

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 capacities (per mass of root, v , or of the whole plant, v_{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 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, 1997, 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 over-expression of nontoxic 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 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 CO₂. 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, CO₂, 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_{\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_{\max} and r values by fixing either V_{\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_{\max} should be infinity: incremental gains in relative growth rate (*RGR*) continue, if at smaller rates, for any increase in V_{\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