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NET FLUXES OF MINERAL NUTRIENTS, WATER, AND CARBOHYDRATE INFLUENCED BY MANGANESE IN ROOT AND SHOOT OF *CUCUMIS SATIVUS* L.[1]

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ABSTRACT: An experiment was conducted with cucumber (*Cucumis sativus* L., cv. Sumter) plants in the vegetative phase of growth to determine effects of manganese deficiency (0.2 μM Mn) and toxicity (182 μM Mn) on fluxes of several mineral nutrients, water, and carbohydrate in the root and shoot, beginning 43 d after germination. Plants were sampled every three days from 34 to 58 d after germination. First and second derivatives of regression equations were used to estimate fluxes and study source/sink phenomena of dry weight (DW), fresh weight (FW), H_2O, Cu, Fe, Mn, Zn, N, P, and K in root and shoot tissues.

With Mn sufficiency (1.8 μM Mn), both root and shoot acted as sinks for of each of the 10 dependent variables through 58 d. In contrast, Mn deficiency caused net loss of K and N from the root beginning at 53 and 56 d, respectively, and net loss of P and Fe from the shoot beginning at 57 and 58 d, respectively. With Mn toxicity, net loss of Cu, N, and K from the root began at 46, 46, and 51 d, respectively, and net loss of Fe from the shoot began at

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55 d. Both Mn deficiency and toxicity increased the shoot:root ratio (S:R) of K and decreased the S:R of Fe, compared to Mn-sufficiency. Manganese deficiency decreased the S:R of DW and H_2O, and Mn toxicity increased the S:R of FW, DW, H_2O, and N. Under the conditions of this experiment, acute Mn toxicity affected fluxes more severely than did Mn deficiency.

INTRODUCTION

The root and shoot of vascular plants are interdependent, since the root supplies the shoot with mineral nutrients and water, while the shoot supplies the root with carbohydrates, and these two organs supply each other with hormones (24). Raper et al. (17) developed a model which shows the transport of total N from the root of tobacco to be dependent upon carbohydrate supply from the shoot. Transport of K from root to shoot of barley seedlings was found to be proportional to the relative growth rate of the shoot (14).

Manganese is an essential mineral nutrient which activates many enzymes in plants and can substitute for Mg to activate phosphate-transferring enzymes (9). Nitrate reductase in the root of pumpkin plants was most efficient when 0.05 $\mu g\ ml^{-1}$ Mn was supplied in nutrient solution, with much lesser efficiencies under Mn-deficient and Mn-toxic conditions (15). Manganese transport to the shoot of oat seedlings was found to be dependent upon the size of a labile fraction of Mn in the root and its rate of turnover to the shoot (13). In tomato, Mn was translocated in the xylem primarily as an inorganic cation, while Fe was translocated strongly bound to citrate in an anionic complex (23). High concentrations of Mn in the root environment increased precipitation of Fe in pineapple root and decreased translocation of Fe to the shoot (19). In wheat, radish, barley and peas, Mn toxicity was reduced or eliminated by application of Fe (1).

Mathematical models have been developed to understand various phenomena in plant physiology (11, 18) and particularly in mineral

nutrition of plants (12). The present work builds on previous studies in which derivatives of regression equations were used to examine ontogenetic aspects of N nutrition of maize (5, 6) and Mn nutrition of the whole cucumber plant (7). An experiment was conducted to test the hypothesis that Mn deficiency and toxicity effect changes in fluxes (net rates of accumulation or loss) of carbohydrate, water and seven elements in cucumber (*Cucumis sativus* L., cv. Sumter) plants, and in various organs of the plants, compared to conditions of Mn sufficiency. The cucumber plant, when considered as a one-compartment system, was found to be a sink for carbon (as indicated by flux of dry weight), H_2O, Cu, Fe, Zn, N, P, and K under conditions of Mn deficiency, sufficiency, and toxicity (7). The present paper examines fluxes of the same variables, source/sink phenomena, and relations between the shoot and root in the same plants, examining the cucumber as a two-compartment system composed of root and shoot.

MATERIALS AND METHODS

Methods of growing, sampling, and analyzing the cucumber plants used in this study have been described previously (7). Briefly, cucumber seedlings were grown under Mn deficient, sufficient, and toxic conditions in nutrient solution in a greenhouse. Uniform plants were selected for Mn treatment 28 d after germination. Sampling whole plants began at that time and continued every third day until the experiment terminated on day 58. Deficient and toxic Mn treatments began on day 43.

Plant parts were rinsed in distilled water prior to determining fresh weight, dry weight and preparation for analysis.

Statistical techniques: Dry and fresh weights of the individual samples of all plant parts were adjusted for initial plant weight at day 28 with covariance analysis. The amount of water per sample was calculated as the difference between the adjusted fresh and dry weights. The amounts of macro- and micro-

nutrients were computed as the products of nutrient concentrations in the dry tissue and adjusted dry weight for each sample. The shoot weights used hereafter were calculated as the sum of the stem and leaf values for each plant.

A regression spline modification (20) of the exponential growth function $y = \beta_0 \exp(\beta_1 t)$, where t equals the number of days after germination, was chosen to estimate the amounts of the measured variables throughout the experiment (20).

The estimated growth functions for the measured variables in this study were derived from the following general spline regression function

$$y = \beta_0 \exp[\beta_1 t + \beta_2 t^2 + \beta_3 t^3 + \beta_{10}(t-43)_+^0 + \beta_{11}(t-43)_+] \quad [1]$$

where $$(t - 43)_+^0 = \begin{cases} 1 & \text{if } t > 43 \quad [2] \\ 0 & \text{if } t \leq 43 \quad [3] \end{cases}$$

and $$(t - 43)_+ = \begin{cases} (t-43) & \text{if } t > 43 \quad [4] \\ 0 & \text{if } t \leq 43 \quad [5] \end{cases}$$

The spline regression function ordinarily is a polynomial wherein the polynomial pieces join at points called knots. The number and degrees of the polynomials as well as the number and position of the knots vary with the situation.

In this study a knot position of 43 d after germination was chosen which represents the time at which the deficient and toxic Mn treatments were initiated. If a single polynomial in the exponent is sufficient to describe the response, then $\beta_{10} = \beta_{11} = 0$ in [1].

The coefficients β_{10} and β_{11}, in particular, were found useful by Crawford, et al. (7) for estimation of major response elevations in the measured variables following the beginning of the three treatments at t=43 d. When $\beta_{10} \neq 0$, the estimated amount, y, of a dependent variable will instantaneously increase at 43 d. Such an instantaneous change of β_{10} units of the amount, y, is highly unlikely for any of the measured variables at 43 d.

Therefore, when $\beta_{10} \neq 0$, a straight line segment with rate β_1 units was used to estimate the amount accumulated between the two measurement days of t=43 and t=46. To facilitate the regression analysis and to stabilize the error variances, the data were transformed to natural logarithms for estimation of the coefficients in equation [1].

The best-fitting models were determined for each variable with standard regression procedures in the SPSSX statistical programs (21). The significant ($p<0.05$) estimated coefficients are shown in Tables 1 and 2 for shoot and root, respectively. The standard deviation of the estimate of any point on the regression curves was computed as the standard deviation, s (Tables 1 and 2), times the estimated value, because the additive error term in the fitted, logarithmic model is multiplicative in the exponential model.

The plots of the flux curves in Figs. 1 through 4 and in 5b were generated from the first derivative, y', of the estimated growth functions. The estimated curves of many of the variables with the toxic Mn treatment had significant β_{10} spline coefficients (Tables 1 and 2) resulting in curves with three segments. In those cases, the flux curves for the toxic treatment are discontinuous as seen in Figs. 1 through 4 and in Fig. 5b.

The time of maximal flux, when it occurred as the inflection of the growth curve, was determined from the second derivative, y", of the estimated growth curve by setting y" = 0 and solving for t. The day at which root or shoot changed from sink to source during the study was determined from the first derivative, y', of the estimated growth curve by setting y' = 0 and solving for t.

Analyses of variance were conducted on root weights and root nutrient concentrations and on S:R of those measurements. Comparisons were made with the LSD test between the pretreatment measurements at 43 d and post treatments of deficient, sufficient and toxic Mn measured at 58 d.

Table 1. Estimated coefficients, standard deviation (s) and coefficient of determination (R^2) of the exponential growth functions for shoot of cucumber.

Variable	Trt[a]	$\ln(b_0)$	b_1	$b_2 \times 10^2$	$b_3 \times 10^3$	b_I	b_{10}	b_{11}	s	R^2
Fresh wgt	D	10.42	-0.81	2.39	-0.19	-	-	-	.09	.99
	S	-6.60	0.36	-0.23	-	-	-	-	.11	.99
	T	-2.44	0.16	-	-	41.52	0.82	-0.12	.12	.99
Dry wgt	D	8.35	-0.79	2.26	-0.18	-	-	-	.10	.99
	S	-4.10	0.14	-	-	-	-	-	.23	.97
	T	-4.10	0.14	-	-	2.55	0.68	-0.09	.14	.98
Water	D	10.06	-0.79	2.37	-0.19	-	-	-	.09	.99
	S	-6.98	0.37	-0.24	-	-	-	-	.11	.99
	T	-2.61	0.16	-	-	38.94	0.83	-0.12	.12	.99
Mn	D	-6.50	0.43	-0.36	-	-	-	-	.23	.91
	S	-1.14	0.15	-	-	-	-	-	.20	.95
	T	0.79	0.09	-	-	2274.59	3.58	0.04	.25	.99
Cu	D	-1.09	0.13	-	-	-	-	-	.13	.98
	S	-0.90	0.13	-	-	-	-	-	.42	.90
	T	1.22	0.07	-	-	46.99	0.82	-	.11	.97
Fe	D	-14.46	0.81	-0.70	-	-	-	-	.35	.90
	S	-15.63	0.85	-0.74	-	-	-	-	.45	.92
	T	-19.28	1.03	-0.94	-	-	-	-	.33	.90
Zn	D	-2.59	0.29	-0.18	-	-	-	-	.13	.98
	S	1.66	0.11	-	-	-	-	-	.33	.92
	T	0.46	0.14	-	-	202.25	0.48	-0.08	.17	.97
N	D	-5.69	0.41	-0.33	-	-	-	-	.12	.98
	S	-3.90	0.33	-0.23	-	-	-	-	.21	.96
	T	-6.08	0.43	-0.36	-	-	-	-	.13	.97
P	D	27.61	-1.97	4.93	-0.38	-	-	-	.15	.98
	S	-1.98	0.14	-	-	-	-	-	.28	.96
	T	-9.99	0.51	-0.41	-	-	-	-	.16	.96
K	D	-3.02	0.28	-0.16	-	-	-	-	.11	.99
	S	0.36	0.13	-	-	-	-	-	.28	.95
	T	-6.81	0.46	-0.37	-	-	-	-	.14	.97

[a] Manganese treatment: D = deficient; S = sufficient; T = toxic.

Table 2. Estimated coefficients, standard deviation (s) and coefficient of determination (R^2) of the exponential growth functions for root of cucumber.

Variable	Trt[a]	$\ln(b_0)$	b_1	$b_2 \times 10^2$	$b_3 \times 10^3$	b_I	b_{10}	b_{11}	s	R^2
Fresh wgt.	D	-7.14	0.38	-0.32	-	-	-	-	.17	.94
	S	-5.82	0.32	-0.25	-	-	-	-	.15	.96
	T	1.36	0.11	-	-	20.78	0.84	-0.15	.16	.94
Dry wgt.	D	-11.09	0.40	-0.34	-	-	-	-	.15	.95
	S	-4.78	0.11	-	-	-	-	-	.18	.96
	T	-5.15	0.12	-	-	0.65	0.77	-0.13	.15	.96
Water	D	-7.20	0.38	-0.32	-	-	-	-	.17	.94
	S	-5.96	0.33	-0.25	-	-	-	-	.15	.96
	T	-1.40	0.11	-	-	20.16	0.85	-0.15	.16	.94
Mn	D	3.62	-	-	-	-	-	-	.34	.99
	S	0.95	0.07	-	-	-	-	-	.38	.62
	T	2.56	0.02	-	-	565.10	3.77	-	.39	.95
Cu	D	2.01	0.06	-	-	20.4	0.27	-	.10	.94
	S	1.68	0.07	-	-	-	-	-	.15	.92
	T	1.36	0.08	-	-	57.31	0.69	-0.09	.13	.94
Fe	D	5.28	0.09	-	-	-	-	-	.10	.96
	S	5.74	0.08	-	-	-	-	-	.21	.92
	T	5.13	0.10	-	-	3765.52	0.41	-0.05	.15	.95
Zn	D	-3.15	0.27	-0.21	-	-	-	-	.18	.92
	S	1.34	0.08	-	-	-	-	-	.24	.89
	T	0.01	0.11	-	-	40.46	0.39	-0.09	.20	.92
N	D	-8.18	0.45	-0.40	-	-	-	-	.21	.89
	S	-5.77	0.33	-0.26	-	-	-	-	.23	.93
	T	-1.80	0.13	-	-	22.55	0.55	-0.15	.21	.89
P	D	-20.68	1.28	-2.37	0.15	-	-	-	.08	.96
	S	-7.04	0.34	-0.27	-	-	-	-	.18	.96
	T	-2.81	0.13	-	-	7.04	0.57	-0.13	.17	.95
K	D	33.16	-2.34	-5.85	-0.46	-	-	-	.23	.93
	S	-4.70	0.30	-0.22	-	-	-	-	.19	.94
	T	-10.82	0.61	-0.60	-	-	-	-	.19	.84

[a] Manganese treatment: D = deficient; S = sufficient; T = toxic.

RESULTS

When influx exceeds efflux, the net flux, or simply "flux" (y') has a positive value, indicating that part of the plant is a sink for a particular substance. As a positive flux approaches zero, the relationship between influx and efflux of the substance flowing through the compartment approaches equilibrium. When the value of the flux is zero, the compartment acts as neither source nor sink for the substance under consideration. When efflux of a substance exceeds influx, the value of flux is negative and the compartment acts as a source of the substance.

Fluxes of Mn: Flux is expressed as the estimated rate of change of mass of a substance in either the root or shoot per day per plant. With Mn sufficiency, the Mn flux continually increased in root and shoot (Figs. 1a, 1c). With Mn deficiency, however, Mn flux in the root was estimated to be at equilibrium during the 30-d experimental period, and Mn flux in the shoot continued to increase until 47 d (Table 3), and then declined until the end of the study. When acute Mn toxicity was induced at 43 d, a relatively large increase in Mn flux occurred in both the root and shoot (Figs. 1b, 1d). After three days, the Mn flux in both root and shoot declined very rapidly to estimated values larger than the estimated fluxes before the Mn-toxic treatment was begun. During the remaining 12 d, Mn flux in the root increased only slightly, but Mn flux in the shoot continued to increase ever more rapidly.

Fluxes of fresh weight, dry weight and water: Fluxes of fresh weight (FW) and water (H_2O) in the root follow similar patterns of increase, maximum flux, and then decline for Mn sufficiency (Figs. 2a and 2c, Table 3). In the Mn-sufficient shoot, however, the fluxes of FW and H_2O continued to increase during the entire experimental period (Figs 2d and 2f). Dry weight (DW) flux in both the root and shoot of Mn-sufficient plants continued to increase during the entire period (Figs. 2b and 2e).

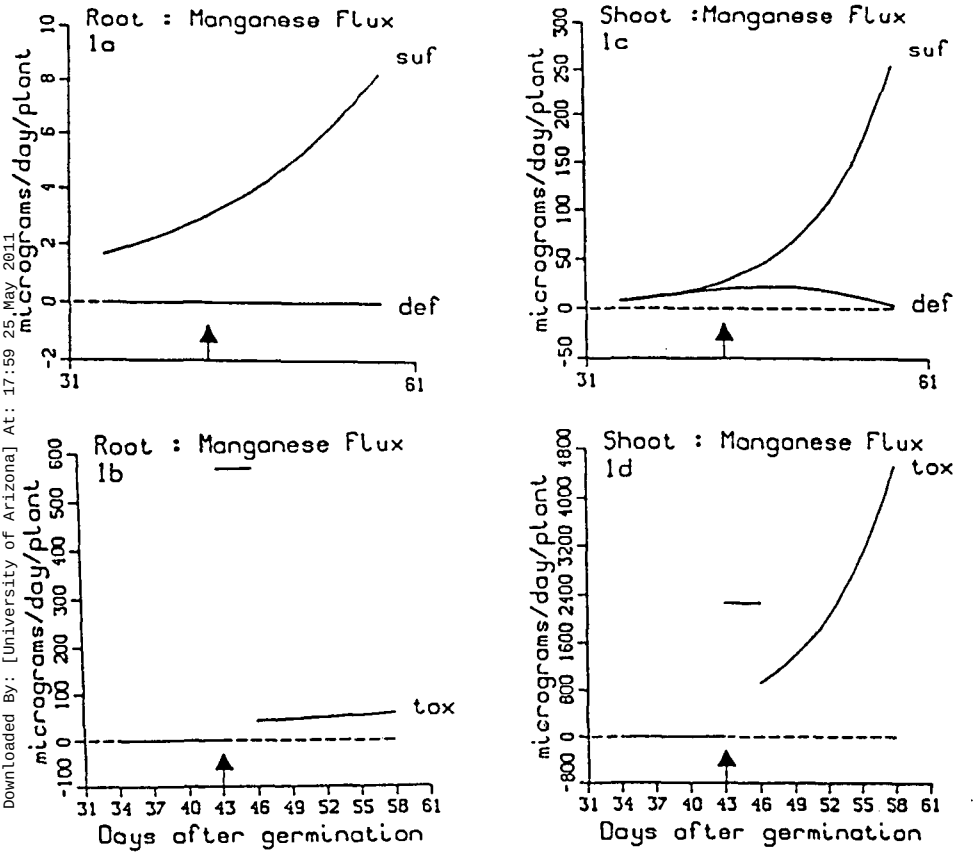

Figure 1. Fluxes of Mn in root of cucumber (a) with Mn sufficiency and Mn deficiency and (b) with Mn toxicity and in shoot of cucumber (c) with Mn sufficiency and Mn deficiency and (d) with Mn toxicity. Arrows indicate the number of days after germination on which Mn deficiency and Mn toxicity were introduced, and dashed lines indicate zero flux.

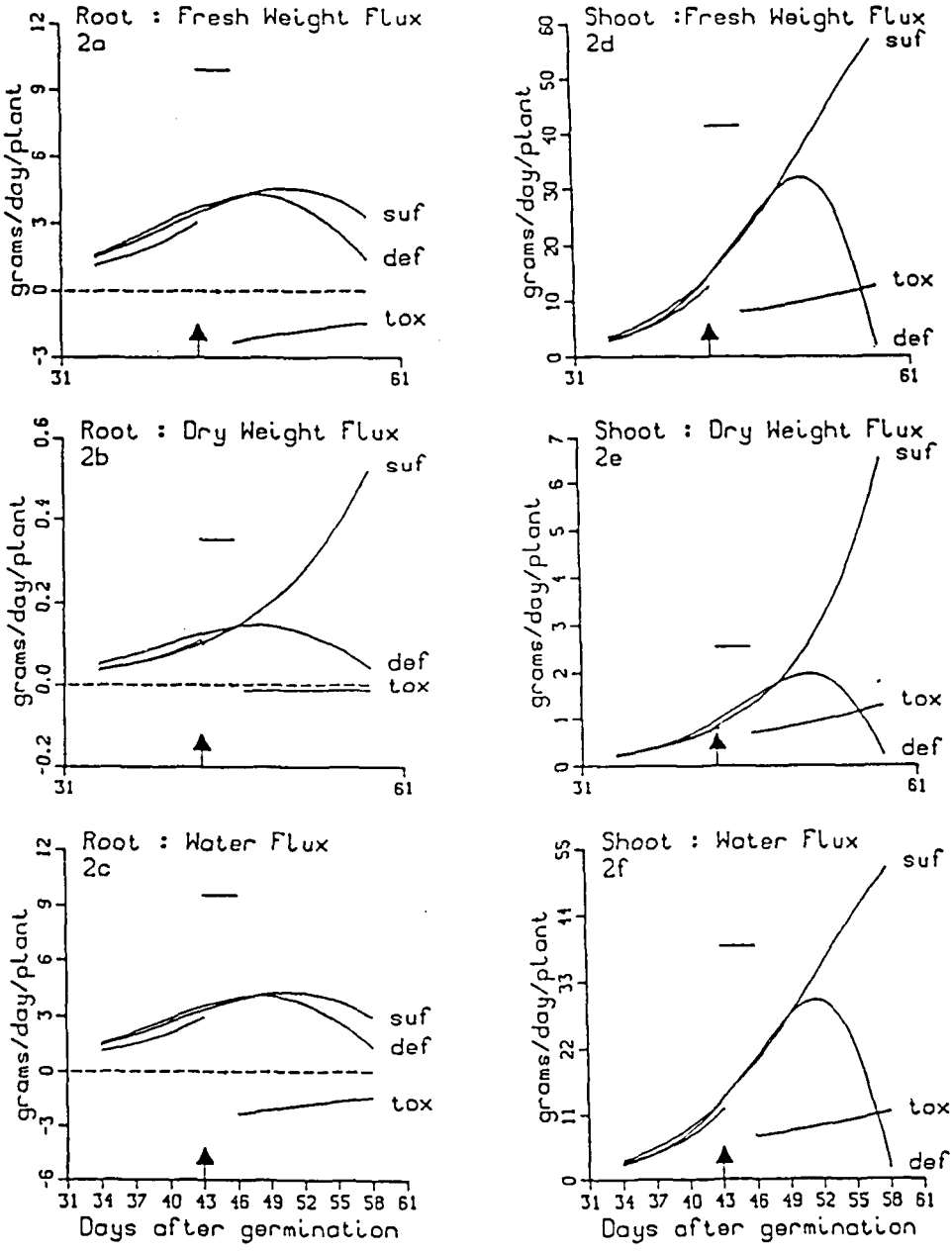

Figure 2. Fluxes of (a) fresh weight, (b) dry weight, and (c) water in root of cucumber and fluxes of (d) fresh weight, (e) dry weight, and (f) water in shoot of cucumber. Arrows indicate the number of days after germination on which Mn deficiency and Mn toxicity were introduced, and dashed lines indicate zero flux.

Table 3. Day after germination when maximum fluxes occurred in root and shoot of cucumber during the 58-day study.

Variable	Deficient	Sufficient	Toxic
Root			
Mn	58	58	43-46
Fresh weight	48	51	43-46
Dry weight	48	58	43-46
Water	48	51	43-46
N	45	50	43-46
P	58	50	43-46
K	47	54	42
Cu	43-46[a]	58	43-46
Fe	58	58	43-46
Zn	50	58	43-46
Shoot			
Mn	47	58	58
Fresh weight	52	58	43-46
Dry weight	51	58	43-46
Water	52	58	43-46
N	50	55	48
P	51	58	51
K	58	58	50
Cu	58	58	43-46
Fe	49	49	47
Zn	58	58	43-46

[a] Maximal flux is estimated to have been constant from 43 d through 46 d after germination.

Deficiency of Mn depressed the flux of FW, DW, and H_2O in both the root and shoot (Figs. 2a through 2f). After reaching maxima (Table 3) the fluxes of FW, DW, and H_2O decreased more precipitously in the shoot (Figs. 2d,e,f) than in the root (Figs. 2a,b,c).

Acute Mn toxicity severely affected fluxes of FW, DW, and H_2O in both the roots and shoots of the cucumber plants (Figs. 2a-f). Fluxes of FW, DW, and H_2O in the root from day 46 through 58 d were negative, indicating that the root had changed from sink

Table 4. Day after germination when root or shoot of cucumber changed from sink to source of fresh weight, dry weight, H_2O, N, P, K, Cu, Fe or Mn.

Variable	Manganese Treatment		
Root	Deficient	Sufficient	Toxic
Fresh weight	46	-	-
Dry weight	46	-	-
Water	46	-	-
N	56	-	46
K	53	-	51
Cu	-[a]	-	46
Shoot			
P	57	-	-
Fe	58	58	55
Mn	-	-	-

[a] A dash (-) indicates that there was no change from sink to source during the experiment.

to source of FW, DW, and H_2O (Table 4). However, during the same period the shoot remained a sink for FW, DW, and H_2O.

Fluxes of N, P and K: Fluxes of N, P, and K in the root of Mn-sufficient plants increased (Table 3) and then decreased (Figs. 3a,b,c). In the Mn-sufficient shoot, the N flux increased (Table 3) then declined (Fig. 3d). In contrast, with sufficiency of Mn, the fluxes of P and K in the shoot continued to steadily increase during the experiment (Figs. 3e,f).

Manganese deficiency imposed at 43 d was accompanied by increased fluxes of N and K in the root until 45 and 47 d, respectively, when maximal fluxes were reached (Table 3). During the subsequent declines of N and K fluxes, the root became a source of N and K at 56 and 53 d, respectively (Table 4). In contrast, P flux in the root continually increased after Mn deficiency was imposed, resulting in P flux about 4 times higher

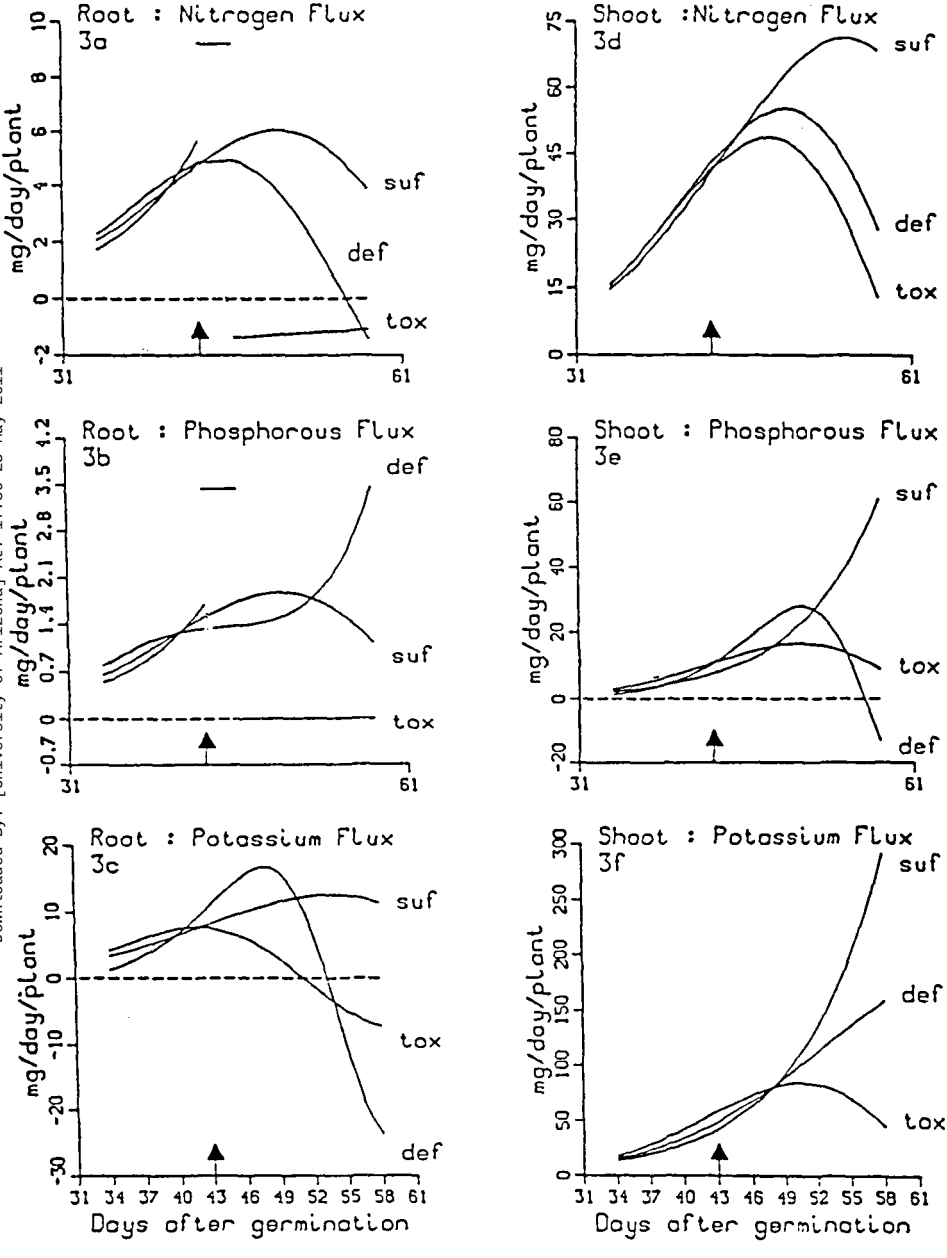

Figure 3. Fluxes of (a) N, (b) P, and (c) K in root of cucumber and fluxes of (d) N, (e) P, and (K) in shoot of cucumber. Arrows indicate the number of days after germination on which Mn deficiency and Mn toxicity were introduced, and dashed lines indicate zero flux.

than the flux with Mn sufficiency at 58 d (Fig. 3b). In the shoot with Mn deficiency, fluxes of N, P, and K were less than with Mn sufficiency (Figs. 3d,e,f).

Toxicity imposed at 43 d resulted in abrupt increases in N and P fluxes in the root, followed by abrupt decreases in flux at 46 d (Figs. 3a,b). At 46 d (Table 4), the root suffering Mn toxicity changed from sink to source of N, but the root was at equilibrium after 46 d with respect to P (Fig. 3b). The root changed from sink to source of K at 51 d (Table 4, Fig. 3c). In the shoot, Mn toxicity diminished flux of N and K relative to sufficiency and deficiency of Mn through the duration of the study. Maximum flux of P into the shoot occurred at 51 d (Table 3) and declined thereafter.

Fluxes of Cu, Fe and Zn: With Mn sufficiency, the familiar pattern of steadily increasing fluxes was observed for Cu, Fe, and Zn in the root (Figs. 4a,b,c) and for Cu and Zn in the shoot (Figs. 4d,f). For Fe in the Mn-sufficient shoot (Fig. 4e), however, flux increased until it reached a maximum at 49 d (Table 3), then decreased with the shoot changing from a sink to source of Fe on 58 d (Table 4).

The root was a sink for Cu, Fe, and Zn under conditions of both Mn sufficiency and deficiency. Manganese deficiency first resulted in an abrupt increase in Cu flux in the root, with an abrupt decrease at 46 d, followed by steadily increasing flux, through 58 d (Fig. 4a). Iron flux in the root of Mn-deficient plants was consistently higher than in the root of Mn-sufficient plants (Fig. 4b). Zinc flux in the root of the plants with Mn deficiency increased from 43 to 50 d (Table 3), then declined at 58 d (Fig. 4c). In the shoot of Mn-deficient plants, Cu flux continued to increase as in the Mn-sufficient plants (Fig. 4d). With both Mn deficiency and Mn sufficiency, Fe flux in the shoot reached a maximum at 49 d (Table 3) and the shoot changed from sink to source of Fe at 58 d (Table 4). Zinc flux in the shoot of Mn-deficient plants continued to increase (Fig. 4f).

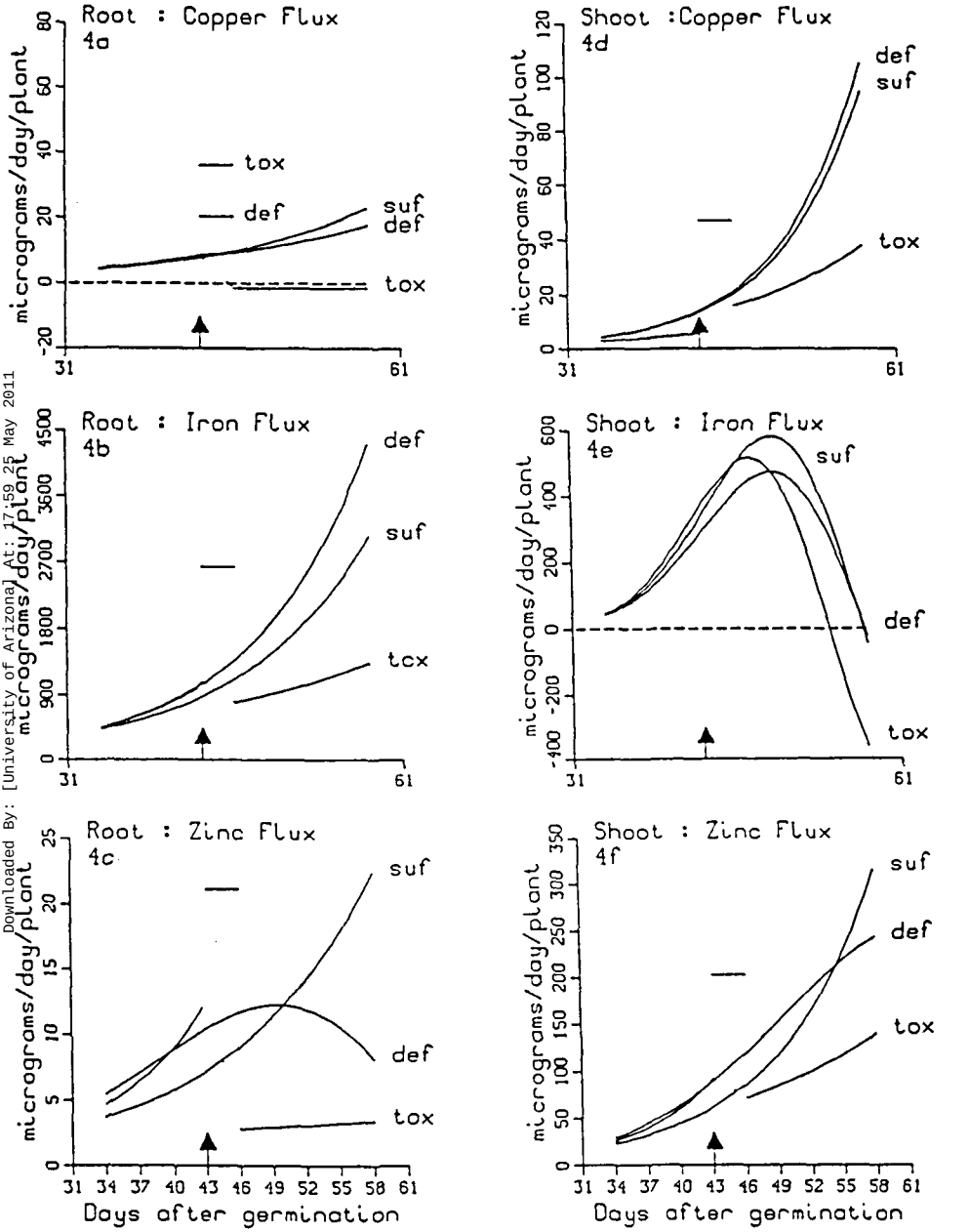

Figure 4. Fluxes of (a) Cu, (b) Fe, and (c) Zn in root of cucumber and fluxes of (d) Cu, (e) Fe, and (f) Zn in shoot of cucumber. Arrows indicate the number of days after germination on which Mn deficiency and Mn toxicity were introduced, and dashed lines indicate zero flux.

In the root with Mn toxicity flux patterns of Cu, Fe, and Zn (Figs. 4a, b, c) are similar to the flux patterns of FW, DW, H_2O (Figs. 2a, b, c), Mn (Fig. 1b), N and P (Figs. 3a, b). This general pattern is characterized by an abrupt increase of flux upon beginning the acute toxicity of Mn, followed by three days of relatively high flux at a rate estimated to be constant, then an abrupt decrease in flux at 46 d, followed by a constant or slowly increasing, relatively low flux. This pattern was also exhibited in the shoot of plants subjected to abrupt imposition of Mn toxicity for the variables FW, DW, H_2O (Figs. 2d,e,f), Cu, and Zn (Figs. 4d,f). With Mn toxicity, Cu appears to have been lost from the root at a constant rate with small absolute value after 46 d. Copper accumulated in the shoot and Zn accumulated in both the root and shoot from the day Mn toxicity was imposed.

Maximum flux of Fe into the shoot occurred at 47 d (Table 3), and at 55 d the shoot became a source of Fe (Table 4). Iron accumulated to a greater extent in the root than in the shoot (Fig. 5a). During the three days following imposition of acute Mn toxicity, the relatively high Fe flux from 43 to 46 d in the root (Fig. 5b) corresponds to the rapid increase in the estimated amount of Fe in the root from 43 d to 46 d (Fig. 5a). The change of Fe flux in the shoot from positive to negative at 55 d (Table 4, Fig. 5b) indicates approximately the day on which the shoot changed from sink to source of Fe under conditions of Mn toxicity. The change of the second derivative for the shoot from positive to negative occurs when $y'' = 0$ at 47 d (Fig. 5c) and indicates the day on which the Fe flux of the shoot reached a maximum (Table 3, Fig. 5b).

Root fresh weight, dry weight and nutrient concentrations: Fresh and dry weights of the root increased between 43 and 58 d with deficiency, sufficiency, and toxicity of Mn (Table 5). After 15 d of Mn deficiency or sufficiency, the Mn concentration in the roots did not differ ($P<0.05$) from the concentration of Mn at 43 d (Table 5). With Mn toxicity treatment, however, the concentration

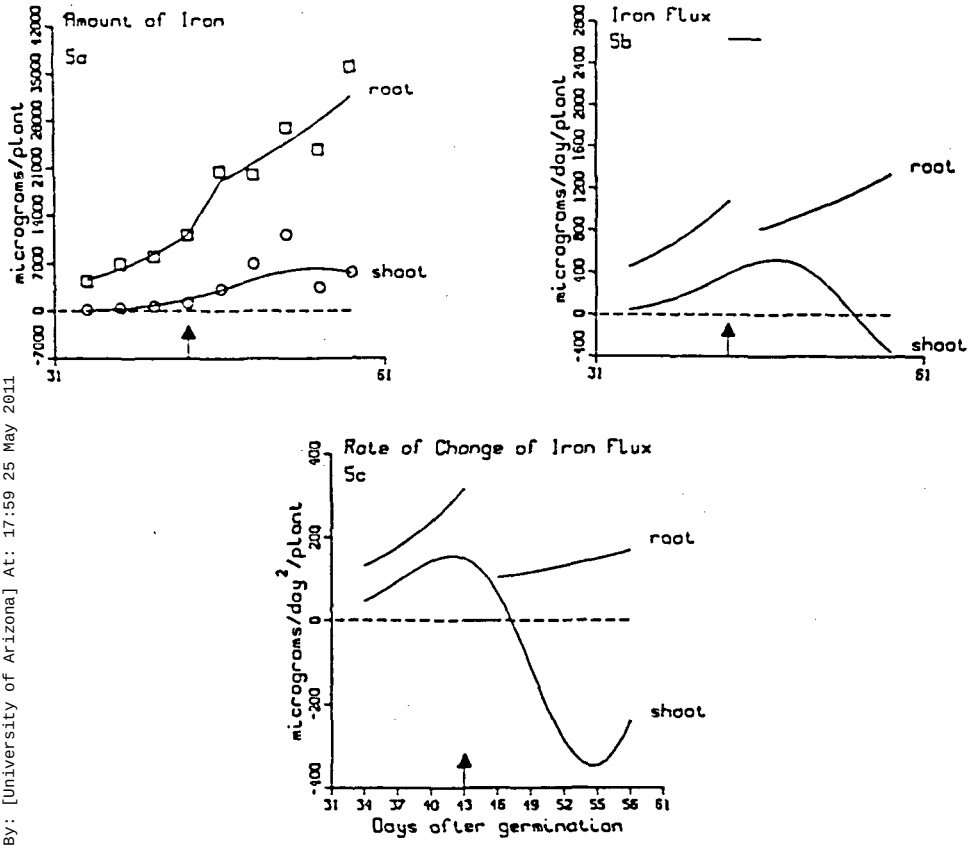

Figure 5. (a) Amounts, y, (b) fluxes, y', and (c) the rate of change of flux, y", of Fe in the root and shoot of cucumber plants treated with Mn sufficiency before day 43 and after day 43 with Mn toxicity. Arrows indicate the number of days after germination on which Mn was introduced, and dashed lines indicate zero amount, flux, or rate of change of flux.

of Mn in the dry root tissue increased about 20-fold from 62 to 1184 μg g^{-1} (Table 5). Dry root tissue concentrations of Cu and Zn did not change from 43 to 58 d with the Mn-deficient and Mn-toxic treatments, but at 58 d, concentrations of Cu and Zn were significantly lower ($P<0.05$) for the Mn-sufficient plants (Table

Table 5. Fresh and dry weights of the root and concentrations of Cu, Fe, Mn, Zn, N, P, and K of the dry root tissue of cucumber at 43 and 58 days after germination

Day	Trt[a]	FW[b]	DW	Cu	Fe	Mn	Zn	N	P	K
		g		$\mu g\ g^{-1}$				% (w/w)		
43	P	28.4[c]	0.95[c]	115[a]	11738[b]	62[b]	111[a]	4.83[a]	1.41[b]	7.12[a]
58	D	91.3[a]	2.92[b]	114[a]	18211[a]	17[b]	117[a]	3.35[b]	1.56[a]	4.96[c]
58	S	95.3[a]	4.19[a]	83[b]	9384[b]	33[b]	72[b]	3.41[b]	0.94[c]	6.03[b]
58	T	40.7[b]	1.87[b]	119[a]	19397[a]	1184[a]	117[a]	3.52[b]	1.40[b]	4.99[c]

[a] Manganese treatment: P = Mn-sufficient pretreatment; D = Mn-deficient; S = Mn-sufficient; T = Mn-toxic.
[b] Means followed by the same letter in the same column are not significantly different at the 5% significance level by protected LSD test.

5). Root tissue concentration of Fe for Mn-sufficient plants did not change between 43 and 58 d, but with Mn deficiency and Mn toxicity Fe concentration did increase.

The concentration of N in the roots decreased from 43 to 58 d for all three treatments, and at 58 d there was no difference among the three treatments (Table 5). Phosphorus concentration in the root was the same at 43 and 58 d with Mn toxicity, but P concentration increased with Mn deficiency and decreased with Mn sufficiency (Table 5). Potassium concentration in the root decreased with all three Mn treatments, but the decreases were greater with the stresses of Mn deficiency and Mn toxicity (Table 5).

Shoot:root ratios: The S:R of DW and H_2O were greater at 58 d than at 43 d for each of the three Mn treatments, and they increased as Mn concentration in the nutrient solution increased from deficient to toxic (Table 6). The S:R of FW also increased, but there was no difference between Mn-deficient and Mn-sufficient plants at 58 d (Table 6). The S:R of Cu increased for all three Mn treatments during the 15-day period following introduction of Mn deficiency and Mn toxicity, but Mn and Zn S:R did not change significantly during the same period (Table 6). The S:R for Fe did not increase significantly with Mn deficiency or toxicity, but in the Mn-sufficient plants, S:R of Fe increased twofold during the same period (Table 6). The S:R of N increased most with Mn toxicity and to a lesser extent with Mn sufficiency and deficiency (Table 6). There was no significant increase in S:R of P with Mn deficiency, but with Mn sufficiency and toxicity, S:R of P increased between two and three times (Table 6). Manganese sufficiency did not significantly increase the S:R of K but with both Mn deficiency and toxicity, there was a significant increase in S:R of K (Table 6).

DISCUSSION AND CONCLUSIONS

The results of this experiment with cucumber show that availability of Mn in the root environment influences fluxes of

Table 6. Shoot:root ratios of dry weight, fresh weight, water, Cu, Fe, Mn, Zn, N, P, and K of the cucumber plant at 43 and 58 days after germination

Day	Trt[a]	DW[b]	FW	H_2O	Cu	Fe	Mn	Zn	N	P	K
43	P	2.8^{d}	6.4^{c}	2.7^{d}	0.8^{b}	0.12^{b}	2.2	5.9	6.9^{c}	3.9^{b}	5.0^{b}
58	D	4.9^{c}	10.1^{b}	4.7^{c}	2.0^{a}	0.12^{b}	7.3	9.5	10.8^{b}	7.3^{ab}	12.8^{a}
58	S	5.5^{b}	10.3^{b}	5.3^{b}	2.0^{a}	0.24^{a}	10.2	9.4	9.1^{b}	9.5^{a}	8.6^{b}
58	T	7.9^{a}	13.0^{a}	7.6^{a}	2.1^{a}	0.15^{b}	14.3	10.7	14.4^{a}	10.0^{a}	14.8^{a}

[a] Manganese treatment: P = Mn-sufficient pretreatment; D = Mn-deficient; S = Mn-sufficient; T = Mn-toxic.
[b] Ratios of all variables are weight:weight and means followed by the same letter in the same column are not significantly different at the 5% significance level by protected LSD test.

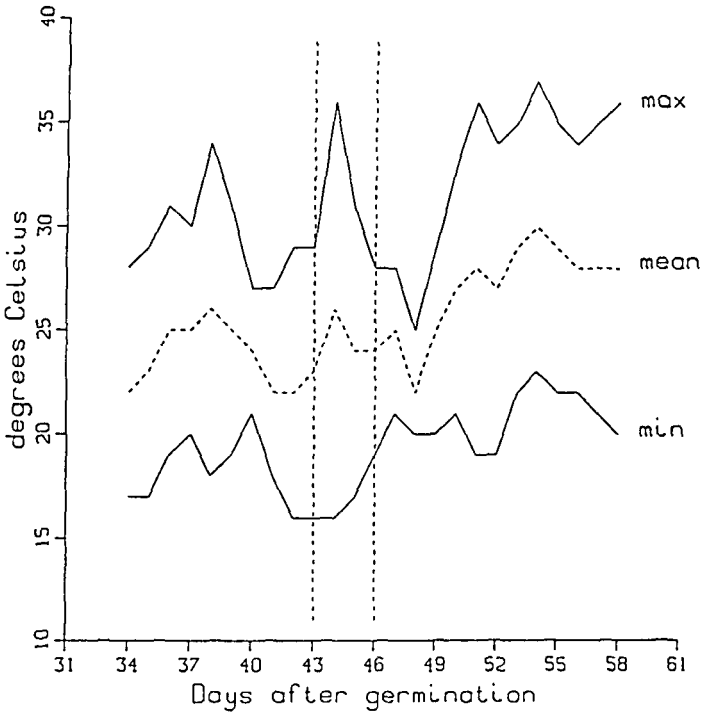

Figure 6. Low, mean, and high daily air temperatures (C) in the glasshouse in which cucumbers of the present study were grown. Vertical dashed lines indicate the three-day period in which temporarily and relatively high fluxes occurred for many variables with the Mn toxicity treatment.

the element itself, and also fluxes of carbohydrate, H_2O,Cu, Fe, Zn, N, P, and K in the root and shoot during the vegetative phase of growth. Of particular interest are the extremely high fluxes of FW, DW, H_2O, N, P, Cu, Fe, Mn, and Zn in the root and of FW, DW, H_2O, Cu, Mn, and Zn in the shoot during a three-day period following the imposition of acute Mn toxicity. Coincidentally, during this period, air temperatures in the greenhouse were relatively high, compared to air temperatures during the preceding and subsequent three-day periods (Fig. 6). Interaction of

temperature and Mn affects the severity of Mn toxicity since greater uptake of Mn can occur at higher temperatures and plants can be more tolerant of Mn at higher temperatures (10). When temperature of the rooting medium for bean plants was increased from 20 to 35°C, shoot growth rate initially increased, but then stopped as the root ceased to function (3).

Levels of important hormones may increase and decline within hours (8), and it has been shown that Mn toxicity accelerates auxin inactivation by means of 1) Mn catalyzing the oxidation of auxin protectors and 2) accelerating the oxidation of IAA by endogenous peroxidases (22). Further research is needed to explain the temporarily high fluxes associated with the onset of acute Mn toxicity in the present study.

In the present study, the root acted as a greater sink for Fe than did the shoot (Table 6). Fluxes of Fe were consistently higher in the root than in the shoot while for the other nine dependent variables, fluxes in the shoot were greater than those in the root in all but one case (P with Mn deficiency during the last two days of the study). In a previous study with pineapple and nutrient solutions, most of the Fe was deposited in the exodermal tissues of the root and was insoluble and unavailable, while a small portion was translocated to the leaves (19). A similar situation occurred in the present experiment. With Mn toxicity, Fe fluxes in both root and shoot were altered (Figs. 5a,b,c) in different ways. Also, at 58 d, the concentration of Fe in the root of the plants with Mn toxicity was about the same as in the root of the plants which were deficient in Mn, and both of these Fe concentrations were between two and three times the Fe concentration in the root of the Mn-sufficient plants (Table 5). Such a difference is explained by the fact that DW flux in the root of both Mn-deficient and Mn-toxic plants decreased, compared to the root of Mn-sufficient plants (Fig. 2b).

From 43 to 58 d in the Mn-sufficient plants, S:R of all variables except Mn, Zn, and K increased, indicating that as the

cucumber developed under conditions of relatively little stress, larger proportions of DW, FW, H_2O, Cu, Fe, N, and P were allocated to growth of the aerial parts of the plant, compared to the root (Table 6). Stress of Mn deficiency resulted in a greater proportion of DW, H_2O, and Fe to the root by 58 d, compared to the Mn-sufficient plants (Table 6). In contrast, by 58 d, the Mn-deficient plants had a higher proportion of K in the shoot than did the Mn-sufficient plants. In an experiment using nutrient solution, the FW S:R of maize decreased when N was omitted from the medium, indicating that root growth was favored under conditions of N deficiency (4). Since FW is a function of both DW and H_2O, it is not clear whether with N deficiency, the fluxes of DW and H_2O in the maize shoot changed. In the present study, although at 58 d, the FW S:R were the same for Mn-sufficient and Mn-deficient plants, the significantly lower DW and H_2O S:R of the Mn-deficient plants (Table 6) resulted from sharply decreasing fluxes of DW and H_2O in the shoot which began at 51 d (DW) and 52 d (H_2O), respectively (Figs. 2e, 2f, Table 3).

After the plants had been stressed by Mn toxicity for 15 d, proportionately more DW, FW, H_2O, N, and K were found in the shoot, compared to the Mn-sufficient plants (Table 6). On the other hand, at 58 d the Mn-toxic plants contained proportionately less Fe in the shoot, compared to the Mn-sufficient plants (Table 6). Manganese toxicity stressed the root more than the shoot, as evidenced by the relatively high S:R's of DW, FW, H_2O, N, and K (Table 6) and by the change of the root, but not the shoot, to a source of DW, FW, H_2O, N, K, and Cu (Figs. 2a,b,c; 3a,c; 4a).

Studying relative growth rates and relative accumulation rates of N and soluble carbohydrates in tobacco, Raper et al. (17) concluded that both root extension and N uptake depend on carbohydrate supply from the shoot. During the present experiment, in plants with Mn-sufficiency, N flux increased, reached a maximum, then gradually decreased in both the root and shoot. The fact that the dry weight flux in both root and shoot

continued to increase during the entire period suggests that C fixation was not limiting the plant growth. Pitman (14) pointed out that during the early stages of development of cereals, uptake of N is rapid, but then decreases, in spite of increasing dry weight. He noted that as the cereals mature, N is remobilized from various sources of stored N to sinks for N. Work on source/sink phenomena in maize has similarly shown that N was remobilized and translocated to the grain (6). The decrease in N accumulation in the root and shoot of the Mn-sufficient plants of the present study suggests that N was being remobilized to support continued vegetative growth.

Relative growth rate (y'/y, where y = amount of dry weight and y' = flux, or net rate of dry weight) has been used to explain S:R relationships of carbohydrates and N in tobacco seedlings (17) and S:R relationships in K nutrition of barley seedlings (14). In both cases, the investigators restricted their analysis to the exponential period of growth described by a simple exponential model, $y = \beta_0 \exp(\beta_1 t)$. As can be seen by Figs. 1 to 5 and Tables 1 and 2, however, our observations also include phenomena which must be described by a more complex exponential model.

Typically, the plants with Mn sufficiency had constant relative growth rates (RGR) and constant relative accumulation rates (RAR, or y'/y, where y = amount of a nutrient and y' = flux, or net rate of accumulation or loss of a nutrient). For example, during the interval from 34 to 58 d, RGR of the Mn-sufficient plants was constantly 0.137 g g^{-1} d^{-1} for the shoot and 0.109 g g^{-1} d^{-1} for the root. In contrast, for the Mn-deficient plants from 43 d to 58 d, RGR of the shoot declined from 0.152 g g^{-1} d^{-1} to 0.008 g $g^{-1}d^{-1}$ and RGR of the root declined from 0.115 g g^{-1} d^{-1} to 0.015 g g^{-1} d^{-1}. From 43 d to 58 d, RGR of cucumber plants with Mn toxicity was estimated as constantly 0.051 g g^{-1} d^{-1} for the shoot and constantly -0.007 g g^{-1} d^{-1} for the root.

As RGR decreased in the shoot of the Mn-deficient plants, the shoot changed from sink to source of Mn at 46 d (Fig. 1c, Table 4). In the shoot of the Mn-sufficient plants, the Mn flux continually increased as the RGR remained constant. From 46 to 58 d, Mn flux increased in the shoots with Mn toxicity while the RGR remained constant. Similar observations can be made regarding the behavior of dependent variables other than Mn. These results show that accumulation and loss of mineral nutrients in roots and shoots can be influenced by variables other than carbohydrate supply from photosynthetic organs. Manganese stress caused changes not only in relative growth rate, but also in relative rates of accumulation of Mn and other essential nutrients.

Noting that the shoot of vascular plants depends upon the root for a supply of essential mineral nutrients, Brouwer (2) has stated that any treatment which increases uptake of minerals and water is likely to increase shoot growth relative to root growth. The results of the present experiment (Table 6) support Brouwer's hypothesis. At the end of the Mn sufficiency pre-treatment period (43 d), dry weight S:R was 2.8. Two weeks later, with Mn deficiency, the ratio was 4.9, with Mn sufficiency it was 5.5, and with Mn toxicity 7.9. Even though the stresses of Mn deficiency and Mn toxicity inhibited the accumulation of dry weight in both shoot and root (Figs. 2b, 2e, Table 5), the S:R of dry weight varied according to Brouwer's hypothesis. Water S:R values at 43 and 58 d show a similar pattern (Table 6), however, the S:R ratios of the other variables do not similarly range from low to high within the deficient to toxic range (Table 6).

Partitioning of mineral nutrients to the shoot and root appears to have been affected by Mn stress only in the cases of Fe, N, and K. With stress of both Mn deficiency and toxicity, S:R for Fe was about one-half that of Mn-sufficient plants, and S:R for K was about 1.6 times higher than that of Mn-sufficient plants at 58 d (Table 6). To understand why the partitioning of Fe and K are so affected by both deficiency and excess of Mn will require

further research. The S:R of N was higher in the Mn-toxic than in the Mn-sufficient and Mn-deficient plants, suggesting that nitrogenous compounds in the shoot tended to be conserved under conditions of Mn toxicity, whereas they may have been translocated to the root to a greater extent in the plants not stressed by Mn toxicity.

Hormones play a part in the regulation of many biochemical processes. Manganese is known to accelerate auxin inactivation, and cotton and morning glory plants showing Mn toxicity symptoms have been shown to have abnormally low levels of IAA (22). It is probable that cucumber stressed by Mn toxicity suffered very low levels of IAA. Manganese deficiency resulted in reduced accumulation of DW in both shoot and root (Figs. 2b, 2e). The DW decreased fluxes may have resulted from decreased activity of enzymatic reactions of the citric acid cycle which require Mn for maximal activity; moreover, photosystem II has been shown to be inhibited by Mn deficiency (16).

This study shows that by dividing a system (the whole plant) into component parts (root and shoot), sources and sinks of carbohydrate (DW), H_2O, and mineral nutrients can be identified. Fluxes and times at which the root and shoot of the plant changed from sink to source have been estimated. Fluxes of DW, H_2O and seven mineral nutrients in cucumber are shown to be affected by Mn deficiency and toxicity. Further research is needed to understand effects of mineral deficiencies and toxicities upon hormonal and enzymatic activity in plants.

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