

# 4 Internal Regulation of Nutrient Uptake by Relative Growth Rate and Nutrient-Use Efficiency

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## 4.1 Introduction

Plants are observed to regulate their uptake of nutrients in elaborate patterns according to their environment of growth and their stage of development. Among the common patterns is that plants reduce their nutrient uptake rates (per mass of root,  $v$ , or of the whole plant,  $v_{\text{plant}}$ ) as nutrient concentrations increase (Clements et al. 1979; Godwin and Blair 1991; Youssefi et al. 1999; see Chap. 6, this Vol.). Similarly, changes in the shoot's environment, such as in  $\text{CO}_2$  partial pressure, also induce changes in nutrient uptake rates ( $v$ ). A number of questions arise – for one, why should a ‘good’ such as nutrient acquisition ever be curtailed, or not expressed at a maximal rate? One must infer that downregulating the acquisition of a beneficial resource confers a net benefit in Darwinian fitness, for which most plants or their immediate ancestors have been heavily selected. Admittedly, long-domesticated plants may diverge from the fitness functions of wild plants (Gutschick 1987, 1997a,b, 1999; Jackson and Koch 1997). In some cases, the explanation lies at the immediate physiological level, in that some nutrients in excess are toxic, such as boron (Nable et al. 1990) and even phosphate (e.g., Romera et al. 1992). Nonetheless, such downregulation occurs even for nutrients that show no apparent toxicity in luxury consumption, such as nitrogen. Plant performance does not follow the guidelines espoused by the actress Mae West, “Too much of a good thing is wonderful”. Some experimental evidence shows that overexpression of non-toxic nutrient acquisition is deleterious to plant growth and fitness – witness the stunting of supernodulating legumes (Carroll et al. 1985), which can perhaps be attributed to excess diversion of photosynthate to  $\text{N}_2$  fixation. Nonetheless, downregulation occurs even at modest, physiological nutrient content, most markedly in woody plants (Gessler et al. 1998).

Prediction of uptake capacity in changing environments, whether for crops or wild plants, is highly desirable for studies of global change. We, as a

research community, might (and must) achieve description suited to wide ranges of plants and environments. This is a worthwhile task, but an unending one, given the infinite continuum of possible environments and of possible landscapes of Darwinian fitness or agronomic value. Far more useful in the long term would be a predictive capability based on demonstrably shared mechanisms (biochemical and genetic), or on a knowledge of the overarching selection pressures for regulation of uptake mechanisms. A comprehensive theoretical framework for uptake capacity should be sought simultaneously on two levels, physiological and ecological/evolutionary.

In the next few pages, we will put forth plausible mass-action forms that fit observations of how plants respond – in nutrient uptake rate, photosynthetic rate, tissue nutrient content, and root allocation – particularly to changes in N availability, or to elevated  $\text{CO}_2$ . The individual rate processes are formulated to respond properly (e.g., the fraction of reduced nitrogen (*RN*) loaded into the xylem should increase if the root *RN* increases). The forms we propose are heuristic (mass actions based on gross pools, not on pools of intermediate metabolites). These are meant to be guides to the origins of the plant responses, specifically to promote considerations of how processes must change relative to each other in order to give observed plant responses. The resultant model extends simple *functional balance* models, which only resolve gross root and shoot capture of resources (nutrients,  $\text{CO}_2$ , light) but do not explain why resource-capture capabilities attain the values observed or how these capabilities might be regulated (Gutschick and Kay 1995).

Foremost, we attempt here to provide a semi-mechanistic ‘explanation’ of how the uptake capacity ( $V_{\text{max}}$ ) and root:shoot ratio (*r*) should acclimate to the growth environment. The functional balance model derived from the experiments of Gutschick and Kay (1995) sought to identify optimal  $V_{\text{max}}$  and *r* values by fixing either  $V_{\text{max}}$  or *r* values and varying the other. One intriguing result was that there should be an optimal root:shoot ratio ( $r=1$ ), independent of environment (N only, not considering water). Second, the optimal  $V_{\text{max}}$  should be infinity: incremental gains in relative growth rate (*RGR*) continue, if at smaller rates, for any increase in  $V_{\text{max}}$ . A mechanistic model obviously would disallow such an extreme; it incorporates responses that evolved despite not maximizing the relative growth rate. If the predictions are realistic, then one might seek an explanation as to why these mechanisms evolved.

We will start our discussion with the question of ‘what sets nutrient demand?’. Demand is surprisingly difficult to formulate, at least in terms of the external environmental variables and the basic growth attributes of the plant, including physiological capacities for nutrient uptake and photosynthesis, and growth patterns of root and shoot. Most of the literature on plant function defines demand as a single point value, the current uptake rate that one might calculate from current growth rate and current tissue nutrient content,  $f_n$ , of the plant. This definition is what economists would call the ‘quantity demanded’. In contrast, ‘demand’ is a mathematical function – the quantity

demanded as a function of price (cost of nutrient acquisition). With this view of demand, we must inquire why the rate of uptake has its current magnitude, and what will be the rate if we change environmental conditions, say,  $\text{CO}_2$  levels.

## 4.2 Phenomenology of Uptake Rate Responding to Nutrient-Use Efficiency and Growth Rate

### 4.2.1 The Evolutionary and Ecological Perspective of Physiological Demand

Economists propose that demand is determined by a rational consumer who knows the utility of a resource, and seeks to maximize net marginal benefit (the utility less the cost, as derivative with respect to quantity consumed) of a resource. For a human consumer, this is monetary value, other values being converted to this as a medium of exchange. For a plant, demand could be defined as the continuous function that relates the mass of nutrient acquired as a function of the cost of acquiring and the benefit of using that nutrient. Cost is a function of, above all, external nutrient concentration – for example, it requires more energy in root growth to obtain dilute nutrients. It is necessary that this mass of nutrient optimize the plant's function, say, its growth or, more importantly, its Darwinian fitness.

This is where the difficulty arises – in what sense(s) and to what extent do plants optimize their performance? Fitness can never be fully maximized (Stenseth and Maynard Smith 1984). Even if fitness is nearly optimized, the relation to readily measured physiology or even simple growth in mass is complicated. Greatest vegetative biomass is not equivalent to greatest fitness. For example, the dispersal dynamics of seeds does matter, and for perennials, reproduction in any one year involves tradeoffs with future reproductive output (Boutin and Harper 1991; Edwards and Crawley 1999). Consider further the relation of total biomass growth to nutrient acquisition. Fast early growth may deplete the soil of nutrients for later reproductive growth. For nutrients that are poorly mobile in plants, this may more than negate benefits of early growth, and may explain why early *RGR* is manifestly held below maximal *RGR* in some plants. Moreover, any prediction of optimal uptake capacity for a specified environment requires that we possess information on aspects such as the availability of nutrients at all future times, especially at times of reproduction. Yet there are uncertain, risky, or stochastic elements in the availability of a nutrient, which may depend on, e.g., weather (precipitation, temperature). The same risk and uncertainty are associated with the utility of a nutrient. Changes in the concurrent availability of water modify the photo-

synthetic utility of nitrogen, as discussed in the following sections. On an ecological level, high N content brings stochastic risks of herbivory; these risks may be the most potent limiters of high nutrient content, particularly for N.

Even for deterministic costs and benefits, the plant cannot accurately sense current availability in a distributed soil volume. Future availability depends as well on other organisms for nutrient mobilization, such as by microbial mineralization. Of course, there are broad, predictable patterns of future availability, such as seasonal flushes, and plants have been naturally selected to respond effectively to these patterns, but the risk lies in the details, especially in competitive growth. Many of the limitations and promises of optimization theory applied to plants have been discussed by, e.g., Bloom et al. (1985) and Gutschick (1987). We shall provisionally accept a number of limitations, and explore some details of what is involved in optimizing *RGR* alone with a known external nutrient concentration, known cost of acquiring and metabolizing the nutrient, and known benefit (current photosynthetic utility) as a function of tissue nutrient content ( $f_n$ ).

#### 4.2.2 A View from Physiology: Response of Growth Rate to Nutrient Availability, Cost, and Utility

An understanding of the regulation of nutrient acquisition and use requires a physiological perspective. Considerable detail at the levels of physiology and gene expression has been achieved in model systems, such as *Arabidopsis*. However, these model systems are somewhat limiting, in that they do not adequately represent the range of selection pressures that have molded diverse physiological patterns among different species and environments. Ecologists and whole-plant physiologists are positioned to broaden this view, generating clues as to the nature of regulatory signals and regulatory actions. One example is in elucidating the roles of nutrient costs (for acquisition and metabolism), and of saturation of benefits in making it beneficial to limit nutrient uptake. Nutrients are costly, in several ways – for example, in the construction of roots, and in metabolism for uptake, reduction, and maintenance (Gutschick 1987; Zerihun et al. 1998). Moreover, as nutrients become more abundant, there is a decline in their marginal benefit, as measured by photosynthetic utility,  $p^*$  (mass of photosynthate made per gram of nutrient per day; Gutschick and Kay 1995). The photosynthetic utility of nitrogen, in particular, is much increased when the shoot is exposed to high  $\text{CO}_2$ .

As a first accounting of such costs and benefits, we present here a model applicable primarily to growth in a steady environment, and omitting the complication of transitions from vegetative to reproductive growth. In this model (elaborated from Gutschick and Kay 1995, Appendix III therein), nutrient uptake and nutrient use for photosynthesis achieve a functional balance – that is, root and shoot functions attain a balance. Such models do appear to

correctly predict the trends in  $f_n$  and in  $RGR$  at high  $CO_2$  (Zerihun et al. 2000; BassiriRad et al. 2000). Can such models also predict trends in  $V_{max}$ ? They can do so only on the basis that a given  $V_{max}$  may maximize growth rate, rather than giving a mechanistic explanation. However, this view must be accommodated, if only to explain why the physiological mechanisms exist and act as they do. We show that yet more physiological and developmental traits must be considered.

Consider the rate of dry-matter gain of a plant limited by its nutrient uptake. Uptake occurs at velocity  $v$  per mass of root. Total root mass is  $m_r$ , so that the uptake rate of the whole plant is  $m_r v$ . New plant tissue has a fractional nutrient content,  $\tilde{f}_n$ , where the tilde indicates increment in new tissue. The uptake-limited growth rate is then

$$\dot{m}^{ul} = m_r v / \tilde{f}_n \quad (4.1)$$

and the relative growth rate of the whole-plant is then divided by whole-plant mass:

$$RGR^{ul} = \frac{m_r v}{(m_r + m_s) \tilde{f}_n} = \frac{rv}{(1+r) \tilde{f}_n} \quad (4.2)$$

Here,  $r$  is the root:shoot ratio, as usual.

The photosynthesis-limited growth rate is simply the whole-plant photosynthetic rate,  $A_{plant}$ , multiplied by the conversion efficiency from raw photosynthate to dry matter,  $\beta$ . Now,  $A_{plant}$  equals the average photosynthetic rate of leaves per mass,  $A_{L,m}$ , multiplied by leaf mass,  $m_L$ . Much photosynthesis is done at light saturation, where the rate per leaf area is proportional to the nitrogen mass per leaf area. Equivalently, then, the rate per leaf mass is proportional to the mass fraction of nitrogen (and perhaps also of phosphorus; see Gutschick 1993), that is,  $A_{L,m} = p^* f_n$ . The leaf mass may be expressed as a fraction of shoot mass,  $\alpha_L = m_L / m_s$ . Thus, the growth rate is

$$\dot{m}^{pl} = \beta p^* f_n \alpha_L m_s \quad (4.3)$$

and the photosynthesis-limited *relative* growth rate is the above divided by total plant mass,

$$RGR^{pl} = \beta p^* \alpha_L \frac{m_s}{m_s + m_r} f_n = \beta p^* \alpha_L f_n / (1+r) \quad (4.4)$$

If root and shoot are in functional balance, the two  $RGR$  expressions above are equal. Dividing out a common factor of  $1/(1+r)$ , we obtain

$$rv / f_n = \beta p^* \alpha_L f_n \quad (4.5)$$

In functional balance, the incremental and average nutrient contents are equal, so that we can solve for  $f_n$  as  $\sqrt{rv/(\beta p^* \alpha_L)}$ . Note that it is determined by functional balance between the root and shoot, and is not freely adjustable as a plant response. Substituting this expression for  $f_n$  into either  $RGR$  expression gives an expression for  $RGR$  in terms of physiology, allocation, and environment:

$$RGR = \frac{\sqrt{rv}}{1+r} \sqrt{\beta p^* \alpha_L} \quad (4.6)$$

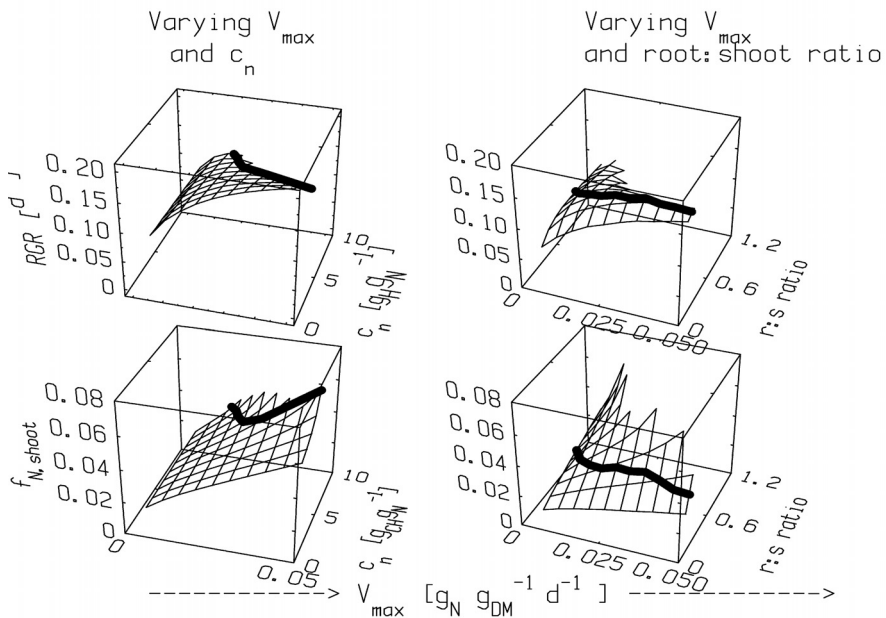
This growth rate is realistic, except that it increases indefinitely as  $v$  or  $p^*$  increases. In order for  $v$ , hence,  $V_{\max}$ , to have an optimum (that is, for  $RGR$  to decline beyond that), it is necessary that there be both a cost to nutrient acquisition and a saturation of the benefit of the nutrient in photosynthesis. The costs have been discussed at length for N by, e.g., Gutschick (1981) and Zerihun et al. (1998). We incorporate them as changing the whole-plant photosynthetic rate in Eq. (4.4) above, introducing a factor  $(1-c_N f_N)$ , with  $c_N$  being the energetic cost of acquiring and metabolizing N. The saturation of photosynthetic carbon assimilation with  $f_N$  is also observed empirically (Sinclair and Horie 1989). It is also interpretable in theory. Consider leaves of a given mass per area – roughly, their thickness; specifying  $f_N$  then determines the carboxylation capacity  $V_{C,\max}$ . For a specified leaf irradiance  $I_L$ , one can derive estimates of leaf (and also whole-plant) assimilation per unit area and per unit mass of N. Both of these functions begin as linear in  $f_N$  at low  $f_N$ , and then approach an asymptote as light, rather than N, begins to be limiting the photosynthetic rate *per mass of leaf*. We thus introduce another factor that decreases the whole-plant photosynthetic rate in Eq. (4.4); one of the simplest mathematical forms with a single saturation parameter  $q$  is  $\exp(-qf_N)$ . Here,  $q$  is the inverse of a ‘saturating’ N content in the shoot,  $f_{N,s,\text{sat}}$ . (Other forms, such as Michaelis-Menten, give very similar results.)

### 4.2.3 Does a Simple Model Predict an Optimal Uptake Capacity and Root Allocation?

We now use this model, with the modified costs and benefits of nutrients, to predict the optimal value of  $V_{\max}$  for nitrogen in particular. We estimate the other physiological and environmental variables, and then vary  $V_{\max}$  to find the value that maximizes  $RGR$ . We consider various values of the N-reduction cost,  $c_N$ , as well. The solution is obtained numerically (we use a binary search in  $f_N$ ; note that our Fortran programs are freely available). The other variables we must set are: the nutrient concentration at the root surface,  $c_e$  (a nominal 100  $\mu\text{M}$  here); the Michaelis constant,  $K_m$  (taken as 30  $\mu\text{M}$ ), in order to com-

pute  $v$  as  $V_{\max}c_e/(c_e+K_m)$ ; the root:shoot ratio,  $r$  (0.4 is taken as a typical value); the biosynthetic conversion efficiency,  $\beta$  (almost invariant among plants, so that we fix it at 0.77, excluding the N-reduction cost; BassiriRad et al. 2000); the fraction of shoot mass as leaves,  $\alpha_L$  (fixed at 0.55, appropriate for a young plant); and  $p^*$ , the photosynthetic utility of the nutrient (fixed at 15.26 g carbohydrate  $g^{-1}$  dry matter  $day^{-1}$ , to represent a modest competitor).

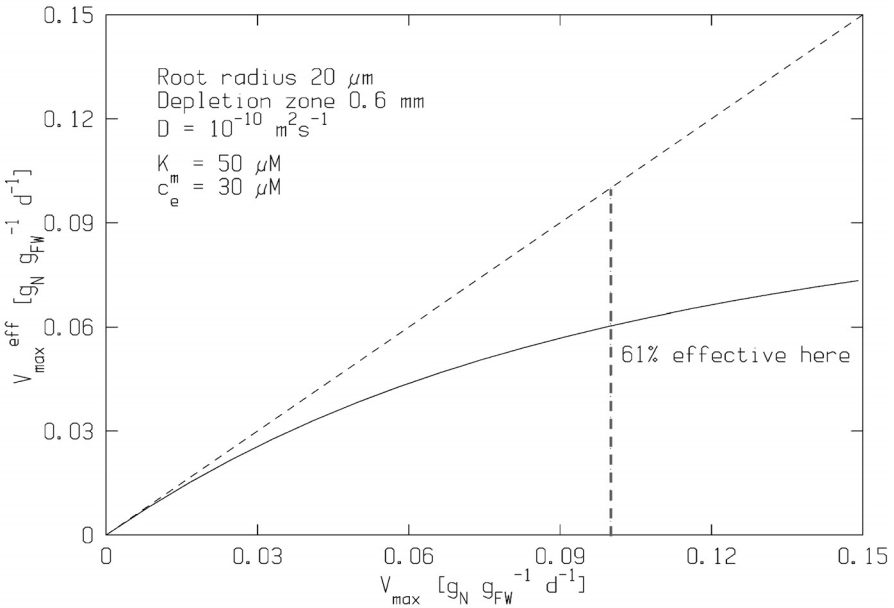
Figure 4.1 presents the results. Note first that  $RGR$  responds more weakly than linearly to changes in uptake capacity. Following the elementary model of Eq. (4.6), it rises initially as the square root of  $v$ , and hence as the square root of  $V_{\max}$ . It then flattens out as N uptake increases, mostly because the photosynthetic capacity saturates in  $f_N$ . Increasing costs of N reduction also exact a penalty in  $RGR$ , as expected. For all cases with relatively high costs ( $>6$  g glucose per g nutrient, there is a clear optimum value of  $V_{\max}$ , above which  $RGR$  declines. At uptake capacities significantly higher than the optimum and at high nutrient cost, however, no functional balance can be attained. For such cases, but also in general, one needs a model with realistic repression of uptake by the accumulation of N in tissue, as we develop below.



**Fig. 4.1.** Predictions of the functional balance model for responses of relative growth rate ( $RGR$ ) and tissue fractional N content ( $f_N$ ) to *left* combinations of N-uptake capacity and nitrate-reduction cost ( $c_n$ ), and *right* combinations of uptake capacity and root:shoot ratio. The model equations are presented in Section 4.2.1. At high  $V_{\max}$  and high  $c_n$ , no functional balance is possible; results are correspondingly absent. *Thick lines* indicate the optimal  $V_{\max}$  (*left*) and optimal root:shoot ratio (*right*)

Predicted tissue N content is only realistic in some regions of the simulations presented here. When  $V_{max}$  is low or moderate, the tissue content,  $f_n$ , is realistic (below 5% N), but not for high  $V_{max}$ . Surprisingly, unrealistically high  $f_n$  occurs when there is a high cost of N that might be assumed to suppress N accumulation. However, this cost penalizes carbon accumulation, not uptake. Feedback to uptake is clearly not represented, nor is it warranted if increased N were really to confer a growth benefit, even a small one. Also unrealistic is that at high  $V_{max}$ , the limited diffusibility of N in soil (even as nitrate) draws down the concentration of N at the root. In essence,  $V_{max}$  is partly ineffective. This phenomenon can be modeled readily, for a specified root geometry and diffusivity (Gutschick and Kay 1995). Figure 4.2 shows such a calculation.

On the right-hand side of Fig. 4.1 are results in which the root:shoot ratio is varied as well as is  $V_{max}$ . This simulation is aimed at determining if there is an optimal value of  $r$  (as real plant behavior implies), when realistic costs and realistic saturation of benefits occur. Indeed, for any  $V_{max}$  there is an optimal



**Fig. 4.2.** Diminishing returns in actual uptake rate at high N-uptake capacity, when diffusibility of N in soil is limited at the stated realistic value. The steady-state uptake rate was computed for cylindrical roots of 20- $\mu\text{m}$  radius with a depletion zone 0.6 mm wide, using standard equations (see Gutschick and Kay 1995). The achieved uptake rate,  $v$ , equals  $V_{max}c_a/(c_a+K_m)$ , where  $c_a$  is the concentration at the root surface. This rate is equated to an effective  $V_{max}$  ( $V_{max}^{eff}$ ) operating at the N concentration in bulk soil,  $c_e$ , as  $V_{max}^{eff}c_e/(c_e+K_m)$

value of  $r$ , and it declines at high uptake rates, following one's intuition that N demand is more readily satisfied in such cases.

Another interesting perspective from physiology is how the benefit of a nutrient is affected by other nutrients, as well as by water and other environmental factors. Consider how a decrease in water availability induces stomatal closure. The ensuing decrease in leaf-interior partial pressure of  $\text{CO}_2$  ( $C_i$ ) reduces the carboxylation rate per Rubisco enzyme by well-known formulae (Farquhar et al. 1980), thus reducing the photosynthetic gain per mass of N per unit time. In the long term (weeks), plants can approach an optimal mixed usage of water and N. We have not entered this consideration in our model.

For greater realism and more insight, we must propose that the uptake capacity  $V_{\max}$  and root allocation are not free parameters, but are both tied to internal indicators of plant status, to achieve optimal values (maximal  $RGR$ ), or to meet other physiological, developmental, and environmental constraints (including risks) that we have not yet considered. Uptake then should respond to N status, although not to that alone, since the optimal  $RGR$  is attained at different magnitudes of  $f_N$  when the photosynthetic utility,  $p^*$ , changes: the magnitude of  $f_N$  is predicted to decrease with increasing  $p^*$ , as is seen in elevated- $\text{CO}_2$  experiments almost uniformly. Evaluating if this is optimal requires more detail. We have presented some detail, but have not answered the question of how optimal uptake shifts as  $p^*$  changes, in other publications (BassiriRad et al. 2000). With the realization that internal N and carbohydrate ( $CH$ ) statuses both represent signals of sub- or supra-optimality, we must proceed to a model that resolves internal pools of N and  $CH$ . Such a model is presented below. Before proceeding to this larger model, we analyze another, little appreciated limit on the utility of nutrients, namely, internal developmental limits on growth rate. This surely must be a strong modifier of growth rate, and of any near-optimizing responses in  $V_{\max}$  and in root allocation.

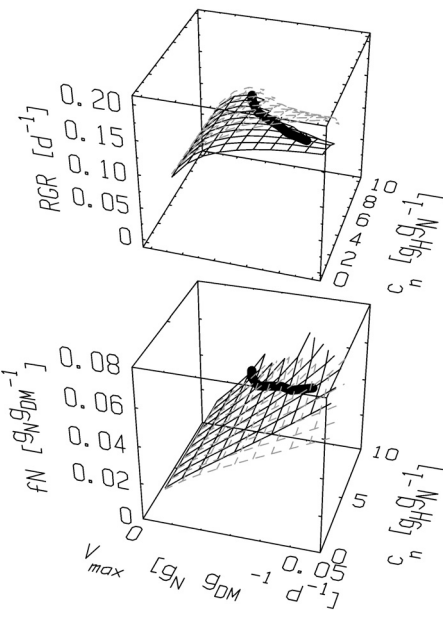
## 4.3 Toward a Model of Uptake Regulation in Response to Nutrient Utility

### 4.3.1 Predicted Response to an Intrinsic, Physiological or Developmental Limit on Relative Growth Rate

A phenomenon that is insufficiently appreciated as determining  $RGR$  and nutrient content or uptake rates is the maximal relative growth rate,  $RGR_{\max}$ . This has been measured by, e.g., Poorter and Remkes (1990), and has been incorporated into a model of  $RGR$  by BassiriRad et al. (2000). Presumably, it arises from the existence of limits on the number of growing points (meristems) in a plant, and of limits on organ expansion rates (e.g., Tardieu and

Granier 2000). This may be taken as a quantitative expression of the qualitative term ‘vigor’. As the environment becomes more favorable,  $RGR$  approaches  $RGR_{max}$ . As the utilization of growth substrates nears saturation, presumably the use of growth substrates stagnates and their internal pools rise markedly. These pools should then function as feedback signals. In our simple model of functional balance with finite  $RGR_{max}$  (BassiriRad et al. 2000; see Fig. 4 therein), the bulk nutrient content,  $f_n$ , does rise sharply, although we do not explain this rise mechanistically.

To explore how the existence of  $RGR_{max}$  is predicted to affect optimization (and thus regulation) of  $V_{max}$ , we use an expanded functional balance model (BassiriRad et al. 2000). To express the origin of  $RGR$  limitation, we resolve a new variable,  $f_c$ , the nominal (molar) concentration of nonstructural carbohydrates internal to the plant.  $RGR$  initially increases with  $f_c$  but reaches an asymptote because growing points saturate in their ability to use carbohydrates. We express  $RGR$ , then, as  $RGR_{max} f_c / (f_c + K_e)$ , with  $k_c$  as a parameter. Photosynthesis, too, is affected (repressed) by high  $f_c$ , being decreased by a factor  $1/(1+k_c f_c)$ . As in BassiriRad et al. (2000), we choose values of  $k_c=1$ , and  $K_e=0.25$ ; both are unitless. The value of  $f_c$  itself is set by the balance between photosynthetic production and consumption in growth – that is, functional balance occurs in carbohydrate generation and use, analogous to the balance for N. As in the model without this developmental limitation, we then explored predicted performance with varied uptake capacity and cost of N reduction. Figure 4.3 shows that  $RGR$  is curtailed even when it is significantly



**Fig. 4.3.** Predictions of growth rate and tissue N content for the functional balance model with a developmental limit ( $RGR_{max}=0.20 \text{ day}^{-1}$ ) imposed. Physiological parameters are as in Fig. 4.1, with the addition of growth-limiting parameters described in the text. *Thick lines* indicate the optimal  $V_{max}$  values. *Shaded lines* represent the simulations of Fig. 4.1 for comparison

below  $RGR_{\max}$ , while tissue N content is higher because use of N for growth is increasingly restricted. Optimal values of  $V_{\max}$  remain apparent, and at closely the same values as for unlimited growth in Fig. 4.1. More signatures of developmental limitation may be discerned if internal pools of metabolites are resolved, as we now proceed to do.

#### 4.3.1.1 Do Internal N and Carbohydrate Pools Explain Responses of $V_{\max}$ to Photosynthetic N Utility and to Developmental Limitations on Relative Growth Rate?

A model with an account of developmental limitations must resolve an internal pool of nonstructural carbohydrates. Further insight might be gained by resolving additional internal pools. The predicted plant performance might thus be more realistic. Conversely, such a model might be useful in predicting the ‘signatures’ (patterns of changes in internal pools) that indicate that a plant is responding either to developmental limitations ( $RGR_{\max}$ ) or to changes in photosynthetic N utility ( $p^*$ ), or to additional internal factors.

There is substantial qualitative evidence, and significant quantitative evidence, that uptake (as  $V_{\max}$ , and  $K_m$ , etc.) responds to internal pools, which are reflected as well in tissue nutrient concentration,  $f_n$  (see Chap. 6, this Vol.). At the root, one observes downregulation of  $\nu$  by high concentrations of the nutrient itself, or of some key pool involving the nutrient. High  $[K^+]$  appears to downregulate  $V_{\max}$  of  $K^+$  (Glass and Dunlop 1979; Siddiqi and Glass 1987); soluble  $K^+$  is, of course, the only significant component of total tissue  $K^+$ . For nitrogen, the situation is more complex;  $\nu$  is regulated by a small pool of reduced-N compounds (King et al. 1992), which broadly track total tissue content. However, rapid transients occur in the regulatory pool in response to sudden (and normal) changes in shoot photosynthesis with time of day, for example (Morcuende et al. 1998), and these are important manifestations of regulation that must occur faster than changes in bulk tissue content. Similar small pools appear to regulate iron uptake, for example (Schmidke et al. 1999). In steady growth, bulk tissue content is related to the regulatory metabolite pools, and thus is correlated with  $V_{\max}$  (see Chap. 6, this Vol.).

Also relevant to the role of internal pools in regulation and any associated optimization are the changes in  $f_n$  induced by changes in the shoot environment, such as light ( $I_L$ =irradiance in the photosynthetically active radiation region or PAR) or  $CO_2$  (expressed as  $C_a$ =partial pressure in ambient air) or temperature. Increases in  $C_a$  cause increases in carboxylation rate per Rubisco molecule (Farquhar et al. 1980), and thus in carbohydrate pools. These commonly cause significant decreases in nitrogen and sulfur contents (Penuelas and Matamala 1990; Peterson et al. 1999). In previous papers (Gutschick 1993; Gutschick and Kay 1995), we expressed this effect solely with the physiological parameter  $p^*$ , the nutrient-use efficiency (or efficacy) in photosynthesis.

In functional balance,  $RGR$  is predicted (and observed; *ibid.*, and Zerihun et al. 2000) to respond directly to  $\sqrt{p^*}$ , while  $f_n$  responds inversely as  $\sqrt{p^*}$ . Here, to explain optimal performance, we must resolve more detailed internal pools of metabolites.

The most parsimonious set of pools is composed of the following: nitrate in the root ( $N_r^o$ , 'o' representing the oxidized form), reduced N in the root and shoot ( $N_r^r$  and  $N_s^r$ , respectively), and nonstructural carbohydrate in the root and shoot ( $C_r$  and  $C_s$ , respectively). Correspondingly, we must resolve the processes of: N uptake; N reduction (taken to be all in the root; this may be generalized readily); growth of root tissue – with attendant incorporation of nitrate, reduced N, and carbohydrate; xylem loading of reduced N; shoot growth with incorporation of reduced N and  $CH$ ; phloem loading of  $CH$ ; and phloem loading (recycling) of reduced N back to the root. We derive a set of kinetic equations for all these processes in terms of the metabolite pools and rate constants for the net metabolic reactions. The rate constants are estimated numerically from 'gross' observables: growth rates under baseline conditions; uptake rate per mass of root and its response to reduced-N accumulation in the root; tissue N contents in the root and shoot ( $N_r^o$ ,  $N_r^r$ ,  $N_s^r$ ) under baseline conditions; the fraction of reduced N recycled to the root; the response of xylem and phloem loading to reduced-N pools; and photosynthetic  $CO_2$  assimilation per mass of N, and its response to tissue N ( $f_N$ ) and to  $CH$  accumulation. These data are not trivial to obtain, but they are much simpler than a more detailed biochemical dataset. Once the rate constants are computed, it is assumed that all acclimations of the plant (to altered N availability, shoot  $CO_2$  or temperature, etc.) are represented by the kinetic scheme with these rate constants fixed – that is, the kinetic scheme captures all the acclimation of the plant.

Many kinetic schemes have been proposed for the various facets of root N uptake, its feedback regulation, root and shoot growth, photosynthesis, and its regulation. (Le Bot et al. 1998). We propose here a similarly parsimonious synthesis of these ideas, and some new ideas. First, we take the evidence that internal or cytoplasmic pools of reduced N, as they increase, can downregulate N uptake from soil (King et al. 1992; Kronzucker et al. 1995; Sivasankar et al. 1997), and propose the simplest functional form for whole-plant N uptake,  $U$ , to be:

$$U = m_r v_0 / (1 + a_U N_r) \quad (4.7)$$

Here,  $v_0$  is the Michaelis-Menten form,  $V_{\max}^0 c_e / (c_e + K_m)$ , where  $V_{\max}^0$  is the fully unrepressed value. The denominator is a downregulating factor, with  $a_U$  being a physiological constant (parameter). Next, we assume that our plant reduces all its nitrate in the root. (The model can readily be generalized to include nitrate reduction partially in the shoot, and also uptake of some N as reduced N. Roughly, the partial uptake of N as reduced N can be simulated by

decreasing the cost of N reduction, ignoring the difference in nitrate and ammonium uptake kinetics.) The reduction rate,  $R_{NR}$ , is taken as simple mass action, responsive to both nitrate and carbohydrate in the root:

$$R_{NR} = m_r k_{NR} N_r^o C_r \quad (4.8)$$

Root growth,  $G_r = dm_r/dt$ , similarly follows mass action in both substrates,

$$G_r = m_r k_{RG} C_r N_r^r \quad (4.9)$$

The individual rates of incorporation of reduced N and of carbohydrates must be specified, in a form that generates consistent fractions of N in tissue. For reduced-N incorporation into root tissue,  $I_{N,r}$ , many empirical forms may be proposed, in advance of detailed experimental evidence. Having tested the behavior of many polynomial forms, we propose a Michaelis-Menten form that realistically generates increased incorporation of N into tissue (increased  $f_N$ ) as the availability of reduced N increases (that is, as  $N_r$  increases):

$$I_{N,r} = R_{NR} N_r^r / (N_r + K_{sel} C_r) \quad (4.10a)$$

$$= k_{NRG} C_r (N_r)^2 / (N_r + K_{sel} C_r) \quad (4.10b)$$

Here, the rate constant for incorporating reduced N into growing tissue,  $k_{NRG}$ , is proportional to the rate constant  $k_{RG}$  for total growth, with a proportionality that produces the proper  $f_N$  at low N availability. A selectivity coefficient,  $K_{sel}$ , prevents excessive incorporation of N relative to C. Similarly, the incorporation of carbohydrate into new tissue,  $I_{C,r}$ , must be consistent with the overall growth rate and with the fraction of biomass deriving from reduced N. We derived the form

$$I_{C,r} = k_{RG} C_r N_r^r - k_{NRG} \frac{C_r (N_r^r)^2}{(N_r + K_{sel} C_r)} + \left[ \frac{1}{f_{N,RN}} - \frac{1}{f_{N,NO}} \right] k_{RG} C_r N_r^r F_{DM} N_r^o \quad (4.11)$$

The third term enforces mass balance of reduced and nitrate N in new tissue. Here,  $f_{N,RN}$  and  $f_{N,NO}$  are the mass fractions of N in the form of reduced N (about 0.18 for amino acids) and of nitrate ( $18/62=0.29$ ), respectively;  $F_{DM}$  is that fraction of fresh mass represented by dry matter.

Proceeding toward the shoot, we describe xylem loading of reduced N,  $X_N$ , as an attenuating quadratic in  $N_r$ ,

$$L_N = k_x (N_r^r)^2 / (1 + a_x N_r^r) \quad (4.12)$$

This is a modification of simple linear kinetics by a Michaelis-Menten factor,  $N_r^r/(1+a_x N_r^r)$ , which increases the export fraction at high  $N_r^r$ . Shoot growth in mass,  $G_s=dm_s/dt$ , is described as by simple mass action,

$$G_s = m_s k_{SG} C_s N_s^r \quad (4.13)$$

Note that the ratio of shoot growth to root growth remains constant (root:shoot fraction is constant) if the C and N pools (which are concentrations) are stable. The incorporation of reduced N into shoot biomass has a form analogous to that in roots, excluding the nitrate term. The shoot as source of carbohydrates is described as in our basic model, with total carbohydrate production rate  $A$  given as

$$A = p^* f_{N,s} m_L = p^* f_{N,s} \alpha_L m_s \quad (4.14)$$

To account for repression by accumulated carbohydrate, we add a simple factor,

$$A \rightarrow A^0 (1 + a_{PS} C_s^0) / (1 + a_{PS} C_s) \quad (4.15)$$

The factor in the numerator simply normalizes  $A$  to its value at a chosen reference environment in which  $A$  attains a known rate  $A^0$  and  $C_s$  has its base value,  $C_s^0$ . The parameter  $a_{PS}$  describes the sensitivity of photosynthesis to repression by free carbohydrate. To describe phloem loading of carbohydrate to circulate to roots,  $P_C$ , we use a model based on the pressure-flow model (admittedly of modest accuracy: Farrar and Jones 2000),

$$L_C = m_s k_{PC} [\Delta\psi + RT(C_s - C_r)] \quad (4.16)$$

Here,  $\Delta\psi$  is the water-potential difference from shoot to root ( $<0$ ),  $R$  is the gas constant, and  $T$  the absolute temperature. Partly as a signal for regulating N uptake, reduced N is also loaded into phloem to return to roots. We take the rate,  $P_N$ , as

$$L_N = L_C N_s^r / (N_s^r + K_{PN} C_s) \quad (4.17)$$

This form makes the fractional return of reduced N increase as reduced N increases – that is, when N supply exceeds growth demand.

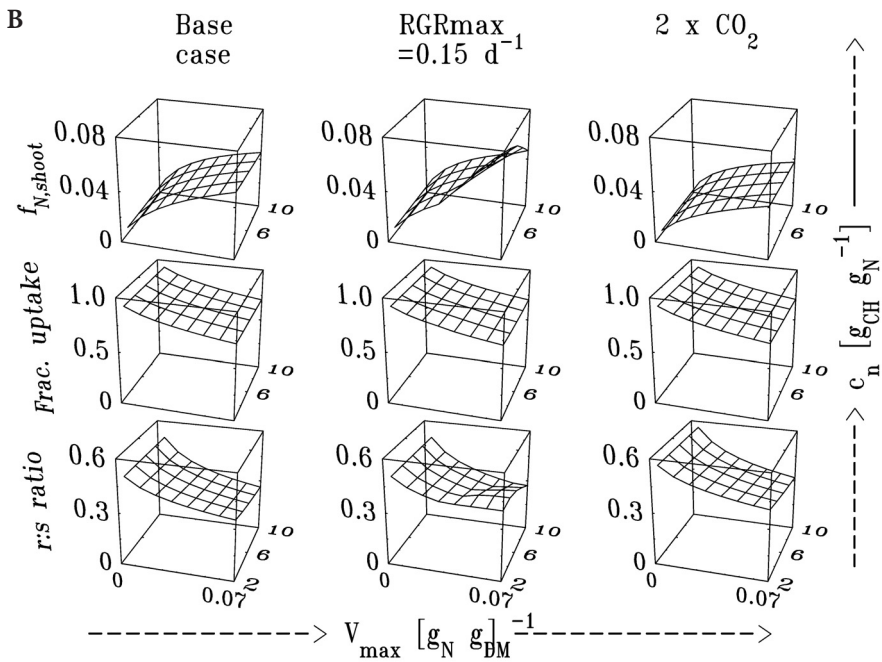
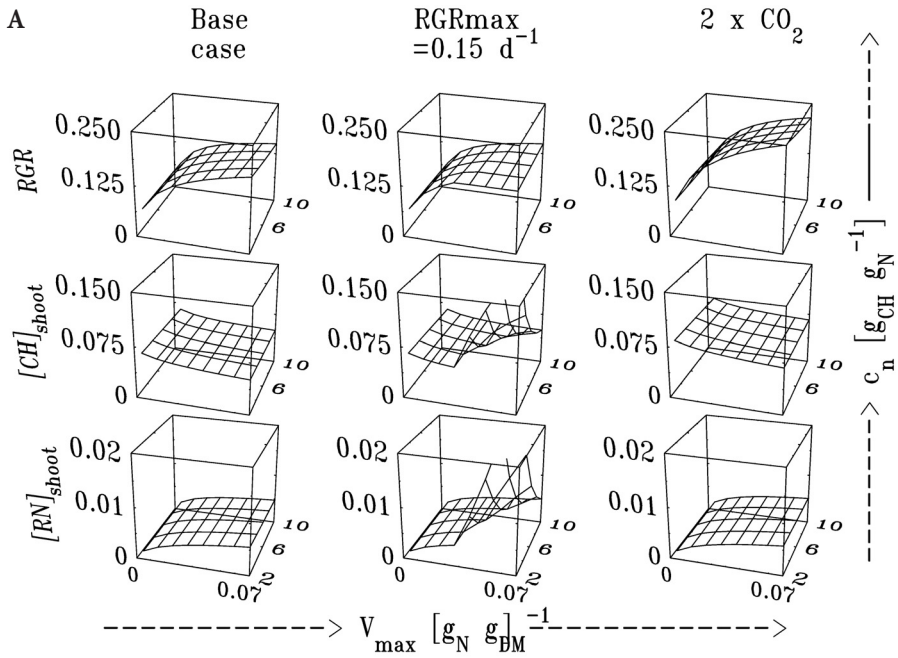
These equations were developed by some trial and error in order to get realistic responses of growth,  $f_N$ , and uptake to changes in external N availability, in  $p^*$  (hence, in  $CO_2$  or irradiance), and in growth potential. It is important to note that a maximal  $RGR$  is implicit in the rate constants  $k_{RG}$ ,  $k_{SG}$ . Most of the rate constants can be fitted from observed values of  $RGR$ ,  $f_N$ , and the pool sizes for a given environment. Other parameters may be estimated to

explore the sensitivity of growth and  $f_N$  to partitioning and feedback parameters such as  $K_{sel}$  and  $a_X$ . The model is coded in Fortran 77 and will be provided to anyone interested (please contact the authors). The code is voluminously commented; the output is pseudo-graphic, providing a schematic printout of pools and flows to a plain ASCII terminal.

### 4.3.2 Applying the Model: Differences from Simple Functional Balance

This explicit carbon–nitrogen pool model (CN model, or CN) has been applied to a few illustrative cases (Fig. 4.4). These are (1) a base case with the same physiology as that used in the FB model above; (2) the same, but with a developmental limit,  $RGR_{max}=0.15$  per day; (3) doubled  $p^*$ , as would be the case if atmospheric  $CO_2$  approximately doubled. The other parameters are similar to the other simulations here: shoot leaf fraction  $\alpha_L=0.55$ ; root:shoot ratio  $r=0.4$ ; external solution concentration of nitrate  $c_e=100$  mmol  $m^{-3}$  (100  $\mu M$ ); uptake Michaelis constant  $K_m=30$  mmol  $m^{-3}$ ; biosynthetic efficiency is 0.77; cost of nitrate reduction  $c_N=6$  g carbohydrate  $g^{-1}$  N; saturation of photosynthetic N utility given with  $f_{N,sat}=0.03$  g N  $g^{-1}$  dry matter;  $p^*=15.3$  g carbohydrate  $g^{-1}$  N day $^{-1}$ ; fresh mass/dry mass ratio=4; free nitrate concentration in roots in base case=12.5 mM; repression parameter for uptake  $a_U=100$  g reduced N  $g^{-1}$  fresh mass; repression parameter for xylem loading  $a_{XL}=500$  g N  $g^{-1}$  fresh mass; recycling ratio in base case=0.33;  $\Delta\psi=0.1$  MPa;  $a_{PS}=5.19$  in the CN model, to give a fractional expression of photosynthesis equal to  $1/1.3=0.77$  in the base case. For N incorporation into new root growth, the parameter  $K_{sel}$  is set to 0.01, making the fraction N in new tissue fairly sensitive to the reduced-N:CH balance in the root.

Several features immediately distinguish the CN model from the simple functional balance model. Most notably, there is no optimal  $V_{max}$  when expressed as unrepressed value,  $V_{max}^0$  –  $RGR$  increases smoothly toward an asymptote, and never decreases (Fig. 4.4A, top row of graphs). Even as  $V_{max}^0$  grows very large, the buildup of reduced N (RN) in the root represses  $V_{max}$  (Eq. 4.7) and forces its decline. The effect is shown in Fig. 4.4C for all three physiological constitutions modeled. The modest repression of root growth at high N availability (Fig. 4.4C, bottom row) acts to further limit N uptake. This consequently limits the associated reduction costs and tissue N buildup. In the shoot, the benefit of increased N is progressively but not inordinately cut by the inefficient partitioning of N (the saturation of photosynthetic rate, as  $f_{N,s}$  increases; Fig. 4.4B, middle row of graphs). Thus, increased N availability – achieved either by high external concentration or by high uptake capacity as  $V_{max}^0$  – again gives *no* optimal value of uptake capacity as  $V_{max}^0$ . The observed control of uptake capacity, particularly to low values, must originate in selection on some traits coupled to nutrition, such as the cation–anion balance that might be adversely affected at high N uptake. Even more likely is the rising



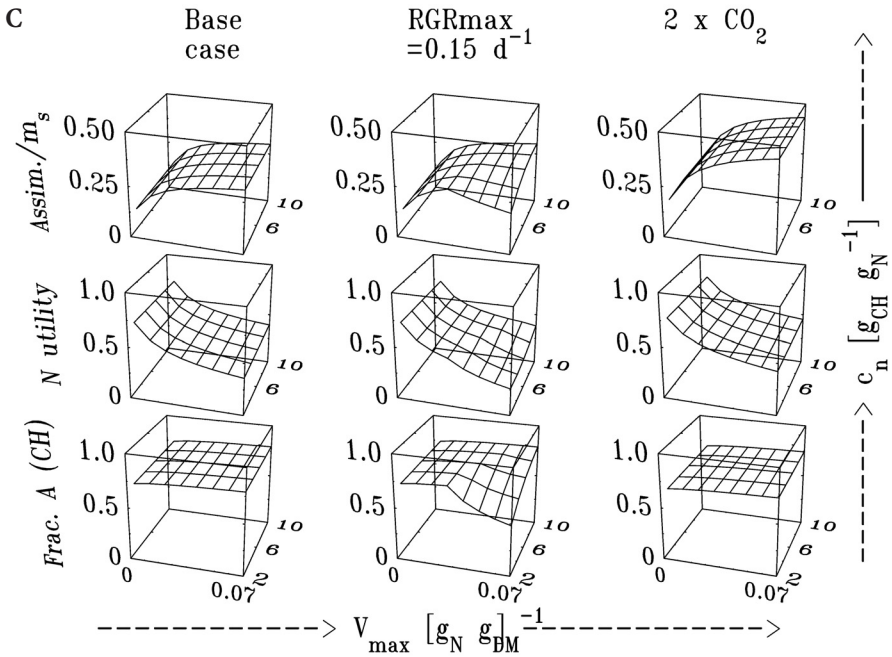


Fig. 4.4A–C. Predictions of the CN model that resolves internal metabolite pools, for a base-case physiology (described in the text); the same physiology with a developmental limitation on  $RGR$ ; and increased photosynthetic N-use efficiency. Responses to combinations of fundamental (unrepressed) uptake capacity ( $V_{max}^0$ ) and N-reduction cost are shown as **A** relative growth rate ( $RGR$ , per day) and in-shoot concentrations of free carbohydrate ( $[CH]_{shoot}$ , g g<sup>-1</sup> dry matter) and free reduced-N compounds ( $[RN]_{shoot}$ , predominantly amino acids); **B** shoot total-N content ( $f_{N,shoot}$ , mass fraction), fraction of maximal N uptake ( $Frac. uptake$ , relative to fully expressed capacity), and root:shoot ratio; **C** photosynthetic carbon assimilation per unit mass of shoot ( $Assim./m_s$ , g carbohydrate g<sup>-1</sup> dry mass day<sup>-1</sup>), fraction of maximal photosynthetic N utility ( $N utility$ , unitless, cf. relative to assimilation linearly proportional to  $f_N$ ), and fraction of maximal photosynthesis not repressed by carbohydrate accumulation [ $Frac. A (CH)$ , unitless].  $CH$  Carbohydrates,  $DM$  dry matter

risk of herbivory at high N and associated high water content (Sect. 4.3.3, below). In our view, the problem of explaining uptake regulation remains open. Second, there is a clear signal of developmental limitation (finite  $RGR_{max}$ ; middle column of graphs), as a sharp rise in both tissue  $CH$  and reduced-N contents as N availability rises. With such growth limitation, the root:shoot ratio is predicted to become insensitive to N at high N availability; this may or may not be realistic.

Other behavior simulated in the model often parallels that in the simple FB model. In all three cases,  $RGR$  initially rises in proportion to the square root of N availability (expressed as  $V_{max}^0$ ). It also increases closely as the square root

of photosynthetic utility – that is, modeled  $RGR$  is about 1.4-fold greater when  $p^*$  is doubled. This increase is maintained at all values of  $V_{\max}^0$  and  $c_n$ . Shoot  $CH$  increases notably because of higher photosynthetic rates, while reduced  $N$  is depleted by faster growth; thus, the repression of photosynthesis by  $CH$  increases, while the saturation of photosynthesis by  $RN$  is relieved. The effect of high  $N$ -reduction cost,  $c_N$ , is modest in all cases, with no more than a 10% reduction of  $RGR$  at  $c_N=10$  relative to  $c_N=0$ ;  $N$  reduction is only a moderate fraction of the energy budget.

Interestingly, the simulated shoot  $CH$  content (Fig. 4.4A, middle row) remains fairly stable as  $V_{\max}$  rises, and so therefore does the fractional repression of photosynthesis by  $CH$  buildup (Fig. 4.4B, bottom row). Simply, high  $N$  enables more  $CH$  production, but in almost the same proportion it increases the consumption of  $CH$  in tissue growth. Shoot  $RN$  content,  $N_s^r$ , rises initially as the square root of  $V_{\max}$ , as in the FB model. It becomes flatter yet at high  $V_{\max}^0$ , as ‘excess’ uptake is repressed.

## 4.4 Additional Questions: Stress, Root Turnover, Low Set Points of Woody Plants

### 4.4.1 Role of Root Lifetime

Chapter 8 (this Vol.) treats a number of the many interesting ways in which root turnover affects growth and nutrient content. Root turnover patterns vary among species and among broad functional groups (Gill and Jackson 2000). The selection pressures favoring faster turnover may include the danger of being parasitized (Aiken and Smucker 1996). Relevant to the current topic is how root turnover affects responses of nutrient uptake to photosynthetic nutrient utility  $p^*$  and to achieved growth rate. In the simplest accounting, turnover represents a capital cost over and above the initial construction costs of the root system (Gutschick 1987; Eissenstat 1992; Comas et al. 2000; Eissenstat et al. 2000; Chap. 8, this Vol.). It therefore inflates the metabolic cost of operating roots. This cost is not incurred per mass of nutrient, so that it is not appropriate to incorporate it into the cost  $c_n$  used above. The cost of turnover resembles the cost of supporting mycorrhizal tissue that is more metabolically active than the bulk of root mass. We have published (BassiriRad et al. 2000) an expanded version of the functional balance model that accounts for mycorrhizal activity, and this version is appropriate for exploring how turnover may affect uptake responsiveness to  $p^*$  and growth rate.

High metabolic activity, such as from high turnover, ‘burns off’ carbohydrates and makes  $f_N$  rise (ibid.). It thus can accentuate sensitivity of uptake to the  $p^*$  and growth rate. However, dilution of this high metabolic activity into a

base of low-metabolism, long-lived roots would correspondingly dilute these changes in uptake sensitivity. Thus, we have not provided simulations of turnover, which can occur in a wide range of rates, fractions of the root system, and costs. We estimate that the effects of turnover may be related more strongly to reducing the local depletion of nutrients in the rhizosphere. Improved access to undepleted soil regions then makes the root kinetic parameters, especially  $V_{\max}$ , more important determinants of uptake rate, as seen in our model (BassiriRad et al. 2000, Fig. 3 therein, using mathematical approximations developed by Gutschick and Kay 1995).

#### 4.4.2 Effects of Water Stress and Salinity

Water stress has at least three effects that are very relevant to the topic of this chapter. First, it reduces growth rates, particularly leaf expansion rates (Granier and Tardieu 1999). It thus acts as a reduction in  $RGR_{\max}$ , and is expected to magnify the downregulation of uptake. It is not yet clear if nutrient uptake at the roots responds directly to stress signals such as ABA (Goldbach et al. 1975; Roberts and Snowman 2000); it may be that downregulation is a response to growth repression with accumulation of reduced N, as in our model. Second, it reduces nutrient availability in the root zone, and thus decreases uptake rates. Third, water stress reduces stomatal conductance. This induces a lowering of leaf-internal  $\text{CO}_2$  ( $C_i$ ) and thus of  $p^*$ , as discussed in the first section of this chapter. Our models in any form predict that lower  $p^*$  will increase the tissue nutrient content,  $f_N$ , and consequently induce additional downregulation of uptake as  $V_{\max}$ . The two effects of stress are not readily separated, except with a simultaneous change in  $\text{CO}_2$  that can restore  $p^*$  under water stress while leaf and whole-plant growth remains repressed. We do not yet have experimental data for experiments in which  $\text{CO}_2$  partial pressure was regulated to control growth repression independently of  $p^*$ , nor in which all the relevant variables, including  $p^*$ ,  $C_i$ ,  $f_N$ , and  $V_{\max}$ , were measured. We look forward to the challenge of such results to interpret with our model. A distinct challenge is interpreting or predicting patterns of recovery from stress. BassiriRad et al. (1999) found contrasting patterns among desert species in N uptake following pulses of water availability. Our model, currently a steady-state model, is not directly amenable to predicting regulation under these conditions, but its extension with resolution of internal N and C pools might be useful.

Salinity stress, like water stress, initially has but minor effects on leaf photosynthetic capacity (Munns and Termaat 1986). Its major effect is on leaf life span and on leaf expansion rate, which are decreasing functions of soil salinity. Thus, an increasing fraction of leaves are senescent or dying. In our model, this acts as a reduction in  $p^*$  averaged over the plant, and one expects a rise in  $f_n$  to accompany a decrease in growth rate as  $RGR$ . This is seen in some exper-

iments in which N fertilization effects are not confounding (e.g., Zidan 1992). Direct effects of anions in salts upon uptake, as by competitive uptake, have the opposite effect of reducing uptake and  $f_n$ , of course.

#### 4.4.3 Why Is Uptake so Low in Some Species?

Some species, particularly woody species, have significantly lower uptake rates than herbaceous species (mostly ruderals) in the same physical location. One must assume that the divergence in uptake rates represents evolutionarily stable strategies of the co-occurring species (Maynard Smith and Price 1973; example of application to plant growth: Vincent and Vincent 1996). Nonetheless, for the low-uptake species, one must ask why the evolved set point of uptake is so low. More significant for the current inquiry in this chapter and for global-change studies is whether a low set point indicates the existence of internal controls that differ fundamentally from those we have considered here. That is, under changes in atmospheric  $\text{CO}_2$ , will woody plants alter their  $V_{\max}$  very differently from herbaceous plants? Some surveys have been made by BassiriRad et al. (2000) on this topic.

Our basic model of functional balance does not predict optimal  $V_{\max}$  directly. Nonetheless, our model with  $V_{\max}$  adjusted to find its optimal value would likely predict a nearly universal curve among species, if basic physiological factors such as  $p^*$  are shared among species. Woody plants do have moderately lower  $p^*$  than herbs (lower photosynthetic rates per unit leaf area, and not much lower N content per unit leaf area). However, the lower value is insufficient to explain the much lower values of  $V_{\max}$ . We must seek explanations in the model that is expanded to resolve internal N and C pools. Several contributing factors are plausible, each of which would generate selection pressure for altered kinetic parameters. First, risks of herbivory rise with higher N content (Letourneau 1997; see also Hartley and Jones 1997 for some qualifications about this relationship). Second, high water content may be needed for high soluble protein content and high photosynthetic capacity (Roderick et al. 1999), and this may also correlate with higher risk of herbivory. Third, woody plants may often exist at climax with low N-mineralization rates relative to demand, and with poorly diffusible ammonium as the dominant form of N. Thus, they operate near the limit of zero concentration at the root surface, which gives minimal effect of  $V_{\max}$  on uptake as well as low  $f_N$ . The first two contributing factors can be expressed in the CN model naturally by setting  $f_N$ , etc., in a base case. One obtains predicted responses, but one does lose some universality, in that base values of  $f_N$  (thus, of  $V_{\max}$  and other physiological parameters) are not optimized, but rather species-specific suboptimal values. The third factor can be expressed in a soil+plant model that includes diffusion in soil. The patterns of response become specific at least to the levels of functional group of plant and of soil type. This may be inescapable.

## 4.5 Conclusions

The trends in  $V_{\max}$  that our models predict are realistic and might guide research into plant responses to new environments that develop with global change. However, the predictions are not universal; different species and ecotypes show variation in their responses. We propose that the variation arises from selection pressures unique to different seasonal patterns of nutrient availability, or to herbivory risks, etc. Some of these formative patterns, such as seasonal nutrient flushes, might be incorporated into the model if it were integrated over time for the whole season. We might then explain a significant fraction of the variation among plants of different functional types and successional status. Other patterns such as herbivory risk are likely to be notably more difficult to account for.

Internal N and carbohydrate pools are being resolved in current experimental research on the biochemical and genetic regulatory basis of uptake regulation. These studies are intensive, and of necessity are focused on a few model species such as *Arabidopsis*. Our models, expanded to resolve a limited number of these internal pools, may offer simpler if somewhat less accurate prediction of uptake responses from a few biochemical assays. These predictions would thus be based on mechanisms specific to species and genotypes. Nonetheless, they would contain implicitly the complexities in physiology, ecology, and evolution for the species, without the need to understand patterns among all species at once. The models thus might be useful to predict responses of some key species that dominate biomass in some ecosystems, or that act as indicators for global change.

## 4.6 Summary

Nitrogen availability is a well-known controlling factor for plant growth. An earlier model of functional balance between the root and shoot offered an explanation of plant relative growth rate in terms of nutrient uptake rate, photosynthetic nitrogen-use efficiency (a notable function of  $\text{CO}_2$  availability), biosynthetic efficiency, and allocation patterns among roots, stems, and leaves. Nitrogen content was determined by functional balance and was not independently adjustable; its responses to environmental factors (concentration of N compounds in soil solution, etc.) were clearly fixed. However, this model left the uptake capacity for nitrogen itself undetermined, having a virtually unconstrained set point, determined genetically. It also presented a dilemma in defining optimal allocation patterns. In this chapter, we offer an expansion of the functional balance model, aimed at explaining how controls over N uptake, allocation, and use in photosynthesis – hence, plant growth –

are exerted via intermediate pools of reduced N and carbohydrates, as well as more detailed bioenergetic costs of their transformations. New physiological parameters are defined for the controls over pool sizes and fluxes; these parameters should be more closely related to identifiable biochemical processes and their genetic bases than are the broader allocation ratios in the original model. We also consider that growth rate may be internally limited by meristem number and developmental rates; this limit affects N uptake and allocation in unique quantitative patterns. New questions are then posed about the variable patterns of performance among diverse plant species, particularly about the role of root lifetime and water stress, and about the occurrence of very low N-uptake capacities in many species.

## Appendix: Definitions of Terms and Symbols

Terms and symbols in the Appendix are given in the text and are detailed in a computer model available on the website: <http://biology-web.nmsu.edu/vince>.

$\alpha_L$	fraction of shoot mass as leaves
$\beta$	conversion efficiency of raw photosynthate into biomass
$A$	carbon assimilation rate
$A^0$	maximal (unrepressed) assimilation rate
$A_{\text{plant}}$	whole-plant photosynthetic rate
$a_U$	parameter for nitrate uptake repression by accumulated reduced N in root
$a_{XL}$	repression parameter for xylem loading
$a_{PS}$	repression parameter for photosynthesis (CN model only)
$CH$	free carbohydrate
CN	carbon–nitrogen pool model
$c_e$	concentration of nutrient external to root
$c_n$	cost of nutrient acquired per unit mass
$C_r$	nonstructural carbohydrate in roots
$C_s$	nonstructural carbohydrate in shoots
DM	dry matter
FB	functional balance model
$f_C$	nominal whole-plant molar concentration of nonstructural carbohydrates
$f_n$	tissue nutrient content, as mass fraction
$\tilde{f}_n$	fractional nutrient concentration in new tissue
$f_N (f_{N,s}, f_{N,r})$	fractional nitrogen content (in shoot, in root)
$f_{N,s,sat}$	63 % saturation point for photosynthesis as $f_N$ in shoot increases

$G_r$	root growth rate
$G_s$	shoot growth rate
$I_{C,r}$	incorporation, carbohydrates into roots
$I_{C,s}$	incorporation, carbohydrates into shoots
$I_{N,r}$	incorporation, nitrogen into roots
$I_{N,s}$	incorporation, nitrogen into shoots
$K_e$	Michaelis parameter in growth response to whole-plant non-structural carbohydrate
$K_{sel,RG}$	selectivity parameter for carbohydrate over reduced-N incorporation in root growth
$K_{PN}$	selectivity parameter for loading <i>CH</i> vs. reduced N into phloem in the shoot
$k_C$	parameter for repression of photosynthesis by carbohydrate buildup
$k_{RG}$	mass-action rate constant for root growth
$k_{SG}$	mass-action rate constant for shoot growth
$L_C$	loading of phloem to circulate carbohydrates to roots
$L_N$	loading of phloem to recycle N
$m_r$	mass of root
$m_s$	mass of shoot
$\dot{m}^{pl}$	photosynthesis-limited growth rate
$\dot{m}^{ul}$	uptake-limited plant growth rate
$N_r^o$	oxidized nitrogen (nitrate) in root
$N_r^r$	reduced nitrogen in root
$N_s^r$	reduced nitrogen in shoot
$p^*$	nutrient-use efficiency (efficacy) in photosynthesis; photosynthetic utility
$P_{LM}$	photosynthetic rate per unit mass tissue
$R_{NR}$	rate of nitrate reduction in roots
$RGR$	relative growth rate (increase in biomass per unit time)
$RGR_{max}$	maximum RGR
$U$	uptake rate of the whole plant
$V_{max}$	maximal uptake velocity per mass of roots
$V_{max}^0$	fully unrepressed $V_{max}$
$V_{C,max}$	maximum carboxylation capacity in photosynthesis
$v$	achieved rate of uptake per mass of roots

## References

- Aikens RM, Smucker AJM (1996) Root system regulation of whole plant growth. *Annu Rev Phytopathol* 34:325–346
- BassiriRad H, Tremmel DC, Virginia RA, Reynolds JF, deSoyza AG, Brunell MH (1999) Short-term patterns in water and nitrogen acquisition by two desert shrubs following a simulated summer rain. *Plant Ecol* 145:27–36
- BassiriRad H, Gutschick VP, Lussenhop J (2000) Root system adjustments: regulation of plant nutrient uptake and growth responses to elevated CO<sub>2</sub>. *Oecologia* 126:305–320
- Bloom AJ, Chapin FS III, Mooney HA (1985) Resource limitation in plants – an economic analogy. *Annu Rev Ecol Syst* 16:363–392
- Boutin C, Harper JL (1991) A comparative study of the population dynamics of five species of *Veronica* in natural habitats. *J Ecol* 79:199–221
- Carroll BJ, McNeil DL, Gresshoff PM (1985) A supernodulation and nitrate-tolerant symbiotic soybean mutant. *Plant Physiol* 78:34–40
- Clements CR, Jones LHP, Hopper MJ (1979) Uptake of nitrogen from free-flowing nutrient solution: effect of termination and intermittent nitrate supplies. In: Hewitt EJ, Cutting CV (eds) *Nitrogen assimilation by plants*. Academic Press, London, pp 123–133
- Comas LH, Eissenstat DM, Lasko AN (2000) Assessing root death and root system dynamics in a study of grape canopy pruning. *New Phytol* 147:171–178
- Edwards GR, Crawley MJ (1999) Herbivores, seed banks and seedling recruitment in mesic grasslands. *J Ecol* 87:423–435
- Eissenstat DM (1992) Cost and benefit of constructing roots of small diameter. *J Plant Nutr* 15:763–782
- Eissenstat DM, Wells CE, Yanai RD, Whitbeck JL (2000) Building roots in a changing environment: implications for root longevity. *New Phytol* 147:33–42
- Farquhar GD, von Caemmerer S, Berry JA (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149:78–90
- Farrar JE, Jones DL (2000) The control of carbon acquisition by roots. *New Phytol* 147:43–53
- Gessler AM, Schultze S, Schrempp S, Rennenberg H (1998) Interaction of phloem-translocated amino compounds with nitrate uptake by roots of beech (*Fagus sylvatica*) seedlings. *J Exp Bot* 49:1529–1537
- Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytol* 147:13–31
- Glass ADM, Dunlop J (1979) The regulation of K<sup>+</sup> influx in excised barley roots. The relationships between K<sup>+</sup> influx and electrochemical potential differences. *Planta* 145:395–397
- Godwin DC, Blair GJ (1991) Phosphorous efficiency in pasture species. V. A comparison of white clover accessions. *Aust J Agric Res* 42:531–540
- Goldbach E, Goldbach H, Wagner H, Michael J (1975) Influence of N-deficiency on abscisic acid content of sunflowers. *Physiol Plant* 34:138–140
- Granier C, Tardieu F (1999) Water deficit and spatial pattern of leaf development. Variability of responses can be simulated using a simple model of leaf development. *Plant Physiol* 119:609–619
- Gutschick VP (1981) Evolved strategies of nitrogen acquisition in plants. *Am Nat* 118:607–637
- Gutschick VP (1987) *A functional biology of crop plants*. Croom Helm, London
- Gutschick VP (1997a) Nutrient-limited growth rates: roles of nutrient-use efficiency and of adaptations to increased uptake rate. *J Exp Bot* 44:41–51

- Gutschick VP (1997b) Photosynthesis, growth rate, and biomass allocation. In: Jackson LE (ed) *Ecology in agriculture*. Academic Press, San Diego, pp 39–78
- Gutschick VP (1999) Biotic and abiotic consequences of differences in leaf structure. *New Phytol* 143:3–18
- Gutschick VP, Kay LE (1995) Nutrient-limited growth rates: quantitative benefits of stress responses and some aspects of regulation. *J Exp Bot* 46:995–1009
- Hartley S, Jones CG (1997) Plant chemistry and herbivory, or why the world is green. In: Crawley MJ (ed) *Plant ecology*, 2nd edn. Blackwell, Oxford, pp 284–324
- Jackson LE, Koch GW (1997) The ecophysiology of crops and their wild relatives. In: Jackson LE (ed) *Ecology in agriculture*. Academic Press, San Diego, pp 3–37
- King BJ, Siddiqi MY, Glass ADM (1992) Studies of the uptake of nitrate in barley. V. Estimates of root cytoplasmic nitrate concentration using nitrate reductase activity – implications for nitrate influx. *Plant Physiol* 99:1582–1589
- Kronzucker HJ, Siddiqi MY, Glass ADM (1995) Compartmentation and flux characteristics of ammonium in spruce. *Planta* 196:691–698
- Le Bot J, Adamowicz S, Robin P (1998) Modelling plant nutrition of horticultural crops: a review. *Sci Hort* 74:47–82
- Letourneau DK (1997) Plant-arthropod interactions in agroecosystems. In: Jackson LE (ed) *Ecology in agriculture*. Academic Press, San Diego, pp 239–290
- Maynard Smith J, Price GR (1973) The logic of animal conflict. *Nature* 246:15–18
- Morcuende R, Krapp A, Hurry V, Stitt M (1998) Sucrose feeding leads to changes in the rates of alpha-oxoglutarate synthesis and increased synthesis of a wide spectrum of amino acids in tobacco leaves. *Planta* 206:394–409
- Munns R, Termaat A (1986) Whole-plant responses to salinity. *Aust J Plant Physiol* 13:143–160
- Nable RO, Lance RCM, Cartwright B (1990) Uptake of boron and silicon by barley genotypes with differing susceptibilities to boron toxicity. *Ann Bot* 66:83–90
- Penuelas J, Matamala R (1990) Changes in N and S leaf content, stomatal density and specific leaf area of 14 plant species during the last three centuries of CO<sub>2</sub> increase. *J Exp Bot* 41:1119–1124
- Peterson AG, Ball JT, Luo Y, Field CB, Reich PB, Curtis PS, Griffin KL, Gunderson CA, Norby RJ, Tissue DT, Forstreuter M, Rey A, Vogel CS, CMEAL Participants (1999) The photosynthesis–leaf nitrogen relationship at ambient and elevated atmospheric carbon dioxide: a meta-analysis. *Global Change Biol* 5:331–346
- Poorter H, Remkes C (1990) Leaf area ratio and net assimilation ratio of 24 wild species differing in relative growth rate. *Oecologia* 83:553–559
- Roberts SK, Snowman BN (2000) The effects of ABA on channel-mediated K<sup>+</sup> transport across higher plants roots. *J Exp Bot* 51:1585–1594
- Roderick ML, Berry SL, Noble IR (1999) The relationship between leaf composition and morphology at elevated CO<sub>2</sub> concentrations. *New Phytol* 143:63–72
- Romera FJ, Alcantara E, de la Guardia MD (1992) Effects of bicarbonate, phosphate and high pH on the reducing capacity of Fe-deficient sunflower and cucumber plants. *J Plant Nutr* 15:1519–1530
- Schmidke I, Kruger C, Frommichen R, Scholz G, Stephan UW (1999) Phloem loading and transport characteristics of iron in interaction with plant-endogenous ligands in castor bean seedlings. *Physiol Plant* 106:82–89
- Siddiqi MY, Glass ADM (1987) Regulation of K<sup>+</sup> influx in barley: evidence for a direct control of influx by K<sup>+</sup> concentration in root cells. *J Exp Bot* 38:935–947
- Sinclair TR, Horie T (1989) Leaf nitrogen, photosynthesis, and crop radiation use efficiency: a review. *Crop Sci* 29:90–98
- Sivasankar S, Rothstein S, Oaks A (1997) Regulation of the accumulation and reduction of nitrate by nitrogen and carbon metabolites in maize seedlings. *Plant Physiol* 114:583–589

- Stenseth NC, Maynard Smith J (1984) Coevolution in ecosystems: Red Queen or stasis? *Evolution* 38:870–880
- Tardieu F, Granier C (2000) Quantitative analysis of cell division in leaves: methods, developmental patterns and effects of environmental conditions. *Plant Mol Biol* 43:555–567
- Vincent TLS, Vincent TL (1996) Using the ESS maximum principle to explore root-shoot allocation, competition and coexistence. *J Theor Biol* 180:111–120
- Youssefi F, Brown PH, Weinbaum SA (1999) Regulation of nitrogen uptake at the whole plant level: a study in almond trees. *Am Soc Hortic Sci* 9:598–600
- Zerihun A, McKenzie BA, Morton JD (1998) Photosynthate costs associated with the utilization of different nitrogen-forms: influence on the carbon balance of plants and shoot-root biomass partitioning. *New Phytol* 138:1–11
- Zerihun A, Gutschick VP, BassiriRad H (2000) Compensatory roles of nitrogen uptake and photosynthetic N-use efficiency in determining plant growth response to elevated CO<sub>2</sub>: evaluation using a functional balance model. *Ann Bot* 86:723–730
- Zidan I, Shaviv A, Ravina I, Neumann PM (1992) Does salinity inhibit maize leaf growth by reducing tissue concentrations of essential mineral nutrients? *J Plant Nutr* 15:1407–1419