
4 Control of Plant Nitrogen Uptake in Native Ecosystems by Rhizospheric Processes

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4.1 NITROGEN AVAILABILITY

4.1.1 MINERALIZATION

Nitrogen (N) availability in crop systems is largely determined by fertilizer application rates. In relatively undisturbed native ecosystems, however, N becomes available largely as a result of internal cycling of this element. Therefore, conceptual or quantitative models of plant N uptake must effectively incorporate processes of N cycling such as decomposition and mineralization. Mineralization of organic N is

particularly important because it is often positively associated with increased net primary productivity (Vitousek and Howarth 1991; Retch et al. 1997; Joshi et al. 2006). This correlation is not surprising, because even in plant communities where a significant proportion of the plant N budget may be provided via amino acids and amino sugars (plant uptake of which will be discussed later), mineral N is still the preferred form for plants.

The amount of N mineralization varies from one system to the next. In temperate forest ecosystems, microbial activities and subsequent N mineralization can release 20 to 120 kg ha⁻¹ of inorganic N annually (Zak et al. 1993; Fan et al. 1998; Rastetter et al. 2005). Estimates of N mineralization in grassland ecosystems range from 30 to 70 kg ha⁻¹ y⁻¹ in xeric to as much as 270 kg ha⁻¹ y⁻¹ in mesic systems. Even in crop production systems, N mineralization can account for as much as 50 kg ha⁻¹ of inorganic N mineralization into the soil during a single growing season (Schomberg and Cabrera 2001).

Despite the clear role of mineralization in determining soil N availability, models of plant N uptake in native systems seldom integrate it with mechanistic parameters such as root uptake kinetics and morphology. This is partly because microbial release of inorganic N is under complex control by soil substrate/litter quality, moisture, temperature, and pH (Groffman and Tiedje 1989; Holmes and Zak 1994), which can vary substantially from one site to another. Additionally, accurate estimation of N mineralization is further complicated by the fact that the dominant microbial types, bacteria and fungi, differ markedly in how rapidly they mineralize organic N (Vinten et al. 2002). Nonetheless, we suggest that robust models of plant N uptake require incorporation of soil mineralization characteristics.

Incorporation of N mineralization into physiological uptake models offers serious challenges. Current models of soil N mineralization can be contrasted as following either a functional approach or a mechanistic approach (Benbi and Richter 2002). Current analysis of the literature does not provide evidence that one approach is consistently more reliable than the other (Wang et al. 2004). The simple functional approach is based on lab incubation results, and in cases where only one soil organic fraction is considered to contribute to mineralization, the results are described by a first-order kinetics. The functional model approach has also been extended to describe cases where two or more soil organic fractions are assumed to control the overall mineralization. To date, the first-order kinetic models, including the single and double exponential models, remain widely used (Wang et al. 2004).

While it is more realistic to assume that there are multiple soil organic fractions that mineralize at distinctly different rates, double- or multiple-compartment functional models remain nonmechanistic. Consequently, and, perhaps more importantly, they are highly site specific. Furthermore, these models do not assess the relative proportion of mineral N that is further nitrified. Therefore, the relative availability of the two inorganic N forms will not be known. Benbi and Richter (2002) suggested, however, that for a given site, a functional approach is a reliable tool to predict soil inorganic N release when it is used with at least two compartments of soil organic N: a rapidly mineralizing fraction and a more recalcitrant (residual) one.

In contrast to simple functional models, the mechanistic mineralization models are process-based, derived from current understanding of how soil moisture, temper-

ature, pH, and texture affect the key processes of the N cycle that affect net mineralization (for example, gross mineralization, immobilization, and nitrification). The mechanistic models range from noncompartmental approaches, where soil organic substrate is considered as a continuum of qualities as opposed to distinct compartments (Agren and Bosatta 1987), to multicompartmental approaches. We know of at least one series of mechanistic models that are based on analytically distinct pools of C and N (including labile and stable plant material, microbial biomass, and labile and stable organic matter) that have explicit compartments for exchangeable ammonium (NH_4^+)-N and nitrate (NO_3^-)-N (Gaunt et al. 2001; Sallih and Pansu 1993).

In general, the mechanistic models are often criticized for lack of robust validation under realistic field conditions and, when compared with the simple functional model approaches, they do not always show a clear advantage. Because these models can incorporate N compartments including NH_4^+ and NO_3^- , we believe that the mechanistic models may be better suited for integration into a physiologically driven uptake model such as the one we present in this chapter. We also suggest that those mineralization models, be they simple functional or mechanistic models, could improve the reliability of the N-uptake models if they capture the high temporal and spatial variability.

4.1.2 ATMOSPHERIC N DEPOSITION

It is estimated that anthropogenic N fixation exceeds biological fixation of this growth-limiting nutrient. Galloway and Cowling (2002) reported that, in 1990, the annual global N production from anthropogenic sources was roughly 140 Tg, the majority of which, about 85 Tg N per year, came from Haber–Bosch processing of N_2 into fertilizers. Fossil fuel combustion and other industrial sources are the remaining major mechanisms of anthropogenic N creation (Galloway and Cowling 2002). On average, Western Europe receives five times more wet N deposition than the United States (Holand et al. 2005). Nevertheless, in the United States, many native communities experience 25 to 100 kg $\text{ha}^{-1} \text{y}^{-1}$ ammonium and nitrate deposition due to farming, industrial activities, and combustion of fossil fuel (Galloway et al. 1995). Because native ecosystems are generally N-limited (Schlesinger 1997; Vitousek et al. 1997), chronic atmospheric deposition represents a novel source of fertilizer that can alter plant N uptake.

Aber et al. (1989) and Schulze (1989) proposed conceptual models that attributed temperate forest decline in North America and Western Europe to increased deposition of anthropogenic nitrogen. These seminal papers brought much needed attention to the alarming increase in atmospheric N deposition in native systems and how it may impact them. While the exact amount of atmospheric N deposition varies from region to region, intensive farming and industrial activities are major culprits in raising ecosystem N load above the background levels by many orders of magnitude. Since the 1950s, atmospheric N deposition has doubled much faster than any other component of the global change, e.g., CO_2 . In addition to N load, the knowledge of the composition of deposition is critically important.

The sources of N pollution are important, as they determine which inorganic N form is deposited. While N deposition originating from industrial sources is domi-

nated by NO_3^- , N deposition associated with farming activities is made of NH_4^+ (Lovett 1994; Schulze 1989; Skeffington 1990). For example, atmospheric deposition in Chicago consists of a 4:1 ratio of nitrate to ammonium (NADP 1997), while atmospheric deposition in the Netherlands consists of at least a 3:1 ratio of ammonium to nitrate (Wilson et al. 1995). Many studies addressing N deposition with long-term fertilization plots have used a 1:1 ratio of nitrate to ammonium (e.g., Tilman 1993; Magill et al. 1997).

The uptake and assimilation of nitrate and ammonium require distinct physiological mechanisms and have different consequences on plant growth (Fernandes and Rossiello 1995). Compared with ammonium nutrition, nitrate nutrition tends to result in greater uptake of cations, higher tissue concentrations of carbohydrates, and smaller root-to-shoot ratios (Fernandes and Rossiello 1995). Assimilation of nitrate may also have a higher energetic cost than assimilation of ammonium. For example, the yield of six perennial grass species supplied with nitrate as a sole nitrogen source was only 22%–48% of the yield when supplied with ammonium (Wiltshire 1973). Although most of the work comparing plant responses to nitrate and ammonium has been done with agricultural species, nonagricultural species also vary in their capacity to take up and assimilate nitrate (Gebauer et al. 1988; Falkengren-Grue 1995). Therefore, we recommend that models of plant uptake pay close attention to the relative availability of the inorganic N form in the deposited N.

It is also important to know how fast the deposited N becomes available for plant uptake. A number of studies have shown that atmospheric N deposition may quickly become tied up, so that the availability at the root surface does not match the deposition rate. McNulty et al. (1991) sampled the forest floor at 11 sites along an N-deposition gradient in New England. They showed that N deposition was positively correlated with percent N in the forest floor and with potential net nitrification and mineralization, but negatively correlated with C:N, lignin:N, and Mg:N ratios in spruce needles in the litter layer. The speed with which forest ecosystems reach the limits of the N they can accumulate depends on forest history. Forests that were clear-cut or farmed accumulated N for a longer time before nitrification rates increased (Aber and Driscoll 1997). A series of 15 burned, logged, or little-disturbed forest sites in northern New Hampshire suggested that the N mineralization to forest floor C:N ratio may be a useful diagnostic of system N accumulation (Goodale and Aber 2001).

Stable isotope experiments suggest that most N added to forests accumulates in the forest floor. The forest floor retained 42%–58% of ^{15}N added to *Quercus velutinal rubra* or *Pinus resinosa* stands in the Harvard Forest, which were receiving 58 kg N $\text{ha}^{-1} \text{y}^{-1}$. The greatest amounts of ^{15}N were retained in fine roots (13%–25%) and in litter plus humus (18%–19%); much smaller amounts of ^{15}N were retained in wood, leaves, and mineral soil (Nadelhoffer et al. 1999). The forest floor also retained the largest amounts (20%–45%) of added ^{15}N in four European coniferous forests that were part of the NITREX experiments (Tietema et al. 1998). At deposition rates of 30–80 kg $\text{ha}^{-1} \text{y}^{-1}$, Tietema et al. (1998) found that less N was retained in the forest floor, and interpreted this to mean that inputs exceeded the capacity of the microbial and plant population to immobilize N.

4.1.3 DISSOLVED OR SOLUBLE ORGANICS N

The fact that soils contain a large pool of soluble organic N (SON) that can be absorbed by plants has been known for some time (Keeney and Bremner 1964). It is only during the last two decades, however, that there has been growing recognition that in many native ecosystems, at least, a portion of plant N demand may be met through the uptake of soluble or dissolved organic N (Lipson and Näsholm 2001; Näsholm and Persson 2001; Schimel and Bennett 2004). This recognition is partly motivated by the fact that in many ecosystems the best estimates of annual inorganic N pools and fluxes could not fully account for the yearly increase in standing N biomass (Kielland 1990; Chapin et al. 1988; Fisk and Schmidt 1995; Chen and Xu 2006). Additionally, much evidence has emerged showing that plant roots, either in association with or without mycorrhizal fungi (Abuzinadah and Read 1988; Raab et al. 1996, 1999; Wallenda and Read 1999; Chapin et al. 1993; Henry and Jefferies 2003; Näsholm et al. 1998; Näsholm et al. 2000; Lipson and Monson 1998), can effectively take up small-molecular-weight organic N such as amino acids though larger molecules such as polypeptides and proteins (Abuzinadah and Read 1986a, 1986b), which have also been shown to be taken up by the root system. Therefore, it is critical that models of plant nitrogen acquisition adequately address the role of soil organic N.

Given that root uptake of amino acids has been shown to be mediated by transporters (Chapin et al. 1993; Wallenda and Read 1999), it should be possible to integrate kinetic parameters as well as concentration of amino acids into uptake models such as that described in the following section. However, incorporation of such parameters is outside the scope of this chapter. Nonetheless, we suggest that some important consideration must guide any such effort. For example, it is important to consider the potential interaction between amino acid and inorganic N uptake. The availability of amino acids and their uptake by plants have been shown to significantly affect uptake of inorganic N. For example, the high availability of amino acids in the root medium leads to reduced uptake as well as reduced subsequent assimilation of nitrate (Padgett et al. 1993; Aslam et al. 2001). Therefore, accurate modeling of N uptake by plants requires a robust understanding of the interactive effects of inorganic N and amino acids uptake.

The majority of the studies that address SON as a source of plant N focus on amino acids. Interestingly, most of these studies deal with plant communities from colder climates such as boreal forest, alpine, and arctic ecosystems. It is currently not known if SON is proportionally more important to the N economy of plants in the colder as opposed to moderate and warmer climates. While amino acids constitute a significant pool of available N in many native systems (1% to 25%) (Chen and Xu 2006; Yu et al. 2002; Senwo and Tabatabai 1998) where plant species exhibit a well-developed absorption capacity, the role of amino acids in the annual N budget of native plants remains quite uncertain. Our current knowledge is limited to those studies that simply illustrate the presence of amino acids in the soil and a plant's ability to take them up. Little quantitative data is available to evaluate the relative contribution of amino acids to the annual plant N budget. In fact, when these N budget studies are conducted in detail, serious doubts emerge as to whether amino acids

are a major source of the plant N economy (Owen and Jones 2001; Jones et al. 2004, 2005; Bennett and Prescott 2004).

In a grazed coastal marsh system, Henry and Jefferies (2002) showed that the uptake of amino acids might only be important when soil inorganic N availability is low. Furthermore, the focus on soil amino acids has taken attention away from a large number of other organic compounds that are often much more prevalent in the soil. For example, in many ecosystems, amino sugars and peptides are much more prevalent in the soil than amino acids (Chen and Xu 2006; Amelung et al. 1999). At the present, we do not know the relative importance of these forms of SON to plant N economy. Even when availability and uptake of soil amino acids are characterized, too often, these studies focus on one or two amino acids (e.g., glycine and glutamine). We suggest that in targeting one or two amino acids, adequate justification be given to such a focus. That is, are the target amino acids available in disproportionately larger concentration than other soil amino acids?

4.2 MODELING ROOT SYSTEM CHARACTERISTICS IMPORTANT TO N UPTAKE

4.2.1 LEVERAGE OF PLANT ATTRIBUTES AND SOIL ENVIRONMENTAL FACTORS IN NUTRIENT ACQUISITION AND GROWTH

A number of attributes of the plant affect the rate of nutrient acquisition per unit mass and, thus, the plant's growth rate, both relative and absolute. These include the root:shoot ratio (r) and the fraction of photosynthate (PSate) allocated to fine roots (f_{FR}); the kinetic parameters of the uptake carrier proteins, V_{max} and K_m , in the Michaelis–Menten formulation of uptake rate, ν (variously per unit area or per unit dry mass), in terms of the concentration, c_a , of nutrient at the root surface

$$\nu = V_{max} \frac{c_a}{c_a + K_m}$$

and the root geometry as mean root radius (a) and mean root spacing ($2b$). One may further consider the roles of mycorrhizae in “expanding” the effective root geometry. In the soil, the bulk concentration of the chosen nutrient (c_b) is important, as is the diffusibility (D), amended by the effect of cation adsorption expressed as the buffering factor (c). Soil water potential directly affects these factors and also the degree of root contact with the soil solution. The rate of renewal of soluble nutrients, particularly mineralization of N, is important for setting the width of depletion zones around roots and, thus, the length of the diffusive pathway. Root growth rates also affect the relative importance of depletion zones, though not as strongly as one might intuit (e.g., Yanai 1994, figure 3). Finally, one may consider plant transpiration rate, which generates mass flow of nutrients and is set by a combination of plant and soil factors.

The roles of all these factors have been discussed at length and ably by a number of authors, including Tinker and Nye (2000) and Yanai (1994). We wish to emphasize

selected factors that are not as widely appreciated as the others, or that have often been misinterpreted, or that have effects that defy some intuitive understanding:

1. the generally high leverage of V_{\max} for uptake rates, in common ranges of other factors, especially bulk nutrient concentration, c_b
2. c_b itself, in soils usually regarded as low in nutrients
3. the low leverage of root:shoot ratio in many conditions, and the apparent primacy of water rather than nutrients in setting r
4. the lack of any substantial affect of mass flow on rates of nutrient uptake

We consider each of these in the following subsections.

4.2.1.1 Control Exerted by Root Kinetics (V_{\max}) and by Soil Properties

Uptake of nutrients ultimately occurs at the root surface, but how much do the carrier proteins control uptake rates, when low nutrient concentration in soil (c_b) or low diffusivity of a nutrient in soil can enforce a low concentration at the root surface? The question is of long standing, and models parameterized with experimental data offer the best route toward a quantitative understanding. In contrast, one cannot adjust V_{\max} and K_m in replicate plants at will in an experimental apparatus, nor the root geometry. Consequently, simulations have been pursued for decades, with an early synthesis presented by Nye and Tinker (1977). Another important effort is modeling the effect of varied root geometries (root diameter, spacing, and vertical distribution) on uptake and growth (Gardner 1960; Lynch and Brown 2001).

The most basic effort toward this goal is then modeling uptake and resultant plant growth rate as functions of important root and soil properties. We will not attempt to reproduce the wide range of simulations done to date, but we do provide a visualization of the sensitivity of growth rate that may be compelling. The focus will be the relative growth rate, RGR, of a young plant, for which plant RGR is a critical trait and one that is most sensitive to nutritional status, uncomplicated by reproductive allocation, stand density, and other effects.

We use as a growth model a functional balance model presented by BassiriRad et al. (2001). This model assumes a tight coupling of uptake to the use of the nutrient in photosynthesis. Thus, one must specify the root uptake capacity and the photosynthetic nutrient-use efficacy (p^* , as grams of photosynthate (PSate) per gram N in leaves per day) as well as an efficiency of converting raw photosynthate into dry matter (β , g DM g⁻¹). Root-uptake capacity can be specified directly as the rate, v , or, for later discussion, derived from the combination of the root's Michaelis–Menten kinetics (V_{\max} , K_m) with a soil nutrient transport model that requires specification of bulk concentration (c_b), diffusivity (D), root radius (a), and mean root spacing ($2b$). The allocations to roots and to leaves are specified as root:shoot ratio (r) and the fraction of shoot mass as leaf mass (α_L). Our model also uses two factors representing product suppression of photosynthesis (significant in some simulations at elevated CO₂) and enforcement of a maximum RGR (from limitation on meristem activity and number).

We choose a base case representing a fast-growing ruderal or crop: $p^* = 40$ g PSate g N d⁻¹, $\beta = 0.5$ g DM g PSate⁻¹, $v = 0.017$ g N g DM_{root}⁻¹ d⁻¹, $r = 0.4$, and $\alpha_L = 0.5$. The molar concentrations of photosynthate that half-repress photosynthesis

and RGR are, respectively, 1.0 and 0.5 (Gutschick and Pushnik 2005, and references therein), which explain more of the starch and sucrose repression of, for example, RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxygenase) gene expression.

Au: There is no corresponding work in the Ref. section.

Subsequently, we explore the effect of varying soil and root properties. In order to generate a single useful plot, we consider variations in the two soil parameters, c_b and D , over ranges covering high stress to high nutrient availability ($0.1\text{--}2.0\text{ mol m}^{-3}$ and 10^{-11} to $2 \times 10^{-10}\text{ m}^2\text{ s}^{-1}$, respectively). We set a single value of V_{\max} , $8 \times 10^{-8}\text{ mol m}^{-2}\text{ s}^{-1}$. With $a = 20\text{ }\mu\text{m}$ and dry matter constituting 25% of fresh mass, this is equivalent to $V_{\max} = 115\text{ }\mu\text{mol g DM}_{\text{root}}^{-1}\text{ h}^{-1}$ or $0.032\text{ g N g DM}_{\text{root}}^{-1}\text{ d}^{-1}$ at an effective 20 h per day uptake, similar to that found experimentally on the ruderal, *Helianthus annuus* (Gutschick 1993; Gutschick and Kay 1995). To test the effect of changes in V_{\max} , we rerun the simulations with 50% larger V_{\max} . We then compute the sensitivity,

$$S = \frac{d(\text{RGR}) / \text{RGR}}{d(V_{\max}) / V_{\max}} = \frac{d \ln(\text{RGR})}{d \ln(V_{\max})}$$

In the functional balance model, the maximal value of S is 0.5, resulting from RGR varying as the square root of uptake rate (e.g., an increase in RGR by a factor $\sqrt{2} = 2^{0.5}$ requires another factor of $\sqrt{2}$ in tissue nutrient content, or a factor of $\sqrt{2} \sqrt{2} = 2$ in nutrient-uptake rate).

The results are shown in figure 4.1. It is clear that RGR is sensitive to c_b and D only at rather low magnitudes of each. At the same time that RGR stabilizes in response to variations in c_b and D , RGR becomes very sensitive to V_{\max} (S approaches 0.4, or 80% of its theoretical maximum). That is, V_{\max} is the controlling factor over the major range of soil conditions. The simulations can be repeated for other choices of plant parameters. For a slower-growing plant, with or without lower V_{\max} , the range of c_b and D where these exert strong control shrinks roughly in proportion to either factor (RGR or V_{\max} ; results not shown).

The conclusion is that V_{\max} is a strong contributor to plant performance. This is supported by many experimental studies showing tight regulation of V_{\max} under varying growth conditions (reviewed in Glass 2005). One might expect that the optimal value of V_{\max} might be predictable, based on balancing the cumulative cost of acquiring and metabolizing nutrients against their declining utility when they are accumulated in excess. However, a number of simulations fail to generate optimal uptake rates of N and optimal tissue N contents in realistic ranges (Gutschick 1993; Gutschick and Kay 1995). Constraints on development and, hence, on nutrient uptake may well be important. So, too, might trade-offs of increased risk of herbivory become important as N content rises, but the quantitative formulation of herbivory as a stochastic risk involves yet another level of modeling.

4.2.1.2 Bulk Concentration of Nutrient and Attendant Concentration in Soil Solution

Studies of root-uptake kinetics consistently show that the high-affinity uptake system (HATS) for a given nutrient has K_m values in the tens of micromoles ($<0.1\text{ mol m}^{-3}$). One might infer that nutrient concentrations at the root surface are similarly

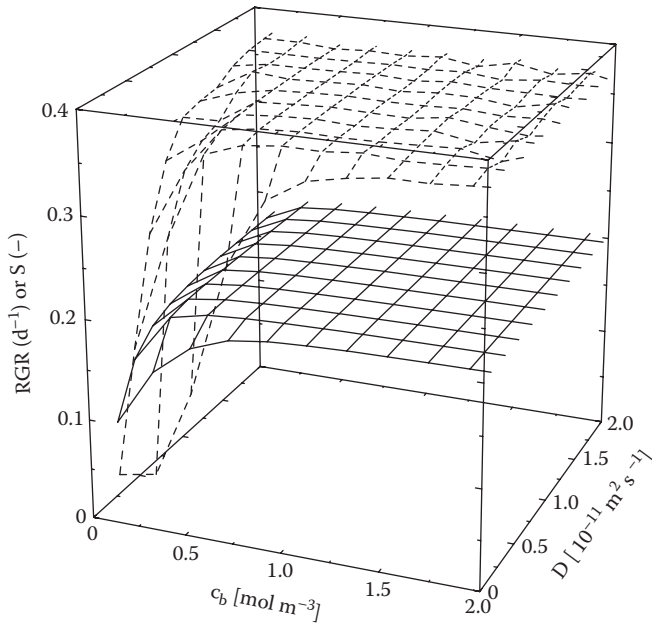


FIGURE 4.1 Modeled response of relative growth rate (RGR) of a ruderal or crop plant, in early growth, to various combinations of nutrient concentration in bulk soil (c_b) and diffusivity in soil (D). Solid lines are RGR (at fixed V_{\max}); gray lines are logarithmic sensitivity to changes in root maximal uptake rate, V_{\max} , as $d \ln(\text{RGR})/d \ln(V_{\max})$.

low. Klipp and Heinrich (1994) argue that natural selection tends to drive K_m to magnitudes at or below substrate concentrations for enzymes in general. We note briefly that c_b is commonly much higher, even in soils considered nutrient poor. The example of nitrogen in desert soils is offered. The data of Schaeffer et al. (2003) and Titus et al. (2002) indicate that, in North America's hottest and most N-poor desert, bulk concentrations average more (often much more) than 2 ppm as mass of N per mass of soil. At a bulk soil density of 1.3 tonnes m^{-3} , this is equivalent to 2.6 g N m^{-3} , or approximately 0.18 mol m^{-3} . The nutrient is actually carried in soil water that represents, on average, about 10% of the soil volume; consequently, concentration in this soil solution is on the order of 1.8 mol m^{-3} or greater. There are undoubtedly episodes when this concentration is depleted, including by rapid growth of plant (or microbial) communities. Otherwise, we should not observe responses of plant growth to added N that would only raise c_b even higher above saturation of the HATS. It is a challenge to resolve the large temporal excursions of c_b . Current experimental techniques, such as the use of bags of ion-exchange resin, are not up to the task. The relative importance of the low-affinity uptake system in natural conditions is also a challenge.

4.2.1.3 Control Exerted by Allocation to Roots

Generally, root:shoot ratios (r) are larger in ecosystems low in nutrients, which includes most "natural" ecosystems, in contrast to agricultural systems. It is also common that r increases with nutrient stress, within a single genotype. Therefore, it

is reasonable to assume that increased r has a significant net benefit and, moreover, that r is relatively close to its optimal value in both unstressed and stressed conditions. However, this assumption has not been rigorously tested on the basis of the fundamental physiology of growth. Such assessments can be addressed by using functional growth models. One simple model, the functional balance model, gives a negative answer, under the presumption that nutrient status is the dominant signal for root allocation. This model has been tested experimentally (Gutschick 1993; Gutschick and Kay 1995; Zerihun et al. 2000) and shown to have acceptable accuracy in explaining RGR and nutrient content under varying nutrient availability. However, the model indicates that the optimal root:shoot ratio is unity, for any growth conditions. We may inspect the final expression for RGR attained when uptake and use of a nutrient are in functional balance. This expression is derived in the cited references:

$$\text{RGR} = \frac{\sqrt{r}}{(1+r)} \sqrt{v\beta\alpha_L P^*} \quad (4.1)$$

Au: There was no eq. 4.1, so we assigned this as eq. 4.1. OK?

The variables have the same meaning as presented earlier. One can use simple calculus to show that the factor involving r is maximal at $r = 1$ (i.e., $(d/dr)[\sqrt{r}/(1+r)] = 0$ at $r = 1$). Note that changes of r by factors of 50% (to 0.5 and 1.5) change the whole factor by a much smaller amount (-6% and -2% , respectively). The cited references note this quandary in some detail.

This conclusion has some vulnerabilities. One assumption is that root properties (root fineness, spacing, V_{\max} , K_m) do not vary as r varies. However, any variations in the other properties do not change the conclusion that RGR would improve under any choice of these properties, if r attains the value of 1. One might also consider that the fraction of root mass as fine roots (f_{FR}) can vary, both with age and with nutrient stress. However, this only introduces the factor f_{FR} under the radical in equation (4.1), separately from the factor r , and RGR should still increase until $r = 1$.

Au: There was no eq. 4.1, so we assigned this as eq. 4.1. OK?

One possible resolution is that r may be set primarily by the need to balance water uptake to plant transpiration, E . The smaller the root system (smaller r), the smaller is the magnitude of E that can be supported. For a given shoot size, lower E requires lower stomatal conductance, g_s , which decreases the photosynthetic rate per leaf area, A . An increased root fraction can allow larger g_s and A . However, these reach plateau values at large r , while the diversion of mass from photosynthetic tissue (the factor $1/(1+r)$ above) eventually curtails RGR. A more detailed argument is given in the appendix at the end of this chapter. Values of r well below unity are supported at typical magnitudes of physiological traits. The problem remains that r varies in response to nutrient stress at high water status, such as in hydroponics. One might invoke the common correlation between low nutrient status and low water status in the field to argue that natural selection has linked the two responses. There is no basis yet to make this assertion.

4.2.1.4 Lack of Substantial Effect of Mass Flow

The argument that we develop here may be succinctly stated: Mass flow sweeps nutrients toward the root surface, but it flattens (or even reverses) the diffusional

gradient. The cancellation of the interference term (mass flow \times diffusion) is almost exact. Consequently, nutrient uptake is expected to be identical with and without mass flow under a very wide range of conditions.

The simplest case to treat, and the case with the most likely contribution of mass flow, is that of a nonadsorbed nutrient such as nitrate. We treat the quasi-steady state, when diffusive gradients have become established; corrections for dynamics are discussed at the end.

Consider a soil with water moving with (vector) velocity \vec{u} at a given location, at or away from the root surface. The soil offers a diffusivity D to the nutrient (taken as isotropic, with no real loss of generality). The nutrient has a concentration c at the given location.

Roots are typically nearly cylindrical and long relative to their diameter. In cylindrical coordinates, nutrient flow in the external solution is typically almost fully in the radial direction only. So, too, is the velocity of water, \vec{u} . We may then write a scalar equation for this radial component of the nutrient flux density. Using J as the magnitude of the total nutrient flux, we have

$$J = -uc - D \frac{\partial c}{\partial r} \rightarrow j = v_w c + D \frac{\partial c}{\partial r} \quad (4.2)$$

On the right side, we have changed to a more intuitive convention, that positive flux ($j = -J$) and positive water flow ($v_w = -u$) are into the root. Let us assume that flow is essentially in steady state, i.e., that new root growth is not fast, nor are nutrient reserves readily depleted. In this case, there is no time dependence, and c depends only upon r ; we may then replace $\partial c/\partial r$ with dc/dr , a total derivative. This formulation is an approximation of more complete equations (e.g., Darrah et al. 2006; Tinker and Nye 2000; Yanai 1994) that account for spatial variation in water content and solid–liquid equilibria of solutes.

In steady state, the flux across any radius (a shell at distance r) is equal to the flux at any other radius. The area that the flux crosses is proportional to r , so that the flux density multiplied by r is a constant. In particular, we can refer all flux densities (of water and of nutrients) to their values (j_a for nutrient, v_a for water) at the root surface, which we take as $r = a$, the root radius:

$$j(r)r = j(a)a \rightarrow j = \frac{j_a a}{r}; \text{ similarly, } v = \frac{v_a a}{r} \quad (4.3)$$

With these substitutions, we may reorder equation (4.2) into a differential equation for $c(r)$:

$$D \frac{dc}{dr} = -\frac{v_a a}{r} c + \frac{j_a a}{r} \quad (4.4)$$

This explicit (analytical) solution of this equation is a bit complicated, but it is readily derived, such as with the adjoint differential equation:

$$c(r) = c_a \left(\frac{r}{a} \right)^{-k} + \frac{j_a a}{kD} \left[1 - \left(\frac{r}{a} \right)^{-k} \right], \text{ with } k = \frac{v_a a}{D} \quad (4.5)$$

An equivalent form was derived by Nye and Spiers (1964). There are interesting limiting cases of behavior. If there is no mass flow ($v_a = 0$; the case of zero transpiration), then $k \neq 0$, and the limit of $(1/k)$ times the quantity in the square brackets reaches a limiting logarithmic form. Consider $(r/a)^{-k}$ as $\exp(-k \ln(r/a))$; for small k , this becomes $1 - k \ln(r/a)$, and we get simply

$$c(r) = c_a + \frac{j_a a}{D} \ln \left(\frac{r}{a} \right) \quad (4.6)$$

That is, there is a logarithmic profile away from the root surface. We shall use this formula to evaluate the contribution of mass flow, by difference from the solution (for flux, not c) from that in equation (4.5). In no case is c_a , the concentration at the root surface, separable into diffusive and mass-flow components.

Uptake rates at the root surface are responsive to the concentration at the root surface, c_a . We need to incorporate an accurate model of uptake to get a complete, consistent solution for both c_a and uptake rate j_a . An essentially universal form for nutrient uptake (review: Tinker and Nye 2000) is the Michaelis–Menten form,

$$j_a = V_{\max} \frac{c_a}{c_a + K_m} \quad (4.7)$$

Here, j_a is the nutrient-uptake rate v expressed specifically per unit area; V_{\max} is the saturated rate; and K_m is the Michaelis–Menten constant, the concentration at which uptake is at half-maximal rate. One can include a back-leakage term, but this is often very small. We may substitute equation (4.7) into equation (4.5) to obtain an equation solely in terms of the concentration c_a . We may solve the combined equation, a quadratic in c_a , for the value of c_a . We can then substitute this value of c_a into equation (4.7) to obtain the estimate of the nutrient-uptake rate.

We have simulated uptake and the role of mass flow for a variety of test cases, ranging over:

1. relatively low bulk concentrations (Mojave Desert; data from Schaeffer et al. 2003; Titus et al. 2002) to high concentrations (taken as 10 times higher); over this modest range, one sees the clear onset of differences in control of uptake by environment and physiology (figure 4.1)
2. soil diffusivities from high ($2 \times 10^{-10} \text{ m}^2 \text{ s}^{-1}$; cf. Tinker and Nye 2000) to low (1/5 of former; at much lower diffusivities, uptake is less important)
3. zero to high transpiration rates, equivalent to water velocities at the root surface from 0 through $5 \times 10^{-10} \text{ m s}^{-1}$ to $1.1 \times 10^{-7} \text{ m s}^{-1}$

The results are shown in table 4.1. Note that the increment in nutrient uptake when mass flow is present is only 0.01% to 1.23%. Mass flow appears large only as the crude measure of concentration multiplied by water velocity. This is the measure commonly cited (e.g., Marshner et al. 1991; Kage 1997). However, this measure omits the interference term (suppression of diffusion) that essentially cancels the crude increment exactly. We offer that mass flow need not be considered in estimating nutrient uptake in general. That is, the rate of nutrient uptake is essentially identical in the presence or absence of mass flow. Nutrient concentration and soil diffusivity remain the controlling factors. The conclusions apply to freely diffusing nutrients such as nitrate and even more strongly to nutrients such as phosphate that are significantly adsorbed on soil constituents. We have omitted consideration of a few phenomena that contribute modestly to uptake. One is mass flow into young root tips, apical to the maturation zone. In our most favorable case, it represents 7% of diffusive uptake, but this is to be weighted by the low fraction of root in this condition, and we may still neglect it (Brady et al. 1993). Uptake by root tips also occurs before the diffusive gradient develops, such that mass flow is again important. Yanai (1994) shows that this generates a modest correction (always less than 20% in her conditions). These and several other factors will be discussed in a later publication.

Our results appear superficially at variance with some experimental indications that the nighttime transpiration is negatively correlated with nutrient status, and enhanced by N amendments (Bucci et al. 2006). The relation that they found may be correlational rather than causal, via some mechanism that acts adaptively for a physiological or ecological activity not directly related to nutrition. Bucci et al. (2006) noted that N and P fertilization changed the full hydraulic architecture of the plants.

4.3 INTEGRATING OTHER ROOT SYSTEM CHARACTERISTICS

Improving our knowledge of plant N uptake and subsequent development of predictive models will ultimately depend on a keen understanding of root system characteristics that collectively control N uptake. A number of important characteristics distinguish nitrogen availability in native vs. managed ecosystems. Unlike crops where fertilizer application minimizes N limitation, native ecosystems are often nitrogen limited. Nitrogen availability in natural ecosystems also differs from that of agroecosystems in terms of temporal and spatial heterogeneity. For example, early-season flushes of N mineralization and pulses of increased N availability after a rain event add an element of uncertainty to N availability that is less dramatic in typical field crop systems, particularly those under irrigation.

These differences have undoubtedly resulted in the evolution of a number of root system characteristics that would not necessarily be favored in crop production practices of today. For example, the degree of mycorrhizal infection in native plants is far more pervasive than that observed in agronomic species. Integrating the relative contribution of mycorrhizal colonization in N-uptake models is a challenging task. While a large number of studies indicate a positive effect on N uptake due to mycorrhizal associations, the enhancement is highly species-specific (BassiriRad et al. 2001; BassiriRad 2006) and varies with the stages of plant development. Previ-

TABLE 4.1
Modeled Concentrations of Nitrate and Uptake Rates under Five
Conditions of Physiological Status and Soil Water Content

Water Status Time of Day Remark	High Day	High a Night	High a Night Low v_a	Low Day	Low Night	High b Day Extreme	High c Day Crop
Parameters							
D (m ² s ⁻¹)	2e-10	2e-10	2e-10	4e-11	4e-11	2e-10	2e-10
v_a (m s ⁻¹)	1.01e-8	2.02e-9	5.05e-10	2.02e-9	5.05e-10	3.24e-8	1.08e-7
k (unitless)	2.53e-3	5.05e-4	1.26e-4	5.05e-4	1.26e-4	8.10e-3	0.027
With Mass Flow							
c_a (mol m ⁻³)	1.01	0.997	0.995	0.997	0.995	0.921	9.845
j_a (mol m ⁻² s ⁻¹)	4.91e-9	4.91e-9	4.91e-9	4.91e-9	4.90e-9	1.07e-8	1.28e-6
Zero Mass Flow							
c_a^0 (mol m ⁻³)	0.995	0.995	0.995	0.995	0.995	0.0890	9.042
j_a^0 (mol m ⁻² s ⁻¹)	4.90e-9	4.90e-9	4.90e-9	4.90e-9	4.90e-9	1.06e-8	1.28e-6
Relative Increment d							
$(j_a - j_a^0)/j_a^0$	0.0005	0.0001	0.0000	0.0001	0.0000	0.0123	0.0004
Crude Increment e							
$c_a v_a / j_a^0$	2.0756	2.0583	2.0550	2.0583	2.0550	0.278	0.831
Suppression f							
$(j_a - j_a^0 - v_a c_a) / j_a^0$	-2.0752	-2.0581	-2.0548	-2.0581	-2.0548	-0.266	-0.831
<p><i>Note:</i> All parameters are as described in text; only variations in the water uptake velocity at the root surface, v_a, and the nitrate diffusion coefficient, D, are considered here, in the first five cases. Cases are described by plant and soil water status (high, low) and time of day. In all entries, “e-n” indicates 10^{-n}, the power of 10 as a multiplier.</p> <p>^a The second and third cases use two different estimates of nocturnal transpiration.</p> <p>^b The sixth case is an extreme (high) estimate of uptake by <i>Larrea tridentata</i>; see text for conditions.</p> <p>^c The seventh case is crop plant under conditions favorable to very high mass flow.</p> <p>^d “Increment” is the fractional increase in uptake as the difference between cases with and without mass flow.</p> <p>^e “Crude increment” is the (misleading, common) estimate of the fractional increment, using (water flow) \times concentration. It is expressed as a fraction of uptake in the absence of mass flow, and can exceed unity.</p> <p>^f “Suppression” is the decrement in uptake from suppression of diffusion, again relative to uptake without mass flow.</p>							

ously, we attempted to integrate the role of mycorrhizal colonization in a similar but simpler version of the functional balance model presented here (BassiriRad et al. 2001). There, we concluded that effects of mycorrhizal fungi on plant N uptake must be viewed in the context of both enhancing plant N status as well as the potential effects on carbon balance. Clearly, more mechanistic understanding of the biology of mycorrhizal fungi needs to emerge before we can quantitatively assess their leverage on plant N uptake via the modeling exercises recommended here.

Another root system characteristic that may have a large leverage on determining plant N uptake is root longevity or life span. Most crop plants are annuals, where root turnover may not confer a significant advantage for N uptake. On the other hand, roots of many native species such as sugar maple may live as long as a year or longer (Hendrick and Pregitzer 1993). While there is some recognition of the importance of root longevity to N uptake (Bloomfield et al. 1996; Eissenstat and Yanai 1997), there is little effort in integrating root life span into models of plant N uptake. We suggest that such integration will improve models of N uptake. Finally, much has been described about root architecture and topological differences among native species and how such differences may have evolved in response to soil N status (Fitter 1991). We suggest that root architecture plays a role in N uptake of plants. However, we are far from being able to determine the extent of that role. It is argued that root systems' branching patterns fall into two categories: herringbone and dichotomous (Fitter 1987, 1991). Fitter (1991) argued that herringbone topology gives rise to a larger specific root length, and thus is more effective than the dichotomous rooting branching pattern in N uptake from infertile sites. However, a number of studies show that such a relationship is not universal (Pregitzer et al. 2002; Einsmann et al. 1999).

4.4 CONCLUDING REMARKS

Development of robust models of N uptake requires greater efforts to integrate factors that control availability of N at the root surface together with the root system characteristics that regulate its absorption into the plant. In this chapter we offer road maps by which mechanistic models of soil N availability can be linked to physiological plant growth models to accomplish that effort. Soil properties that control N transport to the root surface have long been recognized and are well characterized. We offer selected insights as to how such information can be integrated into uptake models.

In particular, we suggested that the relative importance of mass flow to overall N concentration at the root surface in previous studies may have been overestimated. We argued that internal cycling of N via mineralization is a major contributor to N availability in native systems. Efforts to link physiological growth models (e.g., functional balance models) with mechanistic models of N mineralization should significantly improve the predictability of N uptake by native plants. We highlighted the need to characterize and incorporate atmospheric deposition as well as soil organic N sources into models of uptake for improved predictability. We also suggested that adjustments in kinetics of root N uptake have a relatively large effect on plant performance under varying N supply, but efforts to assign optimal values for V_{\max} remain incomplete. It is also concluded that, while increased biomass allocation to roots has beneficial outcomes for N uptake, plant growth is adversely affected, so that optimal

r value appears to be around 1; concurrent improvement of water uptake may drive the allocation patterns. Finally, we encourage studies that further examine the role of root system characteristics that have rarely been incorporated into uptake models, such as mycorrhizal colonization, longevity, and architecture.

To avoid making modeling efforts too cumbersome to parameterize for so many inputs, empirical studies must prove that changes in a given root system characteristic infer a significant change in plant performance in response to varying N availability. Our conclusions do rely heavily on models; they must undergo both modeling refinement and empirical testing. This highlights a major utility of modeling, that of framing hypotheses for such testing. We admit that empirical tests are challenging. They must also be analyzed critically. For example, the attribution to mass flow of a significant role in controlling uptake rates is misleading in the absence of accounting for mass flow's role in flattening the diffusional gradient, leaving total uptake rate unchanged.

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APPENDIX 4.1 OPTIMIZATION OF ROOT:SHOOT RATIO FOR WATER RELATIONS

At any given root:shoot ratio, r , there is a potential rate of water uptake, U , equal to the root mass, m_r , multiplied by the uptake rate per mass of root, v_w . This must match the whole-plant rate of transpiration, E , which equals the leaf area of the plant, a_p , multiplied by the transpiration rate per unit leaf area, E_{La} . This can only occur if E_{La} is adjusted to the sustainable rate by an appropriate magnitude of leaf conductance for water vapor, g_{bs} . (The subscript *bs* refers to the combination of boundary-layer and stomatal conductances.) The relation of E_{La} to the conductance g_{bs} , the vapor-pressure deficit D (leaf-to-air difference in partial pressure of water vapor), and total air pressure P is simple:

$$E_{La} = g_{bs} \frac{D}{P} \quad (\text{A4.1})$$

The plant's leaf area is simply the dry mass of leaves, m_L , divided by the mass per leaf area, m_{La} (inverse of specific leaf area). In turn, the mass of leaves can be expressed as the total shoot mass, m_s , multiplied by the fraction of shoot mass as leaves, α_L . Thus, we have

$$E = \frac{\alpha_L m_s}{m_{La}} g_{bs} \frac{D}{P} = U = m_r v_w \quad (\text{A4.2})$$

Assuming that these parameters are essentially stable at a stage in growth (particularly in early growth, where all leaves experience similar environments), we can solve for the required value of conductance that balances water uptake and water use:

$$g_{bs} = \frac{m_r}{m_s} \frac{v_w m_{La}}{\alpha_L (D/P)} \quad (\text{A4.3})$$

This value of the conductance constrains the rate of photosynthetic CO_2 uptake by the whole plant, A_p , and thus the growth rate, GR, which is A_p multiplied by a biosynthetic efficiency, β (as grams dry matter per gram of photosynthate produced or, if A_p is in mol_{CO_2} per area per time, as grams dry matter per mol_{CO_2}). The whole-plant rate, A_p , is, like water use, a product of whole-plant leaf area with photosynthetic rate per unit leaf area, A_{La} . The latter rate responds to conductance g_{bs} in well-known ways: Its magnitude as a rate of transport of CO_2 across the conductance must equal its magnitude as the enzyme-kinetic rate (Farquhar et al. 1980):

$$A_{La} = g_{bs}' \frac{(C_a - C_i)}{P} = V_{c,\max} \frac{(C_i - \Gamma)}{(C_i + K_{\text{CO}_2})} \quad (\text{A4.4})$$

Here, the conductance for CO_2 , g_{bs} with a prime, is closely related to that for water vapor (about two-thirds of the latter, depending upon the relative importance of

boundary-layer and stomatal conductances); C_a and C_i are, respectively, the CO_2 partial pressures in ambient air and inside the leaf (more precisely, at the site of carboxylation, such that there is an extra resistance in liquid-phase transport inside the leaf, ignored here; see Gutschick, 2006); $V_{c,\max}$ is the maximum rate of carboxylation or CO_2 fixation; Γ is the CO_2 compensation partial pressure; and K_{CO} is the effective Michaelis constant for CO_2 binding to RuBisCO enzyme in the presence of O_2 . The latter two parameters are functions only of leaf temperature and the mixing ratio of O_2 to CO_2 .

The relation above can be rearranged to a quadratic equation for C_i , given the magnitudes of all the parameters g_{bs}' , C_a , P , $V_{c,\max}$, Γ , and K_{CO} . These values are readily obtained for plants growing in normal air and at known temperatures, and with known rates of photosynthesis in unstressed conditions. Once C_i is known, equation (A4.4) can be used to compute the leaf rate of photosynthesis, A_{La} . Finally, we compute the growth rate, as the relative growth rate, RGR, or GR divided by total plant mass, m_p . RGR is relatively stable in various growth periods, and that is critical for competitive growth:

$$\text{RGR} = \beta \frac{A_p}{m_p} = \frac{\beta \alpha_L m_s A_{\text{La}}}{m_{\text{La}} m_p} = \frac{\beta \alpha_L}{(1+r)} \frac{A}{m_{\text{La}}}$$

Here we have used the relation that $m_s/m_p = m_s/(m_s + m_r)$, which becomes $1/(1+r)$ upon dividing numerator and denominator by m_s .

The key trade-off in optimizing r is that increasing r will increase water uptake, U , and allow a higher leaf conductance, A_{La} , but it decreases the fraction of the plant that does photosynthesis. At high conductance (high r), A_{La} saturates, while the factor $1/(1+r)$ cuts into whole-plant photosynthesis.

One may ask if this argument shows the optimum value of r to be near observed values. Let us consider a young herbaceous plant, with $r = 0.5$, a leaf fraction $\alpha_L = 0.5$, an unstressed leaf conductance $g_{\text{bs}}' = 0.25 \text{ mol}_{\text{CO}_2} \text{ m}^{-2} \text{ s}^{-1}$, and leaf photosynthetic capacity $V_{c,\max} = 100 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$ (achieved rate near 20 in same units). We take the environmental descriptors as $P = 10^5 \text{ Pa}$ (about sea-level pressure), $C_a = 38 \text{ Pa}$ (thus, the current CO_2 mixing ratio), and a leaf temperature near 25°C , which puts Γ near 4 Pa and K_{CO} near 90 Pa . The water-balance arguments here then yield $C_i = 26.2 \text{ Pa}$ and $A_{\text{La}} = 19.1 \text{ } \mu\text{mol m}^{-2} \text{ s}^{-1}$, both very representative of such plants. Varying the value of r changes RGR, as shown in figure 4.2. Two points are important. First, the potential uptake rate of roots, v_w , can be notably higher when soil water status is high; r could be lower than posited here. The plant's developmental controls enforce a reserve capacity. Second, the model does not indicate the mode of signaling for adjustments in r when soil water status in the long term is different from our reference conditions; functional balance per se does not yield a clear signal variable. Nonetheless, functional balance for water relations is consistent with realistic root:shoot ratios, while functional balance for nutrients is not thus consistent.

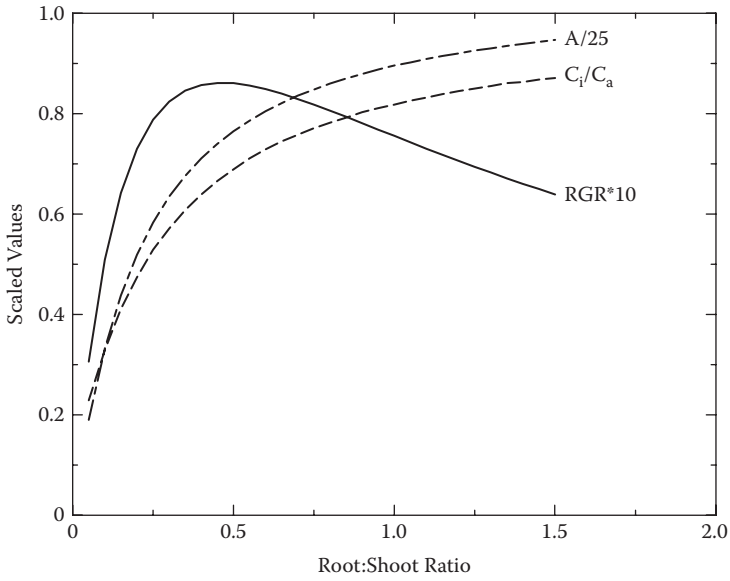


FIGURE 4.2 Occurrence of a root:shoot ratio, r , that optimizes relative growth rate (RGR) in the model of water balance between uptake and transpiration, as presented in the text. Note the continued rise, at higher r , of leaf internal CO₂ partial pressure (C_i , as ratio to ambient value C_a) and leaf photosynthetic rate (A , as ratio to limiting value of about 25 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

