher than that of the dwarfshrubs *Erica* and *Calluna* (Aerts et al. 1990). The higher potential growth rate of *Molinia* enabled this species to increase its biomass much more rapidly than *Erica* after an increase in nutrient supply. In communities where both species are present an increase or decrease in nutrient supply can result in complete dominance of *Molinia* and extinction of *Erica* or vice versa. The changes in such communities were calculated using our model for the competition between plant species (Berendse 1994). This model calculates nutrient and light competition and the losses of biomass and nutrients. The model predicts that species 1 outcompetes species 2 under nutrient-rich conditions, whereas species 2 replaces species 1 under nutrient-poor conditions if

$$\frac{\mathrm{Gmax}_1}{\mathrm{Gmax}_2} > \frac{\mathrm{Ln}_1}{\mathrm{Ln}_2} > 1,$$

in which Gmax_1 and Gmax_2 (g biomass m^{-2} $year^{-1}$) are the potential growth rates in a closed canopy of species 1 and 2, respectively, and Ln_1 and Ln_2 represent the relative nutrient loss rates of the two species, assuming that all other plant features are equal. This relationship leads us to conclude that interspecific competition is responsible for a strong selection pressure on the potential growth rate and the relative nutrient loss rate of species. Slight changes in these plant characteristics may lead to either complete disappearance or complete dominance. But we can conclude as well that species that combine a low nutrient loss rate with a high potential growth rate are superior at all nutrient supply rates. The question to be answered is whether plants can easily combine such characteristics.

The difference in potential growth rate (and nitrogen productivity) between the two species can be attributed to differences in allocation of nitrogen to the photosynthetic system and to differences in biosynthesis costs. At the end of the growing season *Erica* had allocated about 12% of total plant nitrogen to its leaves, whereas in *Molinia* plants 48% of the total plant N was present in leaves and green stems. This difference is not caused by differences in allocation to root biomass, but by the allocation of nitrogen to long-living, woody stems in *Erica*. Possibly, the two species differ as well in the allocation of nitrogen to the different compounds within the leaf. *Erica* leaves live about four times longer than *Molinia* leaves, thanks to their higher lignin content resulting in an increased toughness of the leaf. Lignin is much more expensive to biosynthesize than compounds such as cellulose. In a literature survey, Poorter (1994) did not find any systematic difference in biosynthesis costs of tissues produced by plant species from nutrient-poor and nutrient-rich soils. However, we found that the costs of biosynthesizing *Erica* tissue were higher than those of *Molinia* tissues (1.8 vs. 1.4 g glucose g^{-1} biomass). We conclude that the adaptation to nutrient-poor environments by minimizing the loss of nutrients has important negative side effects: the allocation of nitrogen to the photosynthetic system is reduced and the biosynthesis costs of tissues are increased, which results in reduced nitrogen productivity and reduced potential growth rate, which is an important disadvantage when soil fertility increases. Apparently, plant properties that determine nutrient losses and potential growth rates are strongly interconnected. The combinations low maximum growth rate–low loss rate and high maximum growth–high loss rate strongly correspond with, respectively, the stress-tolerant and competitive strategies that Grime (1979) distinguished much earlier. High maximum growth rates and low biomass losses cannot be easily combined for apparent physiological and morphological reasons.

This leads to the expectation that in plant species adapted to soils with different soil fertilities, biomass turnover rate and maximum growth rate are inversely correlated. In an experiment in growth chambers we measured maximum RGRs in the 14 grassland species, for which we had measured leaf life spans in a garden experiment (cf. Figure 8.5). We found a

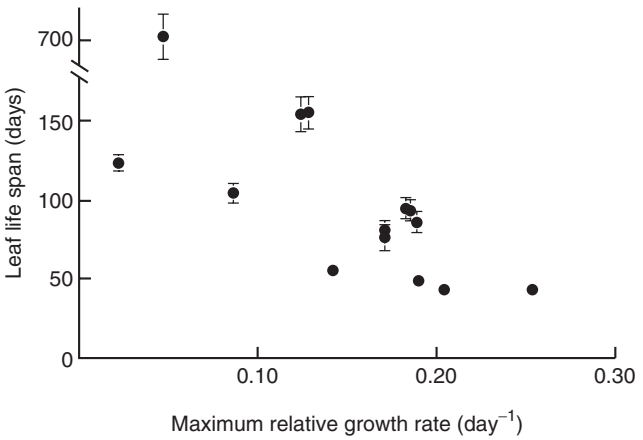

FIGURE 8.6 The average leaf life spans of 14 grassland and heathland species versus their maximum relative growth rate. Life spans were measured as given in the caption of Figure 8.5. Maximum relative growth rates were measured in a growth chamber experiment for seedlings at optimum nutrient supply rates. (From Berendse and Braakhekke, unpublished results.)

significant, negative relationship between leaf life span and maximum RGR which confirms our hypothesis (Figure 8.6). These results show that the differences between *Erica* and *Molinia* reflect a much more general pattern of adaptation of wild plant species to soils with low and high nutrient supplies.

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