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Nutrient-limited growth rates: quantitative benefits of stress responses and some aspects of regulation

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Abstract

Young sunflower plants (*Helianthus annuus* L.) under stress of low nitrate or phosphate availability exhibited increases in root : shoot ratio and in kinetic parameters for uptake. They showed no significant changes in photosynthetic utilization of either nutrient. Increases in root : shoot ratio were achieved by early and persistent suppression of shoot growth, but not root growth. Affinity for phosphate uptake, $1/K_m$(P), increased with phosphate stress, as did affinity for nitrate uptake, $1/K_m$(N), with nitrate stress. Maximal uptake rate, V_{max}, for phosphate uptake increased with phosphorus stress; V_{max} for nitrate did not increase with nitrogen stress. Phosphate V_{max} was related strongly to root nutrient status. Decreases in V_{max} with plant age were not well explained by changes in age structure of roots. Estimated benefits of acclimatory changes in root : shoot ratio and uptake kinetics ranged up to 2-fold increases in relative growth rate, *RGR*. The relation of *RGR* to uptake physiology followed predictions of functional balance moderately well, with some systematic deviations. Analyses of *RGR* using growth models imply no significant growth benefit from regulating V_{max}, specifically, not from down-regulating it at high nutrient availability. Quantitative benefits of increases in root : shoot ratio and uptake parameters are predicted to be quite small under common conditions wherein nutrient concentrations are significantly depleted by uptake. The root : shoot response is estimated to confer the smallest benefit under non-depleting conditions and the largest benefit under depleting conditions. Even then, the absolute benefit is predicted to be small, possibly excepting the case of heterogeneous soils. Depleting and non-depleting conditions are addressed with very different experimental techniques. We note that a theoretical framework is lacking that spans both these cases, other than purely numerical formulations that are not readily interpreted.

Key words: Nutrient stress, nutrient uptake, nutrient use efficiency, relative growth rate, *Helianthus annuus*.

Introduction

Plants subjected to low external concentrations of nitrate or phosphate in the (soil) solution exhibit multiple stress responses. A number of these responses presumably act adaptively to maintain relative growth rate, *RGR*, approximately as high as possible. Particularly common are increases in root : shoot ratio, r (see, for example, Davidson, 1969; Ingestad and Lund, 1979; Kirschbaum *et al.*, 1992; Loneragan and Asher, 1967; Rufty *et al.*, 1984); in maximal velocity of uptake per unit root mass, V_{max} (Cogliatti and Clarkson, 1983; Drew *et al.*, 1984; Kochian and Lucas, 1982); and in the affinity of the uptake system, measured as the inverse of the Michaelis constant, $1/K_m$ (Drew *et al.*, 1984; Kochian and Lucas, 1982). Other responses may be involved, as outlined in Gutschick (1993).

Gutschick (1993) offered an analysis of the quantitative relationship between the set of putatively adaptive responses r, V_{max}, K_m, etc. and the relative growth rate. The analysis also proposed that tissue nutrient content, f_n, is not an independent response that amounts to adjusting nutrient-use efficiency. Rather, f_n can be determined largely by functional balance between roots acquiring nutrient and shoots using that nutrient to support the whole-plant photosynthetic rate.

The current paper extends the analysis of the stress responses in the same experiment to cover three inquiries. (1) What quantitative increase in *RGR* do the responses contribute? (2) Are the responses deployed at appropriate

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times and at appropriate stress levels to optimize the growth benefits? (3) How are the responses co-ordinated and regulated? The last inquiry is restricted here to more phenomenological levels, rather than the proximate, molecular signals involved in regulation such as reviewed by Hoff *et al.* (1994).

In our experiments, young sunflower plants (*Helianthus annuus* L.) were grown in seven different combinations of nitrate and phosphate concentrations maintained constant within practical limits by use of flowing nutrient solution. Plants achieved a range exceeding 2-fold in *RGR* by day 17, when they attained the stage of 3 to 5 leaf nodes. Plants showed 2-fold ranges in the responses of r and V_{max}; larger ranges were achieved in K_m. We obtained detailed time-courses (daily) of r by measuring growth components. Uptake parameters were obtained episodically on two dates. Values of V_{max} were measured by pulse labelling on two cohorts of replicates. Rough estimates of K_m were obtained on these dates by comparing V_{max} with uptake rates in ambient concentrations. Tissue nutrient contents were measured after harvesting.

Materials and methods

Methods

A more complete presentation of methods can be found in Gutschick (1993).

Plant material and growth conditions

Seeds of sunflower (*Helianthus annuus* L., open-pollinated cv. Giant Grey Stripe) were germinated in $CaSO_4$-saturated deionized water and were grown for 10 d, by which time their roots and shoots were sufficiently long to place in our growth apparatus (Kay and Gutschick, 1991). We selected 84 of 200 seedlings for uniformity in fresh weight and also in root : shoot ratio (non-destructive method described below). The selected plants were assigned randomly to seven different treatments of combined nitrate and phosphate concentrations (as potassium salts), imposed over a uniform background of the remaining nutrients (Table 1). A non-recirculating hydroponic system (Kay and Gutschick, 1991) delivered the solution for each treatment to 12 replicate plants. We adjusted flow rates daily to keep solution depletion by plants to 30% or less of inflow concentration. Each plant had separate solution inflow and outflow and aeration connections. Chambers were painted with white epoxy paint to eliminate solar heating of root zones. Carbonic acid–bicarbonate buffering by the vigorous airstream held solution pH in the range of 5.5 to 6. After transfer to treatments, plants grew for 17 d in a naturally-lit greenhouse in Los Alamos, New Mexico (lat. 36°N) during 25 September–12 October 1983. The photoperiod was 12 h. Clouds and shadows were absent 75% of the time, on average. Peak irradiance on plants was typically 1600 μmol m^{-2} s^{-1}. Daytime high temperature averaged 32 °C; night-time temperature was 20 °C.

Measurements of growth and physiology

Every morning at 9 to 10 a.m. local time we measured plant fresh weights and linear dimensions of all leaves. Fresh mass of each surface-dried, whole plant was measured on an automated electronic scale. Root volume, as fresh mass, was measured by displacement of $CaSO_4$-saturated distilled water. On days 7, 12, and 17 (end), 4 randomly selected plants from each treatment were harvested to determine both fresh and dry weights of separated roots and shoots. Dry mass/fresh mass ratios were used to convert fresh masses of plants measured on all days. Details are given in Appendix I.

On treatment days 12 and 17, we measured nitrate and phosphate uptake velocities at three times of day (10 a.m., 3 p.m., midnight) for the 4 plants to be harvested on day 17. Uptake velocity was determined by solution depletion multiplied by flow rate. Nitrate and phosphate concentrations were determined spectrophotometrically (Gutschick, 1993).

On days 12 and 17 we also measured V_{max} for both ions by pulse-labelling roots of intact plants in stirred, aerated nutrient solution spiked with $KH_2{}^{32}PO_4$ and $K^{15}NO_3$. Ten minute pulses were followed by 10 min chases. Phosphate uptake was measured on tissue digests by scintillation counting and nitrate uptake by mass spectrometry (Gutschick, 1993). Tissue digests were also used for determining total tissue N and P contents spectrophotometrically (Gutschick, 1993).

Leaf areas were estimated from daily measurements of lengths. Dry matter per leaf area was determined on harvested plants. The uptake affinity constant, K_m, was estimated roughly by comparing daily peak uptake rate, v_{peak}, at the low nutrient concentration during growth, c, with saturated uptake rate, V_{max}:

$$K_m \approx c \times \left(\frac{V_{max}}{V_{peak}} - 1 \right).$$

Further details are in Gutschick (1993) and in Appendix II. This method of estimating K_m is far less accurate than measuring depletion of concentration with stopped flow (Atkins and Gardner, 1977). However, the latter method could not be done on the tight experimental schedule.

Leaf photosynthetic rate per unit leaf mass, $P_{L,m}$, was inferred from the relationship $RGR = \beta P_{L,m} m_L / m_{total}$, where β is the conversion efficiency from photosynthate to dry matter, adjusted for maintenance respiration. A value of 0.6 was assumed. The values of total leaf mass, m_L, and total plant mass, m_{total}, were available by weighing.

Results

Rapid suppression of shoot growth that increases root : shoot ratio

Plants were transferred on day zero from saturated $CaSO_4$ solution used for germination to their specific nutrient treatments listed in Table 1. On as short a time scale as we could measure (1 d), low N or low P in the external solution led to a strong suppression of shoot relative growth rate, RGR_s, but not of root relative growth rate, RGR_r (Table 2). This response occurred before shoot gross nutrient status was significantly affected, implying that it is a direct response to external nutrient concentration. (The time t_r for tissue nutrient concentration, f_n, to relax from its initial value, f_n^0, according toward its final value, f_n^f, was fairly long, about 5 d. This estimate was obtained by fitting the empirical form $f_n = f_n^0 + (f_n^f - f_n^0)\exp[-t/t_r]$. Very similar estimates for t_r were

Table 1. *Composition of nutrient solutions*

Full details are given in Gutschick (1993).

	Phosphate and nitrate treatments						
	1	2	3	4	7	6	5
Nominal average concentration of NO_3^- (μM)	10	10	10	150	150	7	3
Nominal average concentration of PO_4 (μM)	0.1	0.2	0.2	1	3	3	3
	←P-stress series					N-stress series→	

Table 2. *Significant repression of relative growth rate of shoot* (RGR_s) *but not of root* (RGR_r) *by low external concentrations of nutrient*

Repression is evident from start of treatments (day 1) and continues, as evident in data from representative days 5 (with all 12 replicate plants) and 11 (8 replicate plants left). Each *RGR* is reported as mean ± standard deviation. *P* = statistical significance that RGR_s is less than RGR_s for high-nutrient treatment 7. Last column indicates the difference in RGR_s between indicated treatment and treatment 7 that is significant at $P=0.05$.

Day	Treatment	RGR_r	RGR_s	*P* for $RGR_s < RGR_s$ (treatment 7)	ΔRGR_s for $P=0.05$
P-stress series					
1	1	0.406 ± 0.129	0.082 ± 0.034	0.0000010	0.058
	2	0.349 ± 0.078	0.094 ± 0.024	0.00000036	0.053
	3	0.403 ± 0.081	0.075 ± 0.030	0.000000080	0.067
	4	0.371 ± 0.081	0.147 ± 0.052	0.19	—
	7	0.424 ± 0.173	0.162 ± 0.024	—	—
5	1	0.251 ± 0.054	0.087 ± 0.013	0.000013	0.021
	2	0.203 ± 0.026	0.090 ± 0.014	0.000053	0.017
	3	0.156 ± 0.036	0.081 ± 0.020	0.000018	0.024
	4	0.199 ± 0.029	0.106 ± 0.035	0.10	—
	7	0.211 ± 0.067	0.121 ± 0.018	—	—
11	1	0.155 ± 0.010	0.087 ± 0.016	0.0000000019	0.072
	2	0.158 ± 0.009	0.124 ± 0.016	0.0000018	0.035
	3	0.135 ± 0.020	0.127 ± 0.023	0.000068	0.027
	4	0.172 ± 0.026	0.162 ± 0.027	0.15	—
	7	0.174 ± 0.022	0.173 ± 0.010	—	—
N-stress series					
1	5	0.380 ± 0.088	0.116 ± 0.023	0.000071	0.029
	6	0.352 ± 0.079	0.106 ± 0.029	0.000031	0.036
5	5	0.214 ± 0.041	0.059 ± 0.059	0.0000000029	0.048
	6	0.239 ± 0.032	0.094 ± 0.021	0.0013	0.011
11	5	0.120 ± 0.011	0.054 ± 0.015	0.0000000000	0.105
	6	0.161 ± 0.026	0.136 ± 0.022	0.00035	0.019

obtained using alternative mathematical forms, such as $f_n = f_n^0 + \Delta f_n t/(t+t_r)$, with $\Delta f_n = f_n^f - f_n^0$.) Chapin *et al.* (1988) reported rapid suppression of whole-plant *RGR* upon cessation of nitrate supply. Perhaps this is an allied response of plants already induced for nutrient uptake. Chapin *et al.* (1988) did not localize the response to roots.

The suppression of RGR_s persists for many days (Table 2). This raises the root:shoot ratio, *r*, rapidly and also differentially by nutrient treatment (Fig. 1 in Gutschick, 1993). By days 5 to 7 of treatment, *r* was 20% higher at intermediate nitrate stress in treatment 6, than in luxury treatment 7. The ratio was 30% higher in the highest nitrate stress, treatment 5. By day 17, the enhancements in *r* had reached 45% and 110%, respectively (Table 3; amended from Table 2 of Gutschick, 1993). One may deem the enhancement of root:shoot ratio as occurring early in stress level as well as in time, given that treatment 6 was not very stressful: *RGR* at the end of the experiment was only 7% below that in luxury treatment 7.

Patterns in V_{max}, K_m, diurnal uptake rate, and nutrient utilization

Determinations of V_{max} and K_m for each nutrient N or P were made on days 12 and 17, with the latter date being the final harvest. Limitation to two dates was dictated by the large investment of time required in pulse-chase labelling and in maintaining three harvest cohorts of 28 plants each. In the P-stress series, V_{max} for phosphate [V_{max}(P)] is enhanced moderately under stress (Table 3; see also Fig. 2 in Gutschick, 1993). On day 12, the mean V_{max}(P) is 1.6-fold higher between high-stress treat-

Table 3. *Physiological status and relative growth rate of 28* Helianthus annuus *plants after 17 d growth in seven different nutrient treatments*

Physiological parameters are as defined in text. Symbol (−) for units indicates a dimensionless quantity. At end of each treatment, means and standard deviations of means are reported for each physiological parameter.

Treatment/ replicate	c_e (μM)	r (−)	V_m^{max} (μmol $g^{-1}h^{-1}$)	K_m (μM^{-1})	Shoot f_n (%)	Root f_n (%)	p^* (g PSate $g_n^{-1}d^{-1}$	α_L (−)	RGR (d^{-1})
P-stress series									
1/a	0.076	0.727	24.2	5.6	0.147	0.186	271	0.602	0.083
1/b	0.072	0.928	19.4	2.7	0.083	0.196	384	0.807	0.079
1/c	0.080	0.796	21.5	2.3	0.109	0.232	334	0.605	0.069
1/d	0.064	0.653	20.7	1.9	0.147	0.174	314	0.596	0.098
	0.073	*0.776*	*21.4*	*3.1*	*0.122*	*0.197*	*328*	*0.652*	*0.082*
	±0.003	*±0.058*	*±1.0*	*±0.8*	*±0.016*	*±0.012*	*±23*	*±0.052*	*±0.006*
2/a	0.216	0.707	26.9	4.5	0.228	0.275	239	0.654	0.124
2/b	0.197	0.694	32.5	2.8	0.242	0.199	364	0.569	0.177
2/c	0.221	0.811	29.1	2.9	0.221	0.146	251	0.730	0.111
2/d	0.218	0.706	24.5	2.4	0.160	0.222	357	0.650	0.130
	0.213	*0.730*	*28.2*	*3.2*	*0.213*	*0.210*	*303*	*0.651*	*0.134*
	±0.005	*±0.027*	*±1.7*	*±0.5*	*±0.018*	*±0.027*	*±33*	*±0.033*	*±0.014*
3/a	0.273	0.747	22.9	7.9	0.285	0.393	261	0.471	0.119
3/b	0.269	0.613	25.5	8.8	0.216	0.389	386	0.493	0.151
3/c	0.271	0.695	28.9	13.1	0.217	0.242	226	0.672	0.106
3/d	0.253	0.738	33.8	7.2	0.212	0.220	433	0.529	0.168
	0.266	*0.698*	*27.8*	*9.2*	*0.232*	*0.311*	*326*	*0.541*	*0.136*
	±0.005	*±0.031*	*±2.4*	*±1.3*	*±0.018*	*±0.046*	*±49*	*±0.045*	*±0.014*
4/a	0.817	0.546	19.6	11.7	0.239	0.352	239	0.678	0.172
4/b	0.746	0.577	22.4	13.3	0.183	0.300	517	0.546	0.198
4/c	0.790	0.386	24.7	8.7	0.308	0.380	181	0.725	0.176
4/d	0.769	0.407	28.6	14.6	0.217	0.217	378	0.575	0.201
	0.780	*0.479*	*23.8*	*12.1*	*0.237*	*0.312*	*329*	*0.631*	*0.187*
	±0.015	*±0.048*	*±1.9*	*±1.3*	*±0.026*	*±0.036*	*±75*	*±0.042*	*±0.007*
7/a	2.59	0.313	19.4	7.5	0.267	0.364	305	0.556	0.207
7/b	2.46	0.394	22.3	7.5	0.286	0.411	276	0.553	0.186
7/c	2.67	0.398	19.4	7.5	0.412	0.310	238	0.625	0.212
7/d	2.60	0.467	13.3	7.5	0.298	0.370	247	0.651	0.196
	2.58	*0.393*	*18.6*	*7.5*	*0.316*	*0.364*	*266*	*0.596*	*0.200*
	±0.04	*±0.031*	*±1.9*		*±0.033*	*±0.021*	*±15*	*±0.025*	*±0.006*
N-stress series									
5/a	2.44	0.785	92	24.7	2.20	2.06	26.7	0.395	0.078
5/b	2.12	0.836	84	12.7	2.29	1.96	23.3	0.464	0.082
5/c	1.94	0.870	115	18.0	2.63	2.23	15.0	0.812	0.103
5/d	1.93	0.839	115	16.1	2.73	2.37	21.8	0.511	0.099
	2.11	*0.832*	*102*	*17.9*	*2.46*	*2.16*	*21.7*	*0.546*	*0.090*
	±0.12	*±0.018*	*±8*	*±2.5*	*±0.13*	*±0.09*	*±2.5*	*±0.092*	*±0.006*
6/a	6.86	0.634	68.5	6.1	3.10	2.51	29.2	0.599	0.199
6/b	7.21	0.580	116	25.5	3.52	2.88	22.7	0.532	0.162
6/c	6.83	0.570	65	5.1	3.19	2.74	23.3	0.726	0.203
6/d	7.34	0.546	139	22.5	3.07	2.77	24.4	0.605	0.173
	7.06	*0.582*	*97*	*14.8*	*3.22*	*2.72*	*24.9*	*0.616*	*0.184*
	±0.13	*±0.019*	*±18*	*±5.4*	*±0.10*	*±0.08*	*±1.5*	*±0.040*	*±0.010*
7/a	151	0.313	163	30	3.42	3.73	23.8	0.556	0.207
7/b	150	0.394	98	30	3.56	3.55	22.2	0.553	0.186
7/c	153	0.398	115	30	3.61	3.54	27.1	0.625	0.212
7/d	151	0.467	107	30	3.64	3.24	20.2	0.651	0.196
	151	*0.393*	*121*	*30*	*3.56*	*3.52*	*23.3*	*0.596*	*0.200*
	±1	*±0.031*	*±14*		*±0.05*	*±0.10*	*±1.5*	*±0.025*	*±0.006*

ments 1 to 3 and the luxury treatment 7. The rise in V_{max}(P) is 1.4-fold on day 17. Interestingly, V_{max}(P) at the highest stress in treatment 1 then lags behind V_{max}(P) induced at lesser stress.

It should be noted that values reported here for K_m, as well as for *RGR*, differ somewhat from those reported in Gutschick (1993) from analysis of the same primary data. The re-analyses here removed some biases, without changing the conclusions of Gutschick (1993). Appendix II details the changes and shows the analyses *RGR* as redone with the revised data.

For every nutrient treatment, V_{max} for either nutrient is lower on day 17 than on day 12 (Fig. 2 in Gutschick, 1993). Such a progressive decline of V_{max} with plant age is commonly observed, e.g. by Wild and Breeze (1981) and by Mattsson *et al.* (1992). This decline might be expected if any age-cohort of roots declines in V_{max} with age and if the proportion of new roots declines with plant age because root *RGR* is decreasing. However, root *RGR* is rather stable for the higher-nutrient treatments 3, 4, and 7. We may estimate root-ageing effects simply by composing the weighted sum of (mass increment on day i)*(decay function). Let us choose exp (−age/[decay time]) as the decay function and set the decay time as approximately 4 d. The prediction is then that the ratio V_{max}(P; day 17)/V_{max}(P; day 12) is 0.87, 0.95, 1.03, 1.01, and 1.02 in the P-stress series of treatments 1, 2, 3, 4, and 7. The actual decline is considerably sharper: the ratios are 0.61, 0.80, 0.81, 0.94, and 0.90. Similarly, in the N-stress series of treatments 5, 6, and 7, the predicted ratios for V_{max}(N) are 0.80, 0.93, and 1.02, also not congruent with the observed ratios 1.09, 0.72, and 0.79. The contrast of predicted and observed decline ratios is not sensitive to the choice of decay time. Thus, root ageing alone can not by itself account for as much as half of the decline in whole-root average V_{max} with plant age. A metabolic programme to decrease V_{max} of newer cohorts is likely operating, but its adaptive significance is difficult to formulate.

The uptake-system affinity measured as $1/K_m$ increases markedly and with statistical significance only at the highest stress levels. On final day 17, this encompasses only treatments 1 and 2 in the P-stress series and treatment 5 in the N-stress series. For day 12, the three lowest-P treatments 1, 2, and 3 show large, statistically significant increases in $1/K_m$(P), by factors of 2.3-fold to 3-fold. The respective averages of K_m(P) are $2.8 \pm 1.2\ \mu$M, $2.5 \pm 0.6\ \mu$M, and $3.2 \pm 0.8\ \mu$M, compared with $7.5\ \mu$M assumed for treatment 4 (reference values for treatment 7 were unavailable, because solution samples were compromised). If it had been feasible to measure K_m for both N and P more accurately by concentration depletion (see 'Methods'), it is possible that changes in K_m might be seen at more modest stress levels, and with higher statistical significance in all treatments.

Diurnal variations are apparent in uptake rate (Fig. 1), at least for the high-nutrient treatment 7. The high concentrations of both nitrate and phosphate in this treatment lie well above reported K_m values, so that uptake velocity of either nutrient should represent V_{max} for that nutrient closely. One may infer that V_{max} for the luxury nutrient is down-regulated over much of the day, when nutrient availability is high. Certainly, these plants can achieve uptake sufficient to maintain tissue nutrient concentrations in new growth with such down-regulation. Conversely, plants in low nutrient concentrations need a high 'duty factor' (V_{max} maintained all day at its highest value) to take up nutrients efficiently. Any down-regulation of V_{max} would increase the demand for root investment that is much more costly in energy than the modest investment in root-surface carrier proteins.

Tissue nutrient content decreases very clearly with stress (Table 3). In the P-stress series, mean whole-plant f_P declines 2-fold from treatment 7 to treatment 1. In the N-stress series, f_N declines 1.6-fold from treatment 7 to treatment 5. (Note that tissue N analyses include modest, variable amounts of nitrate, which is unreduced and not metabolically functional in the plant, but which is partially reduced in the Kjeldahl digestion. Moderate amounts of free nitrate are expected only in the highest nitrate treatment, number 7.) As developed in Gutschick (1993)

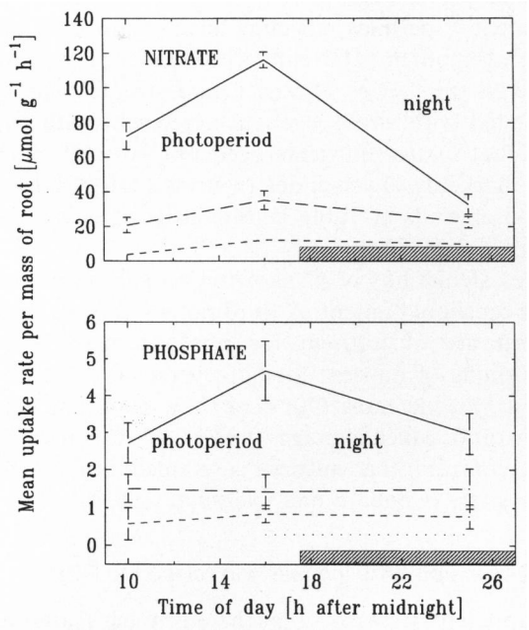

Fig. 1. Diurnal variation in rates of nutrient uptake is apparent only at highest nutrient concentration (treatment 7; topmost segmented line in both plots). In the upper plot for nitrate uptake, successively lower curves are for successively lower concentration treatments, 6 (long dashes) and 5 (short dashes). In the lower plot for phosphate uptake, successively lower curves are for treatments 4 (long dashes), 3 (short dashes), and 1 (dots). Error bars represent standard deviation of the mean; error bars are absent when the deviation is too small for the axis scale.

for the same data set, it is likely that the decline in nutrient contents is passive, driven by a reasonably close functional balance between root uptake and shoot usage of nutrient. The decline is also relative to seedling nutrient contents, which were 4.28% N and 0.30% P in shoots, 2.63% N and 0.36% P in roots. Only plants in high-nutrient treatment 7 maintained f_P as high as the original seedlings. They even gained in root f_N, though they declined in shoot f_N.

One may ask if scarcer nutrients are used with greater efficiency for photosynthesis and growth, perhaps by more efficient partitioning to and within photosynthetic tissues. Let us formulate the whole-plant photosynthetic rate as $P_{plant}=P_{L,m}m_L$, where $P_{L,m}$ is the mean leaf photosynthetic rate per mass and m_L is the leaf mass. Following Gutschick (1993), we in turn formulate $P_{L,m}$ as a photosynthetic utility parameter, p_n^*, times f_n, with $n=$N or P, appropriately. This agrees with much data usually expressing photosynthetic rate per leaf area with nutrient mass per leaf area. To continue, the leaf mass equals a fraction a_L of the total shoot mass. We may then seek stress-related trends in p^*, a_L, or both. In both N and P stress series, a_L varies more than 20% relatively among treatments (Table 3), but the variation has no statistically significant correlation with nutrient concentration c_e, ln c_e, or f_n as measures of stress. The value of p_P^* for phosphorus use varies little among the stress treatments 1 through 4. It is about 20% lower in luxury treatment 7, perhaps reflecting accumulation of a luxury or storage pool not active in or needed for photosynthesis. In the N-stress series, p_N^* varies modestly, 15%, and is not correlated with stress level. In agreement with expectations that luxury nutrients need not be used efficiently, p_P^* is markedly lower under N stress (170 ± 22 for treatment 5, in units of Table 3). Similarly, p_N^* is low under P stress (14.2 ± 0.8).

The calculations of p^* showing no gain in utility were based on shoot content. A third potential contribution to efficient use of nutrient for photosynthesis is greater partitioning of nutrient to shoot versus root, so that the ratio $f_{P,s}/f_{P,r}$ increases. Our data show no significant trend in this ratio, which averages 0.83 ± 0.17. It is often found, to the contrary, that nutrient is retained more in the root under stress (Cogliatti and Clarkson, 1983).

Variation in uptake responses and relation to RGR

It is apparent in Table 3 that there is much scatter among replicate plants in a treatment in their values of r and in the V_{max} or K_m for the appropriate nutrient. Some of this scatter is undoubtedly from measurement error, with largest errors likely in estimating K_m. Residual scatter is genetic or maternal. Nonetheless, pooling treatments shows the eventual dominance of stress in explaining variance. For example, the regression of r against the stress measure f_P is quite significant, yielding $r=-0.71$, $N=20$, and $P=0.0005$.

A particularly informative relation is between the index $I=\sqrt{rv}/(1+r)$ and *RGR*, where v is the uptake velocity per root mass at ambient nutrient concentration, $V_{max}c_e/(c_e+K_m)$. Gutschick (1993) considered the case of functional balance between root uptake of nutrient and shoot usage of nutrient for photosynthetic carbon gain. As summarized in Appendix III, he derived the expected relation $RGR=I\sqrt{\beta\rho^*a_L}$, where β is the conversion efficiency from raw photosynthate to dry matter. Given that the variations in p^* and a_L are both modest and uncorrelated with stress, we expect that the linear regression of *RGR* against I will be very significant. Figure 2 bears this out, showing that I explains 53% of the variance in *RGR* for the P-stress series and 71% for the N-stress series.

The relationship of *RGR* to index I is based on the root and shoot being near to functional balance (FB). When FB obtains, the incremental nutrient content in new tissue, $\tilde{f}_n$, matches the content in existing tissue, f_n. As a measure of deviation, we may calculate what value f_n should attain in functional balance, given the observed daily average uptake rate, $\bar{v}$, and using Eq. (7) in Gutschick (1993). Denoting this as f_n^{FB}, a measure of functional imbalance is the deviation of f_n^{FB}/f_n from unity. Table 4 indicates that plants are often moderately out of FB. There is a 1.4-fold (inverse of 0.7-fold) offset in

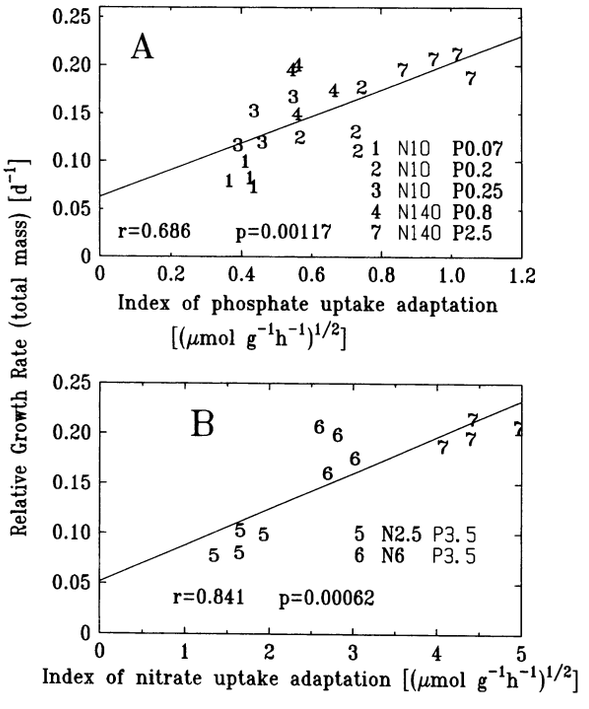

Fig. 2. Relation of relative growth rate, *RGR*, to index of uptake rate, $\sqrt{rv}/(1+r)$, predicted to be linearly related to *RGR*. Here, v is uptake velocity per unit root mass. Individual replicate plants in a treatment are identified with the number of that treatment; see Table 1 for treatment conditions. All data refer to final day 17 of treatment.

moderate P-stress treatment 3 and 1.25-fold offsets in N-stress treatments 5 and 6. For all stress treatments except P-stress treatment 1, f_n^{FB} is less than f_n, as if uptake is (or is becoming) inadequate to maintain f_n and the corresponding *RGR*. The high-nutrient treatment 7 is very close to FB for both N and P use. Table 4 also presents calculations that account for V_{max} varying diurnally, primarily in the higher-nutrient treatments. The calculations simply incorporate uptake rate as its diurnal average, $\bar{v}$, rather than its peak rate, V_{peak}, in using Eq. (7) of Gutschick (1993). With this calculation, offsets from FB are also seen, though in a somewhat different pattern according to nutrient treatment. Significant deviations from FB are not expected if plants are adding tissues similar to existing tissues. Such is the case here, where all leaves, which dominate shoot and thus plant mass, are almost fully exposed to sunlight (plants are well spaced and have little self shading, even at maximal size) and are similarly functional in photosynthesis.

Some aspects of response co-ordination and regulation

The already-noted variations in r, V_{max}, and K_m within a treatment are uncorrelated with each other. Upon pooling the P-stress treatments, r shows a modest correlation with $V_{max}(P)$ ($r=0.58$, $P=0.02$). The correlation is positive, as if both responses covary to increase uptake. Similarly, r is correlated moderately and positively with $1/K_m(P)$, or negatively with $K_m(P)$ itself ($r=-0.46$, $P=0.04$). In the N-stress series, r is correlated moderately with $1/K_m(N)$ ($r=-0.58$, $P=0.05$). Interestingly, $V_{max}(N)$ is correlated positively with $K_m(N)$ ($r=0.57$, $P=0.05$), as if the responses acted antagonistically on uptake. The odd correlation may reflect an anomalous decrease of $V_{max}(N)$ with stress which is, however, not statistically significant itself; see the 'Discussion'.

The increase in $V_{max}(P)$ for phosphate uptake under P stress is correlated well with root P concentration, $f_{P,r}$, on both day 12 and day 17 (Fig. 3). Viewed as the down-regulation of $V_{max}(P)$ with increasing root P status, this is consistent with concepts of homeostasis and with findings of other researchers on a variety of nutrients. For example, see Siddiqi and Glass (1987) concerning potassium and Lee *et al.* (1992) concerning nitrate-N. We could not examine the relationship in much detail, given that we did not independently vary both internal and external concentrations. The N-stress series exhibits no statistically significant change in $V_{max}(N)$ with root N concentration. We discuss below why regulation of $V_{max}(N)$ may not be required on the basis of nitrogen-acquisition costs and benefits.

One aspect of regulation of V_{max} by nutrient content is that V_{max} for the luxury nutrient is markedly down-regulated. This is apparent in Fig. 3 for phosphate uptake in N-stressed plants of treatments 5 and 6. For the P-stressed plants in treatments 1 through 4, $V_{max}(N)$ for nitrate uptake is also down-regulated. Treatment means $\pm$SD of mean) are 37 ± 10, 37 ± 6, 52 ± 10, and 85 ± 16, respectively, all in the common units of μmol g^{-1} root h^{-1}. The lowest values are less than one-third that for high-nutrient treatment 7. Similar down-regulation of

Table 4. *Assessment of approach to functional balance between root uptake and shoot nutrient use in various treatments*

Nutrient content in tissue at functional balance is predicted from Eq. (7) in Gutschick (1993); additional details are given in text here. Second version of prediction uses actual uptake rates on day 17, which accounts for down-regulation of uptake from peak rate over the day as evident in Fig. 1.

Treatment	(f_n at functional balance)/(observed f_n)	
	Assuming continuous uptake at peak rate	With observed diurnal down-regulation
P-stress series		
1 (lowest P)	1.42 ± 0.15	1.19 ± 0.09
2	1.08 ± 0.04	0.91 ± 0.02
3 ↓	0.79 ± 0.09	0.74 ± 0.09
4	0.82 ± 0.02	0.81 ± 0.02
7 (luxury)	1.15 ± 0.06	0.99 ± 0.03
N-stress series		
5 (lowest N)	0.88 ± 0.04	0.79 ± 0.03
6 ↓	0.92 ± 0.05	0.82 ± 0.03
7 (luxury)	1.12 ± 0.05	0.97 ± 0.05

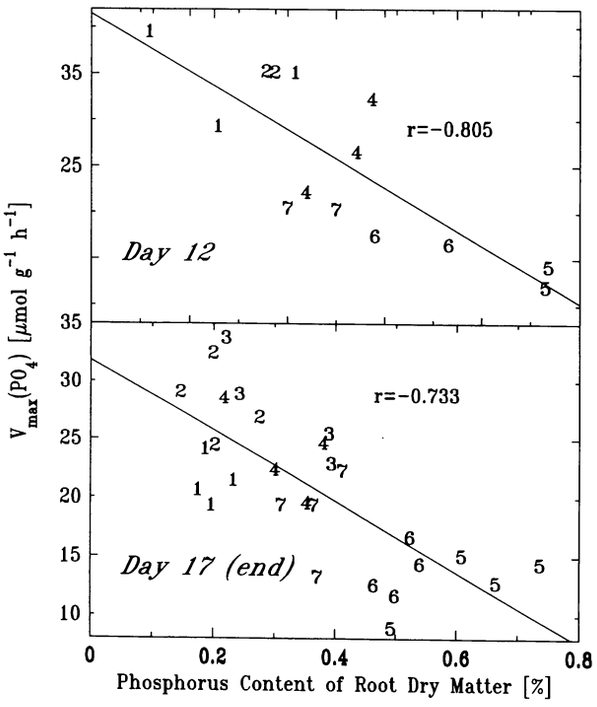

Fig. 3. Relation of V_{max} for phosphate uptake to total phosphorus content in root as fraction of dry matter. Individual replicate plants in a treatment are identified with the number of that treatment; see Table 1 for treatment conditions.

nitrate uptake in P-stressed plants was observed by Rufty *et al.* (1991).

Discussion

Suppression of shoot growth at low nutrient availability

At low external concentrations of either nutrient, c_e, shoot relative growth rate, RGR_s, is much smaller than it is at high c_e. For root relative growth rate, RGR_r, c_e has little effect. The change in RGR_s has been provisionally interpreted as suppression of shoot growth by a signal generated in response to low c_e directly. Alternatively, one might view the differences in RGR_s as shoot growth stimulation at high nutrient availability. The first interpretation is perhaps more likely: in the early days of all nutrient treatments, shoots have similar tissue nutrient contents that may reflect intrinsic growth potential. Whether a negative signal is generated in low-nutrient treatments (RGR_s suppression) or a positive signal is generated in high-nutrient treatments (RGR_s stimulation) can only be resolved when the signal is identified and then blocked. This research might be pursued in the future.

Estimated gain in RGR *from acclimation responses*

The plants began as seedlings with uniform treatment and were then grown in different nutrient treatments. Their differential responses to treatment may be denoted as acclimation. Increases in r, V_{max}, and $1/K_m$ presumably act adaptively to uphold RGR under stress. The most direct estimate of gain is the ratio of RGR with acclimated r, V_{max}, and K_m to RGR with the unacclimated r, V_{max}, and K_m of treatment 7 but at the same external nutrient concentration. The fairest comparison assumes that internal nutrient concentration adjusts to functional balance in each case. As before, we assume that the parameters of photosynthetic utility, β, α_L, and p^* are constant between acclimated and unacclimated plants. Table 5 shows that acclimation enables RGR to be held up to twice as high as without acclimation, under strong P stress. Under N stress, the observed degrees of acclimation offer small gains of about 30%. Nonetheless, even modest gains in RGR compound to large increases in plant mass over time.

Why do plants increase root : shoot ratio early?

Our results show increases in r that are early both in time and in stress level. A first hypothesis is that increases in r offer larger and more persistent gains in RGR than do increases in V_{max} or in $1/K_m$. However, this hypothesis gains only qualified credence under closer inspection. For example, doubling of r as we observe does not double nutrient uptake, nor does it double RGR: higher r dilutes the shoot fraction and thus photosynthesis, and RGR increases only as the square root of the product rv as plants tend toward functional balance. The predicted value of r for improving RGR is proportional to the factor $\sqrt{r}/(1+r)$, according to Gutschick (1993). This factor increases only 10% as r rises from 0.4 to 0.8 as in our data. In contrast, doubling V_{max} might be expected to increase RGR by the factor $\sqrt{2}$, or by 41%.

Table 5. *Estimated increase in relative growth rate provided by acclimatory responses in* r, V_{max}, *and* K_m

RGR with acclimated values of r, V_{max}, and K_m is compared to RGR with unacclimated values in luxury treatment 7. Both RGR values are calculated for actual external concentration of nutrient, c_e, occurring in treatment. Both calculations assume that roots and shoots attain functional balance. Calculations are done for each individual replicate plant, with its own photosynthetic use parameters, and then averaged within treatment group.

Treatment	RGR(acclimated)/RGR(unacclimated)
P-stress series	
1 (lowest P)	2.08±0.04
2	2.08±0.11
3 ↓	1.23±0.10
4	0.94±0.04
5 (luxury)	0.99±0.05
N-stress series	
5 (lowest N)	1.29±0.04
6 ↓	1.31±0.12
7 (luxury)	0.99±0.04

We may turn, then, to estimating the persistence of gains from the different responses. The major factor that compromises long-term gains is the localized depletion of nutrient around a root (Bhat and Nye, 1973). Root uptake then operates under increasingly severe limitations from diffusive transport in the soil. Of course, acclimation responses evolved under conditions in soil and are presumably still triggered by indicators of utility as these indicators operate in soil, not in stirred solution. Consider the simplest case of steady-state transport to a cylindrical root of radius a. Denote the diffusivity of nutrient in bulk soil, including the factor for path tortuosity, as D. Let the boundary condition be that nutrient concentration in soil attains its highest limiting value, c_b, at a radial distance b from the root centre. This distance is roughly the radius of influence of a single root, half the distance to similar, neighbouring roots. The root attains a steady surface flux density, J_a, and the concentration of nutrient at the root surface drops to the value $c_d = c_b - kJ_a$, where $k = [a \ln(b/a)]/D$. Now, J_a itself is a function of c_a, as $J_a = V_{max} c_a/(c_a + K_m)$. It is straightforward, if tedious (Appendix IV), to derive a quadratic equation for c_a having the solution

$$c_a = 0.5[c_b - kV_{max} - K_m \pm \sqrt{(kV_{max} + K_m - c_b)^2 + 4c_b K_m}]. \quad (1)$$

Using this, we can solve for J_a. We may relate this readily to formulations for RGR in terms of uptake per unit root

mass, which is directly proportional to J_a, because $v = 2J_a/(a\rho)$. Here, ρ is the density of root tissue, very close to that for water at 1000 kg m^{-3}.

Numerical studies show that ambient uptake velocity v rises more slowly than does V_{max} or $c_b/(c_b+K_m)$. The limiting case is readily expressed mathematically (Appendix IV) as

$$J_a \rightarrow \frac{c_b}{k}\left[1-\frac{K_m}{kV_{max}}\right]. \quad (2)$$

Concurrently, c_a drops to a small fraction of bulk-soil concentration, c_b:

$$c_a = c_b\left[\frac{K_m}{kV_{max}}\right]. \quad (3)$$

Consider now a small increase in the kinetic ratio V_{max}/K_m, defined as y, from a value y^0 by a fraction ϵ, that is, to $y^0(1+\epsilon)$. A small amount of algebra (again see Appendix IV) leads to the conclusion that J_a/J_a^0 only increases by a smaller factor $1+\epsilon(c_a/c_b)$. Thus, if c_a is drawn down to only 10% of c_b (readily so, for low phosphate concentrations in non-sandy soil), then a 50% increase in V_{max}/K_m leads to only a 5% rise in J_a. Diffusive limitations drastically curtail the effectiveness of acclimation in uptake capacity; see also Nye (1977) and Robinson (1986). Limitations are most severe for phosphate uptake, though nitrate depletion can also occur. This dilution of benefit does not apply to increases in r, which may then become the most important acclimation. The greater importance of r is more relative than absolute. The absolute gains remain fairly small, as discussed earlier.

Increased r may provide a route for positive feedback in *RGR*: if a greater r value affords higher *RGR*, then the root system as a whole has a higher fraction of new roots, therefore greater uptake and greater *RGR*. If uptake by a root age cohort declines as exp(−b*age) as proposed earlier, then whole-root uptake scales as $RGR/(RGR+b)$; a mathematical derivation given in Appendix V. For normal ranges of *RGR*, the gain is small to modest. Note that the root *RGR* can not be adjusted any higher than total *RGR* in the long run. We may put this modifier of uptake into the expression for total *RGR* under functional balance, to obtain

$$RGR = \frac{\sqrt{r v_m^0 \beta a_L p^*}}{1+r}\sqrt{\frac{RGR}{RGR+b}} \equiv \sqrt{Q}\sqrt{\frac{RGR}{RGR+b}}. \quad (4)$$

Here, v_m^0 is the initial uptake rate of newest roots. We may regard $\sqrt{Q}$ as the intrinsic *RGR*. An asymptotic expansion of this expression for $\sqrt{Q} > 0.25b$, that is, for higher growth rates, yields the approximation.

$$RGR = \sqrt{Q} - 0.5b + \frac{b^2}{8\sqrt{Q}}. \quad (5)$$

When $\sqrt{Q}$ is 0.20 d^{-1} and $b = 1/(6\text{ d})$, an increase of 20% in $\sqrt{Q}$ raises *RGR* by the larger factor of 28%; the extra 8% is the contribution from positive feedback. Consider, however, that increasing r alone by 20% increases $\sqrt{Q}$ by only 2.7% and *RGR* by only 3.7%.

The actual temporal pattern of root uptake capacity with root age may be more complicated. Youngest, most apical root segments have relatively low uptake capacity, which attains a peak several mm from the tip (see Lazof *et al.*, 1992, for nitrate uptake). However, the longer-term decline in V_{max} is well-established (see earlier references). If V_{max} varies as (polynomial in time)* exp(−bt), the arguments above on positive feedback are still valid, provided that the polynomial factor is also not a function of nutrient stress level.

A plausible origin for a large adaptive value of increased r—especially relative to increased V_{max} or $1/K_m$—is in finding and exploiting rich pockets of nutrients in soil. Greater r increases both the background uptake rate and the chances of finding such rich pockets. It is beyond the scope of the present discussion to formulate how the exploitation probability, average uptake rate, and *RGR* depend upon the root investment, r. Some considerations are given in Hutchings and de Kroon (1994). One point worth pursuing in the present discussion is that roots of nutrient-stressed plants may reduce lateral branching until they reach richer pockets of nutrients (Drew, 1975; Granato and Raper, 1989). Intuitively, this response would appear to enhance the chance of elongation into, and subsequent investment in, the richer soil areas. As a strategic, adaptive response, it would have to be an early commitment, because its benefits are deferred in time. Its value in uptake enhancement in more homogeneous soils—or in uniform solution culture, as here—would be moderately negative: if, as observed (Drew, 1975; Granato and Raper, 1989), main-axis elongation is not simultaneously enhanced by a redirection of growth substrate, the net effect is to reduce root *RGR* from its maximum. This retards development of high r. However, as long as shoot *RGR* is still suppressed more than root *RGR*, higher r will develop (if more slowly). The very modest benefits of higher r will accrue, somewhat attenuated. This would represent only a very small loss of benefits overall.

Adaptive value of regulating V_{max}

Is it adaptive to reduce V_{max} below the biochemical maximum expressed under stress, when nutrients are more copiously available? This is the converse of the question of whether V_{max} should be scaled up under stress. We can not readily predict the highest V_{max} attainable from first principles, so it is more productive to address the first, inverse question.

There are two ready reasons why *RGR* may be improved if uptake and consequent f_n are held to less

than their maxima. First, there is a cost to acquiring and metabolizing nutrients. Let us set this cost as C_n, in grams of photosynthate per gram of nutrient. This introduces a factor $1-C_n f_n$ into the carbon-limited *RGR* (Eq. 6 in Gutschick, 1993). Second, if f_n becomes large, the leaf photosynthetic rate per mass, $P_{L,m}$, may cease to increase linearly with f_n as generally assumed (Sinclair and Horie (1989) saw substantial curvature). This is especially true for daily-total photosynthesis (Field, 1983). A simple, empirical fit to photosynthetic rate that is linear in f_n at low f_n and that reaches a constant (saturation) at high f_n is

$$P_{L,m}=p^*(1-e^{-qf_n})/q. \tag{6}$$

(Other mathematical forms, such as $(p^*F)f_n/(f_n+F)$, behave similarly and give the same qualitative conclusions as below.)

The combined effect of costs and of benefit saturation is to amend the expression for carbon-limited *RGR* to

$$RGR \rightarrow \frac{\beta a_L p^*}{1+r}(1-C_n f_n)\frac{(1-e^{-qf_n})}{q}. \tag{7}$$

With this transcendental (non-polynomial) equation, it is no longer possible to get an analytical solution for f_n at functional balance, f_n^{FB}. However, numerical explorations are possible. The modifications above have the effect of *increasing* f_n^{FB} and decreasing *RGR*. The counter-intuitive increase in f_n^{FB} arises because uptake rate itself is not cut, but dilution of nutrient content by growth (Jarrell and Beverly, 1981) is curtailed.

The adaptiveness of down-regulating V_{max} may be phrased as, Does a decrease in V_{max} ever increase the predicted *RGR*? We have numerically fitted our N-stress series data on f_n and *RGR*, using $C_n=4$ g photosynthate g_N^{-1} and $q=1/0.06$—that is, photosynthesis is 63% saturated at $f_N=0.06$. For neither treatment does *RGR* increase as V_{max} is decreased notionally. This suggests a hypothesis for detailed experimental testing.

The case of P stress is even clearer. The cost function, C_n, is likely to be even lower than for nitrate, as phosphate is not reduced metabolically. Its only cost may be ion transport, which Bloom *et al.* (1992) have estimated experimentally. Our data show evidence of saturation in the relationship between $P_{L,m}$ and f_P only at the highest P levels, in treatment 7. Here, too, then, we expect that down-regulation of V_{max} provides no gain in *RGR*—rather, a drop. Yet, down-regulation is pronounced in our data and that of others. Our hypothesis is that down-regulation is adaptive in averting costs other than lost-opportunity costs, such as high-phosphate interference with iron nutrient as occasionally reported (citations in Romera *et al.*, 1992).

Conclusions

Plants placed under stress in our conditions show marked increases in r and in V_{max} and $1/K_m$ for the low-availability nutrient. Combined, these three acclimation responses offer a 1.3-fold to 2-fold increase in *RGR*, compared to what an unacclimated plant could attain at low nutrient concentrations. Acclimation upholds nutrient uptake by even larger factors, but *RGR* follows reasonably closely our predictions from functional balance that *RGR* is proportional to the square root of uptake rate. Plants show no significant acclimation in photosynthetic utility of either N or P under stress.

The response of increased r is committed early in both time and stress level. The increase appears to be triggered by external nutrient concentrations. By several lines of argument, we propose that the greatest benefits for *RGR* accrue from increases in r rather than in V_{max} or $1/K_m$. Nonetheless, under conditions in soil, where diffusive transport can become limiting, predicted gains in *RGR* are small from all three responses. This may underlie the non-responsiveness of extremely stress-tolerant species (reviewed by Chapin, 1980). The major way in which increased r may be beneficial may be for finding richer pockets of nutrients to exploit in heterogeneous soil.

We observe down-regulation of uptake, as decreased $V_{max}(P)$ and $1/K_m(P)$, with increasing tissue nutrient status in the P-stress series, though not for $V_{max}(N)$ and $1/K_m(N)$ with the N-stress series. Postulated costs of acquiring nutrients and the saturation of photosynthetic benefits of nutrients do not appear to offer a need for such down-regulation. We hypothesize that down-regulation is protective of iron nutrition, with which phosphate can interfere. There is also a decrease in V_{max} for both N and P, as whole-root average, with plant age. The decrease is not well explained by a change in the age-structure of roots. A metabolic down-regulation is implied, but an adaptive value is difficult to conceive.

The depletability of nutrients around roots was a critical factor in developing several arguments that acclimation benefits can be quite small for roots in soil. We are led to consider the relation of our solution-culture experiments, in which solution concentrations, c_e, are held constant, to other solution-culture experiments and to field conditions. Constant c_e is most relevant to early seedling growth, when plants are small and can not much affect c_e by uptake. A clear contrast is afforded by late growth in dense stands, wherein plants can deplete c_e markedly. This drop in c_e may relieve product inhibition of nitrogen mineralization and increase the rate of nitrate supply. So, too, may root exudation that supports microbial metabolism (Pastor and Post, 1986). In effect, plants partially regulate supply to meet their demand. To this situation, the experimental procedure termed exponential addition (Ingestad and Lund, 1979) is more relevant.

There is a clear need for both theory and experiments to bridge the gap between the two extremes, thus, to get a picture of acclimation benefits over the whole life cycle.

Table of symbols

Symbol	Meaning [units]
b	rate of decline of root uptake capacity with age [d^{-1}]
c_a	nutrient concentration in solution at root surface [mol m^{-3}, or molar]
c_b	nutrient concentration in bulk soil solution [mol m^{-3}, or molar]
c_e	nutrient concentration maintained in solution [mol m^{-3}, or molar]
C_n	metabolic cost of acquiring and metabolizing a nutrient [g photosynthate g^{-1} nutrient]
D	diffusion constant for nutrient in soil solution [$m^2 d^{-1}$]
f_n ($f_{n,r}$; $\tilde{f}_n$)	fractional nutrient content (in roots only; incremental, in new tissue) [unitless, or g nutrient g^{-1} DM]
f_N, f_P	fractional content of nitrogen or phosphorus in tissue [unitless]
FB	functional balance between root and shoot [concept]
J_a	actual rate of nutrient uptake per root area [$g\ m^{-2} d^{-1}$]
K_m	affinity constant in Michaelis-Menten kinetics [mol m^{-3}]
K_m(N), K_m(P)	affinity constant for nitrate, phosphate uptake, specifically
p^*(p_N^*; p_P^*)	photosynthetic utility of nutrient (of nitrogen; of phosphorus) [g glucose d^{-1} g^{-1} nutrient]
$P_{L,m}$	daily-average photosynthesis rate per leaf mass [g glucose g^{-1} nutrient d^{-1}]
q	damping factor for increase of photosynthetic rate with tissue nutrient content [g dry mass g^{-1} nutrient]
r	root : shoot ratio [unitless, or g root g^{-1} shoot] *or* statistical correlation coefficient [unitless]
RGR (RGR_r; RGR_s)	relative growth rate (of root; of shoot) [d^{-1}, or g DM g^{-1} d^{-1}]
v	actual uptake velocity per root mass in growing conditions
$\bar{v}$, v_{peak}	diurnal average, diurnal peak in uptake velocity
v_{total}	uptake velocity of whole plant
V_{max}	maximal uptake velocity by roots, per area or per mass
V_{max}(N), V_{max}(P)	maximal uptake velocity for nitrate, phosphate, specifically
α_L	ratio of leaf mass to total shoot mass [unitless]
β	biosynthetic conversion efficiency [g DM g^{-1} glucose]

Appendix I

Calculating relative growth rates

Fresh masses of root ($m_{f,r}$) and of shoot ($m_{f,s}$) were measured sequentially over 17 d on each individual plant. Conversion to corresponding dry masses, $m_{d,r}$ and $m_{d,s}$, requires knowledge of the ratio of dry to fresh mass. This ratio, d, was determined on harvested replicate plants within each treatment. The magnitude of d differs for roots and shoots, being lower for roots. It also varies as much as 2-fold within any nutrient treatment. The majority of the variance was found to be related to plant size. Thus, we fit d as a linear function of fresh mass, separately for each nutrient treatment. For data sets in which d varied over a significant range, the regression typically accounted for 50% or more of the variance (r was approximately 0.7 or 0.8). To convert any observed fresh mass to dry mass—say, for shoots—we used fresh mass $m_{f,s}$ to compute an estimated mass ratio, d_s. This ratio multiplied by the original fresh mass provided an estimate of dry mass, $m_{f,s}$. When used on the original harvest data, this procedure reproduced actual dry mass with a standard deviation of 6% to 10%. This error was about half the error obtained using a single average d for any nutrient treatment. This error is significant, amounting to about 0.3 to 0.8 of the daily growth increment. Thus it adds noise to calculated RGR values, but it appears to be unavoidable. Higher-order fits (quadratic) were tried, but made little improvement in variance, while adding notably sharper curvatures in dry mass calculated for the final days of the experiment. Values of d for seedlings on day zero were much lower than values on later days. Consequently, inclusion of seedling data skewed the d fit, so it was not pursued.

To get a smoothed representation of RGR as a function of time, the natural logarithm of the dry mass was fitted to a quadratic function of time,

$$\ln m_d = a + bt + ct^2. \qquad \text{(AI-1)}$$

This form was differentiated analytically to yield RGR

$$RGR = \frac{1}{m_d}\frac{dm_d}{dt} = \frac{d}{dt}\ln m_d = b + 2ct. \qquad \text{(AI-2)}$$

The fit of Eq. (AI-1) was done over 7 d segments spanning the day of interest. For day 5, for example, days 2 through 8 were used in the fit. For days near the beginning or end, the 7 d were as close to the central day as possible, e.g. days 1 through 7 were used to fit $\ln m_d$ and RGR for days 1 through 4. All seven days were weighted equally in the fits reported here. Weighting functions that declined with distance from the target day, t^*, were tried, such as $1/|t-t^*|$. They did not materially change the RGR values and they added slightly more variation to RGR within a treatment.

Appendix II

Revised estimates for RGR *and* K_m*, and effects on* RGR *analyses*

The current presentation uses data from the same experiment as used in Gutschick (1993). Here, revised values are given for relative growth rate, RGR, and the Michaelis constant, K_m.

In analysing RGR, one must estimate dry masses of each plant on each day from fresh masses measured daily, non-destructively. Appendix I presents the detailed method. The new analysis here deleted data from seedlings (day zero) in deriving the fresh-to-dry conversion. Seedlings raised in wet paper have a high dry/fresh mass ratio that biased the conversion for all other days.

The magnitude of K_m connects maximal uptake velocity at saturating nutrient concentrations, V_{max}, with actual uptake velocity v at the nutrient concentration, c, used during growth:

$$v_{peak} = V_{max}\frac{c}{c+K_m} \rightarrow K_m = c\left(\frac{V_{max}}{v_{peak}} - 1\right). \quad \text{(AII-1)}$$

The peak uptake rate over the day is taken to represent the full expression of V_{max}, which is apparently down-regulated at various times of day (Fig. 1). In using Eq. (AII-1), an accounting is made for V_{max} of all plants in all treatments being partially down-regulated: v_{peak} is scaled by a factor γ slightly greater than unity. To derive γ, the peak uptake velocity averaged over all replicate plants in the highest-nutrient treatment is made to fit Eq. (AII-1) with V_{max} replaced by γV_{max}. For the current presentation, a previous error in data entry was corrected, giving a new value of γ. This same γ is applied to all treatments, so all K_m calculations were affected. Furthermore, no attempt was made in the new analysis to correct calculated uptake velocities for inequalities in flow rates of nutrient solution to different plants. In Gutschick (1993), the partitioning of total flow rate was estimated so that each plant was assigned the same ratio of time-average uptake rate to daily gain in tissue nutrient content.

The analyses of Table 3 in Gutschick (1993) were re-run with the new values of *RGR* and K_m. Regressions of *RGR* using Eq. (3) of that paper were as unsatisfactory as before. Regressions using Eq. (9) of that paper were as satisfactory as with the old data. Regressions with the new data gave the following results to compare with Table 3 in Gutschick (1993). Note that plant 3/d is no longer an outlier. The regressions include high-nutrient-treatment 7, which is appropriate as an end-point. Regressions without treatment 7 are quite similar, with somewhat lower statistical significance.

P-stress (treatments 1, 2, 3, 4, 7)			
Eq. (9) fit: $r^2=0.63$			
Eq. (9) terms:	$\ln\frac{\sqrt{r}}{1+r}$	$\frac{1}{2}\ln V_{max}$	$-\frac{1}{2}\ln(1+K_m/c_e)$
β value	−3.58	1.26	0.44
t value	−2.05	2.08	2.16
p(H: $\beta=0$)	0.06	0.05	0.05
p(H: $\beta=1$)	0.02	0.67	0.02
N-stress (treatments 5, 6, 7)			
Eq. (9) fit: $r^2=0.88$			
Eq. (9) terms:	$\ln\frac{\sqrt{r}}{1+r}$	$\frac{1}{2}\ln V_{max}$	$-\frac{1}{2}\ln(1+K_m/c_e)$
β value	5.19	1.17	1.22
t value	1.81	1.89	4.48
p(H: $\beta=0$)	0.10	0.09	0.002
p(H: $\beta=1$)	0.18	0.79	0.44

Consider the beta coefficients for the second and third terms involving V_{max} and K_m (the coefficient for the first term, involving r, is never important, statistically). As in the old analysis, these coefficients are near the expected value of unity, except for one coefficient (in the P-stress series, there is one value of 0.44). The statistical significance is modestly improved over the old analysis. The probability that a beta coefficient is zero (that the corresponding physiological response is irrelevant) is only 2% to 10%. In the old analysis, the range was 2% to 17%. The probability that a coefficient is near the expected value of 1.0 is greater than 2/3 for two of the four important coefficients. It was this high only for one coefficient in the old analysis.

Appendix III

Relation of relative growth rate to uptake and photosynthetic utility of nutrient

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 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

$$\dot{m}^{pl} = m_r v/\tilde{f}_n \quad \text{(AIII-1)}$$

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

$$RGR^{ul} = \frac{m_r v}{(m_r+m_s)\tilde{f}_n} = \frac{rv}{(1+r)\tilde{f}_n}. \quad \text{(AIII-2)}$$

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

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

$$\dot{m}^{pl} = \beta p^* f_r \alpha_L m_s \quad \text{(AIII-3)}$$

and the photosynthesis-limited relative growth rate is

$$RGR^{pl} = \beta p^* \alpha_L \frac{m_s}{m_s+m_r} f_n = \beta p^* \alpha_L f_n/(1+r). \quad \text{(AIII-4)}$$

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

$$rv/\tilde{f}_n = \beta p^* \alpha_L f_n. \quad \text{(AIII-5)}$$

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 root and shoot and is not freely adjustable as a plant response. Substituting this expression for f_n into either *RGR* expression gives the expression in the text,

$$RGR = \frac{\sqrt{rv}}{1+r}\sqrt{\beta p^* \alpha_L}. \quad \text{(AIII-6)}$$

Appendix IV

Calculating uptake rates strongly limited by soil diffusivity

As in the text, consider steady-state transport in soil of diffusivity D toward a cylindrical root of radius a. In all cylindrical shells of radius r centred around the root, total transport is equal. This specifies how flux density J_r scales with r: by integrating J over the area of a shell of length L, we get $J_r 2\pi r L = \text{constant}$. (Mathematically this is equivalent to the form $\nabla J = 0$). We may use the flux density at the root surface,

J_a, to set the scale, as $J_r = J_a a/r$. This allows us to rewrite the diffusion equation for the behaviour of concentration c:

$$J_r = J_a \frac{a}{r} = -D \frac{\partial c}{\partial r} \qquad \text{(AIV-1)}$$

or

$$\frac{\partial c}{\partial r} = \left[\frac{J_a a}{D}\right] \frac{1}{r}.$$

This equation indicates that c varies in proportion to $\ln r$. Mathematically, J here is negative, toward the root. Let us change the sign to use J as a positive quantity. We may incorporate the boundary condition that concentration attains the bulk soil value, c_b, at a radius b from the root centre, to get

$$c = c_b - \left[\frac{J_a a}{D}\right] \ln \frac{b}{r}. \qquad \text{(AIV-2)}$$

Now, J_a is itself a function of c_a and the root uptake parameters, V_{max} and K_m, namely the Michaelis-Menten form $J_a = V_{max} c_a/(c_a + K_m)$. We may express $c = c_a$ above in these terms to get a quadratic equation for c_a, which can then be used to solve for J_a:

$$c_a = c_b - \left[\frac{J_a a}{D}\right] \ln \frac{b}{a} = c_b - V_{max} \left[\frac{a}{D} \ln \frac{b}{a}\right] \frac{c_a}{c_a + K_m}. \qquad \text{(AIV-3)}$$

Let us denote the combination of parameters in the rightmost brackets as k. If we multiply both sides of the equation by $(c_a + K_m)$ and gather terms on to the left-hand side of the equation, we get

$$(c_a - c_b)(c_a + K_m) + k V_{max} c_a = 0. \qquad \text{(AIV-4)}$$

The terms can be multiplied out simply. The formula for solving a quadratic equation readily gives Eq. (1) of the text. Only the equation root with the positive sign is physically real.

We may proceed to derive Eq. (2) of the text. Consider that a high uptake capacity, as large V_{max} or small K_m or both, will increase J_a, but the flux to the root must be sustained by a greater gradient in c. This decreases c_a and thus 'self-limits' the rate J_a. When uptake capacity is large, we may develop a power-series approximation to the square root (radical) in Eq. (1), as follows. First, let $x = kV_{max} + K_m - c_b$. Then, especially when V_{max} is large, x^2 will be large compared to $4c_b K_m$. We may then write the radical as $x\sqrt{1 + 4c_b K_m/x^2}$, with the second term inside being small compared to 1. The square root of 1 plus a small number ϵ is represented by a rapidly converging power series, of which the first terms are just $1 + \epsilon/2$. This approximation yields

$$c_a \approx [-x + x(1 + 2c_b K_m/x^2)]/2 \approx c_b K_m/x. \qquad \text{(AIV-5)}$$

We may substitute this into the Michaelis-Menten form for uptake flux density, attaining

$$J_a = \frac{V_{max} c_a}{c_a + K_m} = \frac{V_{max} c_b K_m/x}{c_b K_m/x + K_m}. \qquad \text{(AIV-6)}$$

We multiply both numerator and denominator by x/K_m to get $J_a = V_{max} c_b/(c_b + x)$. Substituting for x, the denominator becomes simply $kV_{max} + K_m$. Now, for large V_{max}, kV_{max} is much larger than K_m. We may then write

$$J_a \approx \frac{V_{max} c_b}{kV_{max}(1 + K_m/[kV_{max}])} \approx \frac{c_b}{k}\left[1 - \frac{K_m}{kV_{max}}\right]. \qquad \text{(AIV-7)}$$

To obtain the final form, we cancelled factors of V_{max}. We also used the approximation (the first terms in exact power series) that $1/(1+\epsilon)$ equals $1-\epsilon$ when ϵ is much smaller than 1. The equation above is exactly Eq. (2) of the text.

The justification of the argument following Eq. (3) in the text proceeds as follows. We may rewrite Eq. (AIV-7) above as

$$J_a = \frac{c_b}{k}\left[1 - \frac{1}{ky^0}\right], \qquad \text{(AIV-8)}$$

where $y^0 = V^0_{max}/K^0_m$ as in the text. If a plant increases y by a small fraction ϵ, so that y^0 becomes $y^0(1+\epsilon)$, then the ratio of new uptake rate to original uptake rate is

$$\frac{J_a}{J^0_a} = \left[1 - \frac{1}{ky^0(1+\epsilon)}\right] \Big/ \left[1 - \frac{1}{ky^0}\right]. \qquad \text{(AIV-9)}$$

The common factor of c_b/k has been removed. Again expanding $1/(1+\epsilon)$ as $1-\epsilon$, we get

$$\frac{J_a}{J^0_a} \approx \left[1 - \frac{1}{ky^0} + \frac{\epsilon}{ky^0}\right] \Big/ \left[1 - \frac{1}{ky^0}\right] = 1 + \frac{\epsilon}{ky^0(1 - 1/ky^0)}. \qquad \text{(AIV-10)}$$

Now, $1/ky^0$ is just the concentration ratio c_a/c_b. It is also much less than 1, so that we will approximate $(1 - 1/ky^0)$ as 1. Then we may write the ratio of new to old uptake rates, in a close approximation, as $1 + \epsilon(c_a/c_b)$. This is the expression cited in the text.

Appendix V

Potential for positive feedback in relative growth rate

Higher relative growth rate implies that the average age of roots is lower and, thus, that these roots are more active on the average than roots in a plant with lower *RGR*. Consider roots in a cohort of age t, such as $t = 3$ d. For the sake of making the argument quantitative, assume that uptake velocity per mass of root, v_m, declines exponentially with root age, as

$$v_m = v^0_m e^{-bt}. \qquad \text{(AV-1)}$$

If a plant maintains constant *RGR*, the root mass increases exponentially as $m = m^0 e^{Rt}$; here, R is used as a single-letter symbol for *RGR*, for simplicity. (This entire analysis can be done for the case that *RGR* depends on time, too, but it affords no more insight into the current topic.) In a time interval from t to $t + dt$, the amount of root mass added is $dm = m^0 R e^{Rt} dt$. The uptake rate of the whole root system will be the sum of all root mass increments in root mass, multiplied by their age-adjusted uptake rate per mass. Expressed as an integral, the root uptake rate at a 'final' time t_f is

$$\begin{aligned} v_{total}(t_f) &= \int_0^{t_f} dm(t) v^0_m e^{-b(t_f - t)} \\ &= v^0_m m^0 R \int_0^{t_f} dt\, e^{Rt} e^{-b(t_f - t)} \\ &= v^0_m m^0 R e^{-bt_f} \int_0^{t_f} dt\, e^{(R+b)t} \end{aligned} \qquad \text{(AV-2)}$$

The time integral of $e^{(R+b)t} \equiv e^{at}$ is just $(e^{at_f} - 1)/a$. The first term in parentheses dominates at times greater than a few mass-doubling times, so that we may approximate

$$v_{total} \approx v^0_m m^0 R e^{Rt}/(R + b). \qquad \text{(AV-3)}$$

We may divide this by root mass at time t_f to get the uptake

rate per mass,

$$v_{m,\,total} = v_m^0 \frac{R}{R+b}. \qquad \text{(AV-4)}$$

This is a relation postulated in the text. Next, consider the *RGR* equation derived as Eq. (8) in Gutschick (1993) and as Eq. (AIII-6) above:

$$RGR = \frac{\sqrt{r}}{1+r}\sqrt{v_m \beta \alpha_L P^*}. \qquad \text{(AV-5)}$$

Substituting for v_m using Eq. (AV-4) yields Eq. (4) in the text here.

To derive the asymptotic expansion of relative growth rate, Eq. (5) in the text, we first square Eq. (4). Again letting $RGR = R$ for algebraic ease, we get

$$R^2 = Q\frac{R}{R+b}. \qquad \text{(AV-5)}$$

We can cancel out a common factor of R on both sides. Then, we may multiply both sides by $(R+b)$ and collect all terms on the left-hand side to get the quadratic equation and its explicit solution:

$$R^2 + Rb - Q = 0 \qquad \text{(AV-6)}$$

$$R = (-b + \sqrt{b^2+4Q})/2.$$

For the case of interest, the intrinsic *RGR*, or Q, is considerably larger than b. We may write the square root as $\sqrt{Q}\sqrt{1+b^2/4Q}$. The term $b^2/4Q$ is small. We use the approximation that $\sqrt{1+\epsilon} \approx 1+\epsilon/2$ to get Eq. (5) in the text:

$$R = -\frac{b}{2} + \sqrt{Q}\left(1 + \frac{b^2}{8Q}\right)$$

$$= -\frac{b}{2} + \sqrt{Q} + \frac{b^2}{8\sqrt{Q}}. \qquad \text{(AV-7)}$$

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