Compensatory Changes in the Partitioning of Dry Matter in Relation to Nitrogen Uptake and Optimal Variations in Growth

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ABSTRACT

Equations are derived relating relative growth rate (RGR) to root:shoot ratio, root length, nitrogen inflow rate, leaf area, photosynthesis and carbon and nitrogen concentrations in the plant. The extents to which changes in specific root length and root:shoot ratio can compensate for the effects of low N availability upon RGR are examined. Such responses could have several compensatory functions: maximizing RGR; maintaining growth in which the activities of root and shoot limit RGR equally; and maximizing the efficiency of increase in RGR.

Key words: Growth, nitrogen, carbon, dry matter, partitioning, root:shoot ratio, relative growth rate.

INTRODUCTION

The partitioning of biomass between and within the root and shoot systems of a plant can be changed significantly by environmental conditions. Partitioning between roots and shoot varies according to the availabilities of nutrients, water and light, above- and below-ground temperatures, and physical disturbance. Striking illustrations of the plasticity of growth within the organs of a single plant are provided by the localized branching of roots in a region of high nutrient availability (Drew and Saker, 1975) and variations in the size and shape of leaves caused by uneven distributions of light in a canopy (Fitter and Hay, 1981, p. 53). Further, different species exhibit degrees of morphological plasticity that can be related to their life-histories and to the potential productivity of their environments (Hunt and Burnett, 1973; Hunt and Nicholls, 1986).

Such changes in partitioning have been interpreted as allowing a plant to compensate for potentially growth-limiting conditions. Experiments have, however, been unable to differentiate in this respect between causes and effects, nor able to suggest for what condition(s) in the plant these mechanisms have evolved to compensate. Consequently, the mechanistic interactions between morphological changes and the growth of the plant remain obscure. It is the aim of this paper to address this problem using a simple mathematical model. No attempt is made to model growth rigorously. The model is used only to illustrate relationships between parameters and to examine possible consequences of changes in these relationships which could reveal how they might act as compensatory mechanisms.

THE MODEL

The environmental variable that is considered is nitrogen (N) availability; this is the major factor limiting the growth of plants in many natural and agricultural environments. The effects of nitrogen availability are examined via its influence upon the rate of net N uptake per unit root length, i.e. inflow rate, since the depletion of a nutrient from soil

is related primarily to the length of the root system rather than its mass (Brewster and Tinker, 1972). Variations in inflow determine the amount of N that the plant can potentially use for producing more dry matter. In practice, such variations could arise from changes in the absolute or relative concentrations of ammonium and nitrate in the soil solution, the amount of root having access to these ions, the extent of inter-root competition or the plant's demand for N (Robinson, 1986).

The amount of N absorbed daily by a unit mass of root is given by the product IL if I is in g cm^{-1} d^{-1} (symbols are defined in Table 1). If the root:shoot ratio is known, the amount of N absorbed by a unit mass of the whole plant is $IL/[(1/K)+1]$. This

TABLE 1. *Definitions of symbols*

Symbol	Definition	Units
A	Specific leaf area (leaf area per unit leaf d.wt)	cm^2 g^{-1}
C	Total carbon concn in dry matter	(g carbon) g^{-1}
F	Net rate of C assimilation	(g carbon) cm^{-2} d^{-1}
I	Net rate of N inflow	(g nitrogen) cm^{-1} d^{-1} or (mol nitrogen) cm^{-1} s^{-1}
K	Root:shoot d. wt ratio	—
L	Specific root length (root length per unit root d. wt)	cm g^{-1}
N	Total nitrogen concn in dry matter	(g nitrogen) g^{-1}
R	Relative growth rate	d^{-1}

amount of N can be equated to an increment of dry matter produced by the existing biomass using the concentration of N in the dry matter (Agren, 1985), assuming that any new growth uses N absorbed from the soil and not N re-translocated from mature or senescent tissues. Such an increment is, by the conventional definition in plant growth analysis, a relative growth rate (RGR; see Hunt, 1982). Therefore, the *potential* RGR of the plant in terms of the amount of N available for growth is

$$R(N) = IL/[(N/K)+N]. \tag{1}$$

An analogous equation can be derived defining the potential RGR as a function of the amount of carbon (C) assimilated by the plant:

$$R(C) = FA/[(CK)+C]. \tag{2}$$

The actual RGR is defined by the smaller of the values calculated by these equations. When $R(N) = R(C)$, RGR is limited equally by rates of N inflow and C assimilation (see Tilman, 1982, p. 35). When this condition obtains, root:shoot ratio is defined by

$$K = FAN/ILC, \tag{3}$$

which is equivalent to the relationship derived by Davidson (1969).

Using these equations and the parameter values listed in Table 2, the interactions between N inflow rate, biomass partitioning (defined in terms of K and L) and biomass production (R) can be examined.

RESULTS AND DISCUSSION

Relationships between parameters

The RGRs predicted by the model for a N inflow rate of 10 pmol cm^{-1} s^{-1} (see Table 2) were about five times higher than those measured for plants growing under favourable environmental conditions (Grime and Hunt, 1975). This is because eqn (1) implies that

TABLE 2. *Parameter values. Except where stated otherwise, units are as given in Table* 1

Parameter	Value(s)	Notes and references
A	500	Assuming a leaf thickness of 0·02 cm (Charles-Edwards 1981, p. 42) and a water content of 90% (Fitter and Hay, 1981, p. 118)
C	0·4	Charles-Edwards (1979)
F	1·89 mg cm^{-2} d^{-1}	Charles-Edwards (1981, p.42)
I	0·1–10 pmol cm s^{-1}	Representing low (Robinson and Rorison, 1985) and high (Robinson, 1986) N availabilities, respectively
K	0·1–1·0	Realistic range (Hunt and Burnett, 1973)
	0·01–100	Range used for calculations
L	10–80 cm mg^{-1}	Realistic range (Fitter, 1985)
	10–100 cm mg^{-1}	Range used for calculations
N	0·03	Pate and Layzell (1981)

all of the root system absorbs N at a single rate. In practice, high inflow rates are restricted to only certain parts of the root system by spatial heterogeneity of available nutrients in the soil, by ontogenetic changes in the capacity of a root to absorb nutrients, and by inter-root competition (Robinson, 1986). Similarly, self-shading by leaves and the production of non-photosynthetic tissues reduce the theoretical rate of C assimilation in the shoot system. The five-fold difference between theoretical and experimentally-measured RGRs suggests that only approx. 20 per cent of the root mass is needed to supply enough N to satisfy the plant's demand, provided that this fraction can attain a high rate of N inflow, 10 pmol cm^{-1} s^{-1}, for example. This is comparable with Burns' (1980) conclusion that the N demands of many crops could be met if as little as 15 per cent of their root systems absorbed N at a maximal rate. To make the predicted RGRs comparable with those that have been measured experimentally, they were re-scaled by a factor of 0·2; RGRs predicted using a N inflow rate of 0·1 pmol cm^{-1} s^{-1} (see Table 2) were not, since they were not unrealistically high.

Representative relationships between specific root length and RGR are shown in Fig. 1 for different root:shoot ratios. For a constant root:shoot ratio, R is defined by a linear increase in specific root length until $R(N) = R(C)$, after which further increases in L have no effect upon RGR. For a given value of L, the maximum RGR attainable is that at which $R(N) = R(C)$. If K and L are allowed to vary freely, maximum RGRs occur at the points where $R(N) = R(C)$. The line joining these points, shown in Fig. 1, represents the 'optimal variation' (see Cowan, 1982) between L and K in the sense that no other combinations of these parameters can produce higher RGRs. To maintain R at a maximum value, therefore, variations in L and K must follow the optimal variation curve. A similar conclusion was reached by Tilman (1982, p. 33 *et seq.*). Note that the optimal variation curve is described mathematically by a rectangular hyperbola, $R = IL/[(ILC/FA)+N]$ but this expression masks the influence that K has upon R, as shown in Fig. 1.

The optimal variation curve for a N inflow rate of 0·1 pmol cm^{-1} s^{-1} is shown as the broken line in Fig. 1. In this case, the value of K needed to maintain R on the optimal variation curve is 100 times greater than that with a N inflow rate of 10 pmol cm^{-1} s^{-1}, for a given specific root length.

These relationships are emphasized in Fig. 2 in which isopleths of RGR are plotted as functions of L and K. Combinations of L and K lying to the left of the optimal variation curves cause RGR to be limited by N inflow rate; those to the right, limit RGR via C assimilation rate. Over the same range of specific root length, a reduction in I from 10 to 0·1 pmol cm^{-1} s^{-1} causes a 100-fold increase in the range of K needed to attain growth
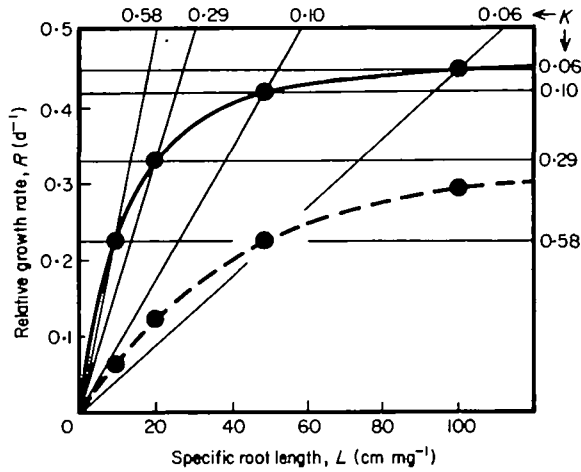
FIG. 1. Relationships between specific root length and RGR at various root:shoot ratios. Straight lines passing through the origin are derived from eqn (1), horizontal lines from eqn (2), for the same N inflow rate of 10 pmol cm^{-1} s^{-1}. Intersections of lines with the same value of K are denoted by closed circles. The solid curve joining these points represents the optimal variation between L and K. The broken curve is the optimal variation for a N inflow rate of 0·1 pmol cm^{-1} s^{-1}; values of K on this curve corresponding with the closed circles on the solid curve are, from left to right, 58, 29, 10 and 6.
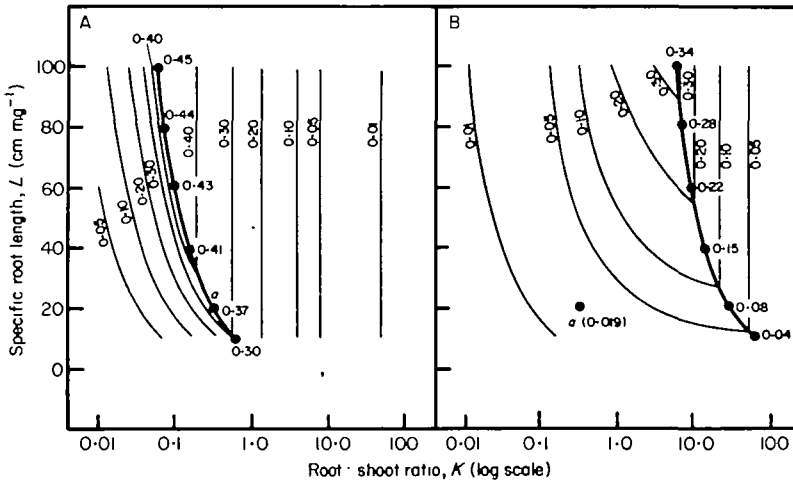

FIG. 2. A, Isopleths of RGR as a function of root:shoot ratio and specific root length for a N inflow rate of 10 pmol cm^{-1} s^{-1}. The bold curve represents the optimal variations between L and K. Numbers on this curve are RGRs at the points indicated by closed circles. Numbers on other curves are the RGRs represented by the curves. Point a defines the RGR (0·37 d^{-1}) of a plant in which $L = 20$ cm mg^{-1} and $K = 0·3$. B, As for A, but with a N inflow rate of 0·1 pmol cm^{-1} s^{-1}. The RGR at point a is 0·019 d^{-1}.

with optimal variation between L and K. Comparison of Fig. 2A with B shows that if other parameters remain constant, this reduction in N inflow rate decreases the potential RGR for any combination of L and K. For example, a plant having a specific root length of 20 cm mg^{-1} and a root:shoot ratio of 0·3 (as shown at point a in Fig. 2A) has a (re-scaled) RGR of 0·37 d^{-1}. This is the maximum RGR possible with this combination of parameters; the plant is growing with optimal variation between L and K. If the N

inflow rate in this plant was limited to 0·1 pmol cm^{-1} s^{-1}, RGR would be reduced to 0·019 d^{-1} (point *a* in Fig. 2B).

Compensatory responses

By how much could changes in specific root length and root:shoot ratio compensate for the reduction in RGR caused by a low N inflow rate in the example described above? Possible changes in these parameters are shown in Fig. 3. Within realistic limits, the greatest increase in RGR would occur if *K* and *L* increased to their maxima (point *d* in Fig. 3). An increase in *K* alone (*c*) leads to a smaller increase in RGR than does an increase in *L* alone (*b*). In this example, however, full compensation (i.e. an increase in
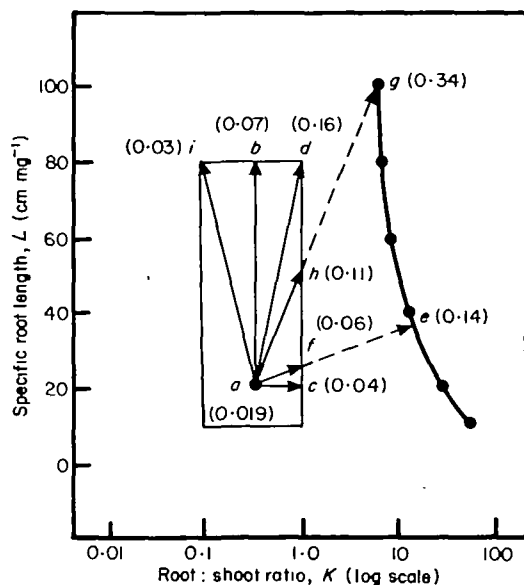

FIG. 3. Possible responses of *L* and *K*. Point *a* and the optimal variation curve are those shown in Fig. 2B. The rectangle represents the realistic limits of *L* and *K* (see Table 2). Trajectories of changes in *L* or *K* are shown as arrows, the letters *b-i* are points along these trajectories, and the numbers in parentheses are the RGRs at these points. *b*, Maximal increase in *L* only; *K* constant. *c*, Maximal increase in *K* only; *L* constant. *d*, Maximal increase in both *K* and *L*. *e*, 'Shortest route' to the optimal variation curve, but limited at *f*. *g*, Increases in *K* and *L* to an arbitrary maximum point on the optimal variation curve, but limited in *h*. *i*, Maximal increase in *L* and a decrease in *K* to its minimum value. (Note that the opposite response, maximum *K* and minimum *L*, would decrease RGR and so is not considered as a possible compensatory response).

RGR to 0·37 d^{-1}), could not be achieved without an increase in inflow rate. This could occur if the roots encountered a localized high concentration of N in the soil, but this itself is likely to be dependent upon appropriate changes in root morphology. Drew and Saker (1975) found that by such a response, a barley plant in which only a fraction of the root system was supplied with N could, after a temporary check, restore its growth rate to that attained by a plant receiving an unrestricted N supply.

An upper limit to the extent to which *L* can increase could be set by a high resistance to water flow along the root, which, according to the Poiseuille-Hagen equation (Newman, 1976), decreases with the fourth power of the radius of the conducting vessel, i.e. the xylem. This can be related directly to the radius of the root and, hence, inversely to its specific length (Fitter, 1985).

An upper limit to root:shoot ratio could be determined by the extent to which the acquisition of nutrients and water by the roots is offset by the respiratory load imposed by roots upon the shoot system (Schulze, 1983). A possible compensatory response in N-deficient plants could be, therefore, to restore growth with optimal variation in order to resolve this conflict; this would not necessarily be the same, initially, as restoring the maximum possible RGR. This type of response could account for the periodic oscillations in root:shoot ratio (Szaniawski, 1985) and nitrate uptake rate (Tolley and Raper, 1985) which have been measured experimentally. Such responses (*e* and *g* in Fig. 3) are, in this example, limited to their maximum realistic values (*f* and *h*, respectively). The RGRs attained at *f* and *h* are less than those achieved by response *d* (see above) and do not restore growth with optimal variation, but this should not rule out the possibility that such responses could occur.

Hunt and Nicholls (1986) suggested that the 'efficiency' of partitioning quantified on a 'return for effort' basis as the increase in RGR obtained for a change in dry matter partitioning has important implications for the survival of plants in habitats of potentially low productivity. For the present example, this can be calculated as the proportional increase in RGR achieved for a proportional change in specific root length and root:shoot ratio, using the expression

$$[R(x)/R(a)]/[L(x)K(x)/L(a)K(a)],$$

where *a* refers to the values of the parameter at point *a* in Fig. 3 and *x* refers to those at any of the points *b–i*. Table 3 shows that response *i* has the highest efficiency when quantified on this basis, but this is an unlikely response given the known facts about

TABLE 3. *Efficiences of the compensatory responses shown in Fig.* 3, *calculated as described in the text*

Response	Efficiency
b	0·97
c	0·63
d	0·63
e	0·12
f	0·63
g	0·19
h	0·63
i	1·14

the effects of nutrient deficiency upon root:shoot partitioning (see Hunt and Nicholls, 1986). *Response b is the most efficient of those which are likely to occur.* Moreover, there is a diminishing-returns relationship between the increase in RGR arising from an increase in *K*. This predicts that if such efficiency is important in allowing some plants to survive N-deficient conditions, they should maintain a constant root:shoot ratio at the expense of a variable specific root length. This prediction is supported by experimental evidence (Robinson and Rorison, 1985), although Hunt and Nicholls (1986) found that in a potentially slow-growing species subjected to nutrient deficiency, large changes in root:shoot partitioning could occur.

Another compensatory function that could involve growth responses is the homeostatic maintenance of nutrient concentrations or turgor in intracellular compartments The maintenance of N-containing solutes within a certain concentration range in the cytoplasm (Leigh and Wyn Jones, 1986) is likely to determine the extent to which *N* can vary. A decrease in the concentration of N in dry matter would decrease the plant's

demand for N (per unit biomass) and allow a higher RGR to be attained with the same inflow rate. Such a decrease in concentration occurs if N in intracellular storage pools is metabolized and used to produce dry matter when the plant is N-deficient (Barniex *et al.*, 1976), or if dry matter low in N (e.g. fibre) is produced. It is likely that changes in *N* act in conjunction with those in *I*, *L* and *K* that have been considered here.

CONCLUSIONS

It is suggested that responses of plants to N deficiency could have several different compensatory functions. These are: (1) to maximize RGR; (2) to maintain growth with optimal variation between and within various parts of the plant; and (3) to maximize the efficiency with which RGR is increased by any morphological adjustments. These may or may not be mutually exclusive, depending upon the species and the nature and degree of the 'stress' (see Hunt and Nicholls, 1986) that it experiences. The results of certain experiments support the possibility that these compensatory mechanisms occur in plants. More experiments are needed to test the wider applicability of the general predictions made here.

LITERATURE CITED

AGREN, G. I., 1985. Theory for the growth of plants derived from the nitrogen productivity concept. *Physiologia Plantarum* **64**, 17–28.

BARNIEX, A. J., JAMES, D. M., WATSON, E. F. and HEWITT, E. J., 1984. Some effects of nitrate abundance and starvation on metabolism and accumulation of nitrogen in barley (*Hordeum vulgare* L. cv. Sonja). *Planta* **162**, 469–76.

BREWSTER, J. L. and TINKER, P. B., 1972. Nutrient flow rates into roots. *Soils and Fertilizers* **35**, 355–59.

BURNS, I. G., 1980. Influence of the spatial distribution of nitrate on the uptake of N by plants: a review and a model for rooting depth. *Journal of Soil Science* **31**, 155–73.

CHARLES-EDWARDS, D. A., 1979. Photosynthesis and crop growth, pp. 111–64. In *Photosynthesis and Plant Development*, eds R. Marcelle, H. Clijsters and M. van Proucke, 376 pp. Junk, The Hague.

—— 1981. *The Mathematics of Photosynthesis and Productivity*, 127 pp. Academic Press, London.

COWAN, I. R., 1982. Regulation of water use in relation to carbon gain in higher plants, pp. 589–613. In *Encyclopedia of Plant Physiology, New Series*, vol. 12B, eds O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler. Springer-Verlag, Heidelberg.

DAVIDSON, R. L., 1969. Effects of soil nutrients and moisture on root/shoot ratios in *Lolium perenne* L. and *Trifolium repens* L. *Annals of Botany* **33**, 571–7.

DREW, M. C. and SAKER, L. R., 1975. Nutrient supply and the growth of the seminal root system in barley. II. Localized, compensatory increases in lateral root growth and rates of nitrate uptake when nitrate is restricted to only part of the root system. *Journal of Experimental Botany* **90**, 79–90.

FITTER, A. H., 1985. Functional significance of root morphology and root system architecture, pp. 87–106. In *Ecological Interactions in Soil*, eds A. H. Fitter, D. Atkinson, D. J. Read and M. B. Usher, Blackwell Scientific Publications, Oxford.

—— and HAY, R. K. M., 1981. *Environmental Physiology of Plants*, Academic Press, London.

GRIME, J. P. and HUNT, R., 1975. Relative growth rate: its range and adaptive significance in a local flora. *Journal of Ecology* **63**, 393–422.

HUNT, R., 1982. *Plant Growth Curves: The Functional Approach to Plant Growth Analysis*, 248 pp. Edward Arnold, London.

—— and BURNETT, J. A., 1973. The effects of light intensity and external potassium level on root/shoot ratio and rates of potassium uptake in perennial ryegrass (*Lolium perenne* L.). *Annals of Botany* **37**, 519–37.

—— and NICHOLLS, A. O., 1986. Stress and the coarse control of growth and root–shoot partitioning in herbaceous plants. *Oikos* **47** (in press).

LEIGH, R. A. and WYN JONES, R. G., 1986. Cellular compartmentation in plant nutrition: the selective cytoplasm and the promiscuous vacuole. *Advances in Plant Nutrition* **2**, 249–79.

NEWMAN, E. I. 1976. Water movement through root systems. *Philosophical Transactions of the Royal Society* B **273**, 463–78.

PATE, J. S. and LAYZELL, D. B., 1981. Carbon and nitrogen partitioning in the whole plant – a thesis based upon empirical modelling, pp. 94–134. In *Nitrogen and Carbon Metabolism*, ed. J. D. Bewley. Junk, The Hague.

ROBINSON, D., 1986. Limits to nutrient inflow rate in roots and root systems. *Physiologia Plantarum* (in press).
—— and RORISON, I. H., 1985. A quantitative analysis of the relationships between root distribution and nitrogen uptake from soil by two grass species. *Journal of Soil Science* **36**, 71–85.
SCHULZE, E.-D., 1983. Root–shoot interactions and plant life-forms. *Netherlands Journal of Agricultural Science* **31**, 291–303.
SZANIAWSKI, R. K., 1985. Homeostasis in cucumber plants during low temperature stress. *Physiologia Plantarum* **64**, 212–16.
TILMAN, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton.
TOLLEY, R. C. and RAPER, C. D., 1985. Cyclic variations in nitrogen uptake rate in soybean plants. *Plant Physiology* **78**, 320–22.