

Modeling Nutrient Uptake in Chrysanthemum as a Function of Growth Rate

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Abstract. The results of six experiments conducted over 3 years were analyzed to develop a relationship between nutrient uptake rate and growth rate in hydroponically grown *Dendranthema ×grandiflorum* (Ramat.) Kitamura, cv. Fiesta. Plants subjected to two levels of CO₂ and three levels of irradiance in four greenhouses were periodically analyzed for growth and the internal concentration of 11 mineral elements. The resulting data were used to determine relative accumulation rate and relative growth rate, which were included in linear regression analyses to determine the dependence of uptake on growth. The regression equations were significant, with a slight trend toward nonlinearity in some elements. This nonlinearity seems to be related to the aging of the plant and suggests a process in the plant capable of controlling uptake rate, perhaps as a result of changes in the rate of formation of different types of tissues.

Increasing concern about environmental pollution, coupled with recent advances in the ability to control the environment of greenhouses via computers, have made it both necessary and possible to consider adjusting nutrient solutions to minimize waste and maximize growth. If nutrient uptake rate can be predicted accurately under differing conditions, it should be possible to devise systems that deliver only the quantity of minerals necessary for growth, thereby minimizing the pollution potential of the waste. Further, it should be possible to anticipate periods of high demand and adjust the concentration of nutrients accordingly, so that growth is not compromised by nutrient deficiency.

The relationship between growth rate and nutrient uptake rate has been examined in numerous studies (Ingestad, 1982, 1987; Ingestad and Agren, 1988; Ingestad and Lund, 1979; Raper et al., 1977a, 1977b). Ingestad (1987) and Ingestad and Agren (1988) suggest that unless nutrient uptake research is conducted under steady-state conditions, errors in interpretation are likely to result. They define steady-state for a particular element as the case where the internal concentration of that nutrient is unchanging with time. This requires that the relative accumulation rate (RAR) for that nutrient equal the relative growth rate (RGR) of the plant; thus, RAR becomes a linear function of RGR, with slope 1.0 and intercept 0.0. The case is made that failure to maintain a constant internal concentration of an element implies that the element was in limited supply and that this must hold independent of species or climatic variables.

In the simplest of cases, two conditions must be met for RAR to equal RGR: 1) the relative proportions of any plant parts (e.g., leaves, stems, roots, flower buds) differing in nutrient composition must remain the same throughout the period of interest, and 2) the nutrient composition of the different plant parts must remain constant over time. Alternatively, nutrient composition of the part(s) may change so long as the relative proportions of the parts adjust to offset the imbalance.

Ingestad and Agren (1988) address the relative proportions

of plant parts by drawing upon work by Ingestad and Lund (1979), Ingestad (1982), and Ericsson and Ingestad (1988), on birch (*Betula*) and gray alder (*Alnus*) seedlings, to postulate that the RGRs of different plant parts are nearly identical under steady-state nutrition. Raper et al. (1977b), however, found that cotton (*Gossypium hirsutum* L.) plants grown over the interval from 22 to 56 days after planting exhibited root RGRs not different than those for leaves; however, both were lower than the RGR for stems.

In this paper, we use some of the evidence presented above to develop a model for predicting the relative uptake rates of 11 mineral elements as functions of the whole-plant RGR of *Dendranthema ×grandiflorum*, cv. Fiesta.

Materials and Methods

Six experiments were conducted over a period of 3 years to determine the influence of CO₂ and irradiance on growth and nutrient uptake rates in hydroponically grown chrysanthemums (Table 1). Experiments 1-4 included only the first 4 weeks following pinching while Expts. 5 and 6 included growth through the 7th week (point of color break).

Facilities and equipment. The plants were grown in four double-polyethylene-covered greenhouses. Each was equipped with a natural-gas-fired unit heater, a two-speed fan, and an evaporative-pad cooling system. Two of the greenhouses had rockbeds attached for providing closed-loop cooling to facilitate CO₂ enrichment (Willits and Peet, 1989).

The environment was controlled via computer. Dry and wet bulb air temperature, leaf and solution temperatures, outside

Table 1. Experiment dates and treatments for chrysanthemums.

Experiment	Start date	Duration of expt. (wks)	Treatments ^z					
			CO ₂ (μl·liter ⁻¹)		Irradiance (μmol·m ⁻² ·s ⁻¹)			
			L	H	XL	L	M	H
1	25 Apr. 1985	5	330	675		830	1100	1400
2	7 Aug. 1985	5	330			830	1100	1400
3	8 Nov. 1985	5	330	675	550	830	1100	
4	29 Jan. 1986	5	330	675		830	1100	1400
5	8 Jan. 1987	8	330	675		830	1100	1400
6	19 Mar. 1987	8	330	675		830	1100	1400

^zXL = extra low; L = low; M = medium; H = high.

Abbreviations: RAR, relative accumulation rate; RGT, relative growth rate.

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solar radiation, and irradiance at canopy level were monitored every 75 sec by an Esterline Angus PD-2064 datalogger (Esterline Angus Instrument Co., Indianapolis) and recorded as 30-min averages.

Heating setpoints were 21C day/16.7C night. Venting was set to 26.7/28.1/29.4C for low vent, medium vent, and evaporative pad cooling, respectively. Means and SD of day and night air temperatures for each experiment are presented in Table 2. The highest mean temperatures were observed in Expt. 2 (28.1C day/24.6C night); the lowest in Expts. 4 and 5.

The two greenhouses with rockbeds attached were CO₂-enriched using setpoints of 675 µl-liter⁻¹ (except for Expt. 2, when the temperature was too high for enrichment) while the remaining two houses were not allowed to fall below 350 µl-liter⁻¹. Carbon dioxide was supplied as a liquid in cylinders and released via pressure regulators into the houses using conductometric controllers (Kimball and Mitchell, 1979). Table 2 presents the means and SD of the CO₂ concentrations measured in the houses for each experiment averaged over the two replications. The mean daytime CO₂ levels in the ambient treatments ranged from 340 to 423 µl-liter⁻¹ while the enriched treatments ranged from 558 to 693 µl-liter⁻¹. Ambient levels tended to be slightly higher in the winter experiments because of human respiration in the houses during periods of no ventilation.

Within each house, three levels of irradiance were maintained by shading and/or supplemental high-pressure sodium lighting to provide maximum photosynthetic photon flux (PPF) levels at solar noon of 1400, 1100, or 830 pmol-m⁻²·s⁻¹. The high level was based on the expected maximum solar noon irradiance inside the greenhouses on 21 June, and the low was based on the expected maximum solar noon irradiance on 21 Dec. Experiment 3 was an exception in that the high irradiance treatment was omitted and replaced by one of 550 µmol-m⁻²·s⁻¹.

Actual PPF levels were monitored at the tops of the plant canopies via six LI-COR Model 190 quantum sensors (LI-COR, Lincoln, Neb.) rotated weekly among the various irradiance treatments. The resulting data were regressed against outside solar radiation measured at the top of one of the greenhouses using an Eppley black-and-white pyranometer (Eppley Laboratory, Newport, R.I.). Canopy PPF levels were then predicted from the outside solar radiation data using the regressions developed above. Means and SD of daily PPF derived from this data are presented in Table 2.

Plant growth procedures. Unrooted cuttings of 'Fiesta' chrysanthemum were placed in 20-liter aerated tanks filled with distilled water and held on heated mist beds for 1 week. At the

end of the week, the tanks were moved to the greenhouses, and the distilled water was replaced with one-half strength modified Hoagland's solution. After 4 days, the half-strength solution was replaced with a full-strength solution. The concentrations of the major nutrients in the full-strength solution were (mM): 12 NO₃⁻, 2 NH₄⁺, 1 PO₄⁻³, 6 K⁺, 4 Ca²⁺, 2 Mg²⁺, 2 SO₄⁻²; those for micronutrients were (mM): 72 Fe²⁺, 93 B³⁺, 18 Mn²⁺, 1.5 Zn²⁺, 1.6 Cu²⁺, and 0.1 Mo²⁺.

The plants were transferred to 42-liter tanks at the end of the 2nd week. Two tanks were placed under each irradiance treatment, 30 plants per tank. Throughout each experiment, water was added daily to each tank to replace losses due to evaporation and transpiration. The tanks were vigorously aerated via two submerged fritted-glass diffusers connected to an air pump delivering ≈5 liters/min per tank.

Long days, either natural or forced (150-W incandescent light bulb above each 32 m² of greenhouse space, applied from midnight to 0200 HR), were imposed throughout rooting and the first week of each experiment. The plants were then pinched and given short days, either natural or forced (black plastic sheeting), for the remainder of each experiment.

In Expts. 1-4, 10 plants were randomly harvested from each tank at the end of the first week, with five plants being harvested from each tank each week thereafter. In Expts. 5 and 6, four plants were taken from each treatment (2 tanks) each week. Plants from each tank (Expts. 1-4) or each treatment (Expts. 5 and 6) were combined for weight and nutrient analysis.

Leaf area and stem length were determined, and the plants were separated into leaves, stems, roots, and flower buds, and then washed for 1 min in 0.2 N HCl and rinsed in distilled water to remove any nutrient solution residue. The parts were then dried for 24 h at 70C in a forced-air oven to obtain dry weights. Components were then ground and analyzed for nutrient content.

A sample of tissue was dry ashed at 500C and the levels of K, Ca, Mg, Fe, Mn, Zn, and Cu determined using atomic absorption spectrophotometry (Depa, 1987; Kuehny, 1988). Another sample was treated with a solution of MgNO₃, dissolved in methanol, and ashed at 450C. A turbidimetric procedure was used for S in which barium sulfate was suspended with polyvinylpyrrolidone. Spectrophotometric methods were used for the analysis of P and B. Total N was determined by a micro-Kjeldahl procedure.

Evidence of non limiting nutrient supply. Nutrient solutions were changed each week. Samples were taken of both the old and new solutions for analysis of NO₃ and NH₃, nitrogen, P, K, Mg, Ca, S, pH, and conductivity. Solution pH ranged from

Table 2. Overall means and SD² of mean daily air temperature (d = day, n = night) (°C), mean daily CO₂ concentration (µl-liter⁻¹) during daylight hours and daily total PPF (mol-m⁻²·day⁻¹).

Expt.	Air temp				CO ₂				Irradiance							
	T _d		T _n		L		H		XL		L		M		H	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	26.2	0.4	20.3	0.8	368	14	558	26	---	---	11.9	1.4	17.9	2.2	24.5	2.9
2	28.1	0.9	24.6	1.2	375	12	---	---	---	---	10.0	1.2	14.7	1.7	19.8	2.3
3	24.0	1.1	18.6	0.6	422	43	645	14	5.8	1.0	8.3	1.3	15.8	1.4	---	---
4	22.8	0.6	17.7	0.1	423	10	693	15	---	---	7.0	2.0	12.7	2.9	20.7	1.6
5	22.7	0.7	17.5	0.1	377	40	660	34	---	---	8.8	2.2	14.6	3.0	19.6	3.4
6	24.9	0.8	18.3	0.8	340	13	625	62	---	---	10.7	1.9	16.1	2.8	23.4	3.9

²SD are of the weekly (or bi-weekly in the case of Expt. 5, weeks 1 and 3) means and thus represent the variability of the associated factor from growth interval to growth interval to growth interval for each experiment.

6.5-6.8 in the fresh solutions and from 5.0-6.4 in the depleted solutions, with the lower pH values occurring toward the end of the experiments in the treatments with the highest biomass accumulation. Solution conductivities ranged from 2.0-2.2 mmh_ocm⁻¹ initially to 1.8-2.1 mmh_ocm⁻¹ at each solution change, again with the lower values occurring toward the end of the experiments in the treatments with the largest biomass accumulation.

To avoid nutrient stress, the ratio of biomass : tank volume was chosen to limit the depletion of the nutrients to <50% (depletions were generally <30% and in no case >55%), and the tanks were well stirred by the aeration pumps so that concentration gradients were minimized. The internal nutrient status of the plants did not at any time indicate that nutrients were in limited supply.

Root : shoot ratios ranged from 0.28 immediately following pinching to 0.09 during Week 8. The decrease with age was approximately logarithmic in a fashion similar to that observed by Hunt and Burnett (1973). High irradiance/high CO₂ treatments tended to produce root : shoot ratios slightly higher than low irradiance/low CO₂ treatments, corresponding to the findings of Hunt and Burnett (1973) and the extensive literature cited by Enoch and Zieslin (1988).

Data analysis. Mean RGRs for each plant part and the total plant were calculated for each interval for each treatment and replicate (tank) of the six experiments (Hunt, 1982):

$$RGR_i = (\ln W_{i+1} - \ln W_i) / N \quad [1]$$

where *i* is the interval number, *W* is dry weight (grams), and *N* is the length of the interval (days).

Weekly RARs of each plant part and the total plant for the 11 mineral elements for the six experiments were calculated for each treatment and replicate as:

$$RAR_{ji} = (\ln (C_{j,i+1} * W_{i+1}) - \ln (C_{j,i} * W_i)) / N, \quad [2]$$

where *j* represents the element and *C* is the concentration of that element.

One-week intervals were used for all calculations except Expt. 5, when the second and fourth harvests were skipped by design. We originally assumed that the first, third, and fifth harvests would be enough to match the data to the earlier, 5-week experiments. This turned out not to be the case; therefore, all eight harvests were included in Expt. 6. Thus, RAR/RGR values were found for Weeks 1-4 in Expts. 1-4, Weeks 1, 3, and 5-7 for Expt. 5 and Weeks 1-7 in Expt. 6.

Regression analysis. Raper et al. (1977a, 1977b) regressed the RAR of the whole plant against the RGR of the roots, on the assumption that uptake should be related to root mass. We regressed whole-plant RAR against RGR of the roots and whole-plant RGR, with better fits generally associated with whole-plant RGR. The results presented here, then, are based on the regressions of whole-plant RAR vs. whole-plant RGR, on the assumption that nutrient uptake might be more closely related to total plant demand, rather than amount of root mass.

The data were analyzed using simple linear regression models of RAR on RGR. Although strictly speaking, there was no prior basis for choosing RAR as the dependent variable, it is convenient, for the purposes of future modeling efforts, to be able to predict nutrient uptake rates based on RGRs. Precedent for this approach was provided by Raper et al. (1977a, 1987b).

Treatment effects [carbon dioxide (CO₂), and irradiance (IRR)], and time effects [experiment (EXP) and week (WK)] were included as class variables in the linear model

$$RAR = a + b * RGR \quad [3]$$

for each element, using the GLM procedure of SAS (SAS, 1985), and the technique suggested by Freund and Littell (1981). Terms of the model were judged to be significant or nonsignificant and included or discarded based on the Type I and Type III sum of squares (SAS Institute, 1985) with $\alpha = 0.01$. No more than two terms were discarded at the end of any given run to minimize the chance of mistakenly discarding significant terms.

Results and Discussion

Initially, only CO₂, IRR, and EXP were included as class effects in the model. Of these, only the IRR effect on intercept for two elements (N and P) and the EXP effect on the slope and intercept for some elements (P, Fe, Mn, Zn, and Cu) were found to be significant at $\alpha = 0.01$. In all but one case, however, the contribution of the corresponding class term to the model sum of squares was <4.0%. The one exception was Zn, with the effect of EXP on intercept producing a contribution to the sum of squares of 7.8%. The only significant environmental effect, that of IRR on the intercepts of N and P, contributed < 0.5% and 0.7% to the model sum of squares, respectively.

Because of the small effects of EXP and IRR on the model, and the relatively small amount of information conveyed by class variables in a model of this type, the equations are presented without these effects (Table 3). All of the regressions produced R² values > 0.70 except for Fe and Mn, which produced 0.60 and 0.50, respectively. Plots of N, P, K, and Mn illustrate the general fit of the model to the data (Fig. 1).

Corrected-intercept model. Although the data of Fig. 1 were reasonably well represented by straight lines, the deviation of the slopes from 1.0 and intercepts from 0.0 was disturbing (only Ca, B, and S had slopes not different from 1.0, and only B and Fe had intercepts not different from 0.0, all at $\alpha = 0.05$). The studies of Ingestad and Lund (1979), Ingestad (1987), and Ingestad and Agren (1988) suggest that these results indicate a limited nutrient supply, which we are reasonably confident was not the case.

Since our results appeared to deviate from the norm, we again examined our data and found that when the observations were identified by week, the data grouped into a series of straight lines, rather than a single straight line. This difference suggested a WK effect of the intercept of the linear model (no effect on the slope of the lines was observed). Lacking any information as to the expected form of this effect, polynomials of up to the 5th order in WK were used to represent the intercept, 'a', in Eq. [3], with the significance of each parameter being judged by its standard error of estimate. For all elements except B

Table 3. Estimated linear model parameters, as defined by Eq. [3], with associated SE of estimate.

Element	a	b	R ²
N	-0.014 ± 0.001	1.11 ± 0.01	0.94
P	-0.026 ± 0.003	1.32 ± 0.03	0.78
K	-0.012 ± 0.002	1.14 ± 0.02	0.90
Ca	-0.007 ± 0.002	1.00 ± 0.02	0.82
Mg	-0.010 ± 0.002	0.95 ± 0.02	0.82
S	-0.011 ± 0.002	1.02 ± 0.02	0.78
B	0.004 ± 0.002	0.96 ± 0.02	0.76
Fe	-0.016 ± 0.006	1.29 ± 0.06	0.50
Mn	-0.008 ± 0.004	1.16 ± 0.04	0.60
Zn	-0.001 ± 0.002	0.80 ± 0.02	0.71
Cu	-0.016 ± 0.003	1.14 ± 0.03	0.72

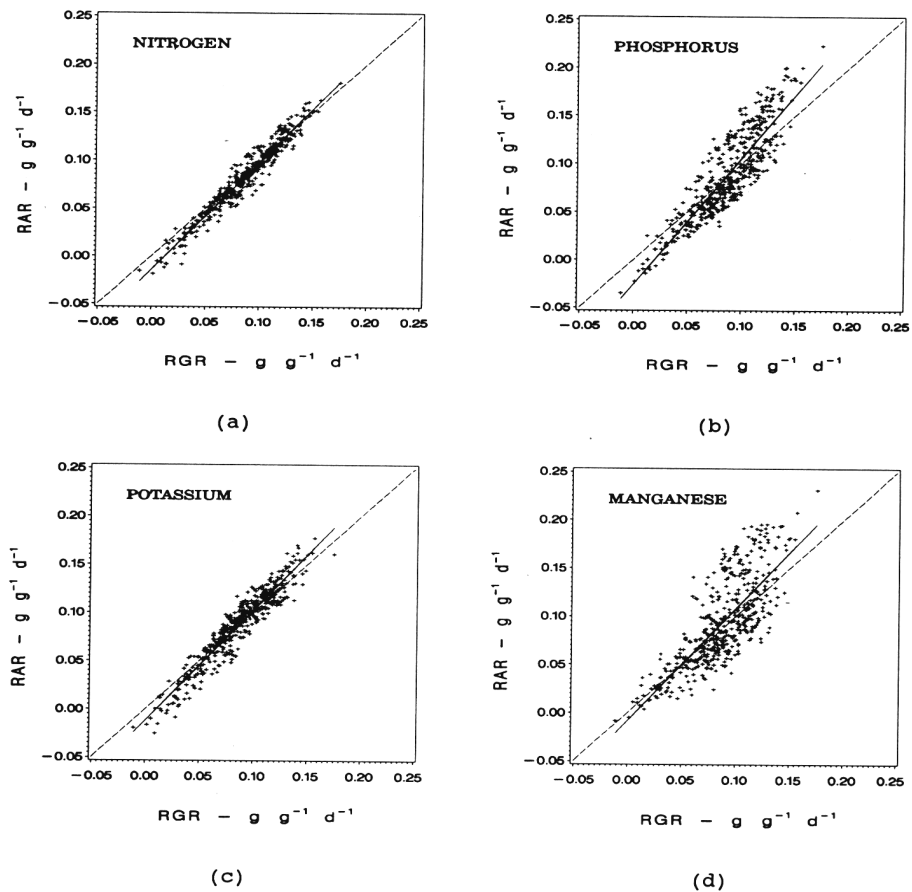


Fig. 1. RAR ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) as a function of RGR ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) for: (a) N, (b) P, (c) K, and (d) Mn for all experiments. Dashed line is slope 1.0 and intercept 0.0, solid line is Eq. [3].

(which did best with a quadratic form) the best results were obtained with a cubic function of WK,

$$a = c + d * WK + e * WK^2 + f * WK^3. \quad [4]$$

Class effects of EXP, CO_2 , and IRR were tested on the parameters c, d, e, and f of Eq. [4], as substituted into Eq [3]. Only EXP was found to be significant at $\alpha = 0.01$ (for N, P, B, Mn, and Zn). A α of 0.01 was chosen to minimize the chances of incorrectly including an effect, considering Ingstedt's (1987) statement that environmental factors should not play a role in the relationship between RAR and RGR.

Since the information provided by EXP is minimal, we determined if a further reduction in the number of equations could be accomplished. The output from the multiple equations produced for N, P, B, Mn, and Zn when EXP was included was compared with the output from individual equations for each element obtained when EXP was omitted. When the individual equation for an element produced the same shape as the multiple equations and the predicted RARs for the single equation fell within 10% of those for the multiple equations, the individual equation was deemed acceptable. The resulting estimated parameters of Eqs. [3] and [4] are presented in Table 4, along with their SE of estimate. As noted above, the 'f' term for the element B was not significant, resulting in a quadratic function of WK for 'a'. Comparing the fit of this model to that of the linear model, the correction for WK greatly improved the prediction of RAR for P, K, Ca, B, Mn, and Cu, moderately

improved the prediction for N, Mg, and Zn, and only barely improved the prediction for S and Fe.

Model behavior. The general effect of the corrected-intercept model is that RAR tends to decline with increasing age, over and above the decline associated with decreasing RGR; K and B (Expt. 4 only) were the only exceptions. In some cases, the decline was slight, as with N; in some cases it appeared to recover slightly in weeks 5 and 6, but then fell again in week 7 as in P, Ca, Mg, S, Fe, Mn, Zn, and Cu. In the exceptions noted for K and B, RAR for K increased in week 2 with a gradual decline thereafter, while RAR for B (Expt. 4) increased in week 2 and did not begin to decline until week 4. Three-dimensional plots of the equations for N, P, K, and Mn illustrate the various types of behavior (Fig. 2).

Intercept. Although the true functional dependence of 'a' on WK is unknown, we speculate that it may be a result of the different types of plant tissue being formed as the plant develops. It is known, for example, that the nutrient composition of the various plant parts changes with time, as do the proportions of the tissue type formed as the plant progresses from vegetative to reproductive growth (Duncan and Sutton, 1987; Martin-Prevel et al., 1987). Evidence for this in our data is presented in Fig. 3. The data for this plot was taken from Expt. 6 (Fig. 3) because it contained the longest continuous record over time (the trends from other experiments were similar). Although the total plant N and K followed stem concentrations most closely (after week 3, stems comprised the largest single component by weight),

Table 4. Estimates of corrected-intercept model parameters, as defined by Eqs. [3] and [4], with associated SE of estimate.

Element	Expt.	b	c	d	e	f	R ²
N	All	1.01 ± 0.01	0.0133 ± 0.003	-0.0136 ± 0.003	0.0031 ± 0.008	-0.00025 ± 0.00007	0.96
P	All	1.08 ± 0.03	0.0918 ± 0.006	-0.0853 ± 0.005	0.0208 ± 0.002	-0.00157 ± 0.00014	0.90
K	All	1.00 ± 0.02	-0.0173 ± 0.004	0.0302 ± 0.003	-0.0100 ± 0.001	0.00809 ± 0.00008	0.95
Ca	All	0.88 ± 0.02	0.0590 ± 0.005	-0.0476 ± 0.004	0.0113 ± 0.001	-0.00823 ± 0.00011	0.89
Mg	All	0.91 ± 0.03	0.0230 ± 0.005	-0.0325 ± 0.005	0.0095 ± 0.001	-0.00806 ± 0.00013	0.84
S	All	0.98 ± 0.03	0.0088 ± 0.007	-0.0169 ± 0.006	0.0050 ± 0.002	-0.00442 ± 0.00016	0.79
B	1-3,5-6	0.91 ± 0.03	0.0338 ± 0.004	-0.0135 ± 0.002	0.0014 ± 0.0002	---	0.84
	4	0.91 ± 0.03	-0.0714 ± 0.008	0.0747 ± 0.007	-0.0147 ± 0.001	---	0.84
Fe	All	1.23 ± 0.08	0.0462 ± 0.002	-0.0548 ± 0.001	0.0144 ± 0.004	-0.00111 ± 0.00038	0.52
Mn	All	0.88 ± 0.04	0.1372 ± 0.008	-0.0983 ± 0.007	0.0218 ± 0.002	-0.00149 ± 0.00018	0.84
Zn	All	0.78 ± 0.03	0.0344 ± 0.006	-0.0422 ± 0.005	0.0132 ± 0.002	-0.00115 ± 0.00014	0.75
Cu	A	0.94 ± 0.06	0.0856 ± 0.007	-0.0749 ± 0.002	0.0188 ± 0.002	-0.00146 ± 0.00017	0.83

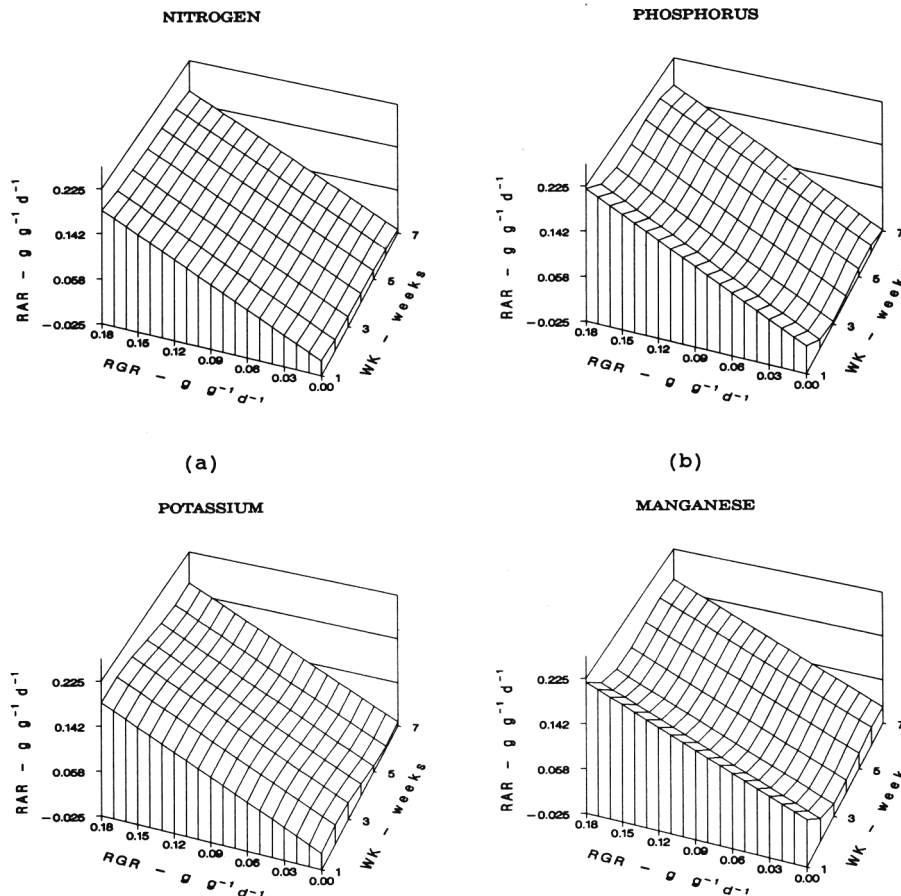


Fig. 2. RAR ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) as a function of RGR ($\text{g} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$) and time for : (a) N, (b) P, (c) K, and (d) Mn for all experiments.

they were influenced by concentrations in leaves toward the end of the experiment. Root concentrations of N and K were relatively constant and thus had little influence on the total concentrations of these elements. Zinc and Cu concentrations declined sharply in the first few weeks in leaves and roots, despite a gain in stems; thus, total concentration of Zn and Cu followed that in roots and leaves more closely than that in stems.

Rates of uptake of specific elements that adjust to meet plant needs at the time of uptake suggest a dependence on physiological rather than chronological age, and may be the reason for the statistical differences observed with EXP. The physiological age of the plants in the various experiments may well have been

different at the same chronological age because of different growing conditions; however, this experiment was not designed to test for such differences.

Systematic errors in nutrient analysis could also be responsible for the WK effect; however, it seems likely that any systematic errors would have affected the analyses of the plant parts nearly equally on any given harvest. Further, the opposing trends in concentration of the various plant parts shown in Fig. 3 suggest that any systematic errors present were small.

Slope. The corrected-intercept model reduced the estimated slope, 'b', for each element (compared to the linear model). Four elements produced slopes not significantly different from

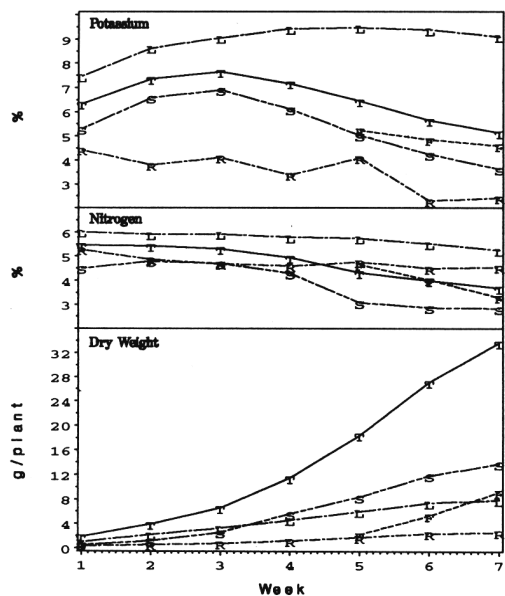


Fig. 3. Weekly dry weight and N and K concentrations in leaves (L), stems (S), roots (R), flowers (F), and total plant (T) for Expt. 6.

1.0: N ($P = 0.308$); K ($P = 0.869$); S ($P = 0.539$); and Cu ($P = 0.056$). Calcium, Mg, B, and Zn produced slopes significantly <1.0 ($P > 0.996$) while Fe produced a slope significantly >1.0 ($P = 0.997$).

The case for Ca and Mg producing slopes <1.0 is supported by Raper et al. (1977a), in their work with tobacco; however, we were unable to find support in the literature for the slopes observed for B and Zn. Slopes <1.0 suggest that the rate of dry matter production per unit of nutrient uptake is not constant with growth rate and would imply that tissue production for these elements is not equally efficient at all rates of growth or ages. This pattern may be related to the establishment and usage of storage pools and/or the conversion of storage pools to structural carbon.

The present data do not permit much insight into the meaning of slopes different from 1.0. Since RGR changes with age and with environmental factors, the fact that WK did not have a significant effect on slope may only mean that the "age" effect had already been accounted for (by the deviation from 1.0); thus, it is not clear whether a slope different from 1.0 represents an additional correction for age (beyond that of the corrected intercept)- or a correction for growth rate independent of age.

Model usage. The mechanism by which RAR is corrected is not sufficiently well known to develop a mechanistically based model at this time. Until it can be developed, the models presented here provide a means of predicting uptake rates if growth rates are known or can be predicted. Acock et al. (1979), for example, present a model for predicting growth rate in chrysanthemum. Undoubtedly, increasing demands for precision and accuracy will require that additional quantitative work be done

to better understand the effect of aging and growth on nutrient uptake.

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