Plant Physiol. (1980) 65, 286–290
0032-0889/80/65/0286/05/$00.50/0

Nitrate Uptake by Roots as Regulated by Nitrate Assimilation in the Shoot of Castor Oil Plants

Received for publication February 5, 1979 and in revised form August 21, 1979

ERNEST A. KIRKBY AND MICHAEL J. ARMSTRONG
Department of Plant Sciences, The University of Leeds, Leeds LS2 9JT England

ABSTRACT

Ricinus communis was used to test the Ben Zioni-Dijkshoorn hypothesis that NO_3 uptake by roots can be regulated by NO_3 assimilation in the shoot. The rate of the anion charge from assimilated NO_3^- (and SO_4^{2-}) was followed in its distribution between organic acid anion accumulation and HCO_3^- efflux into the nutrient solution. In plants adequately supplied with NO_3^-, HCO_3^- efflux accounted for between 56 and 63% of the anion charge. When the plants were subjected to a low NO_3 regime HCO_3^- excretion accounted for only 23% of the charge. A comparison of mature plants growing for a 10-day period at the two levels of NO_3 nutrition revealed that the uptake of NO_3^- at the higher level was increased 3-fold, whereas K uptake was unaltered. To trace ion movement within the plant, the ionic constituents of xylem and phloem sap were determined. In xylem sap these constituents were found to be predominantly K^+, Ca^{2+}, and NO_3^-, whereas in the phloem sap they were mainly K^+ and organic acid anions. Results have been obtained which may be interpreted as providing direct eivdence of NO_3 uptake by roots regulated by NO_3 reduction in the tops, the process being facilitated by the recirculation of K^+ in the plant.

Following the work of Dijkshoorn (7), Ben Zioni *et al.* (4) have proposed a mechanism by which NO_3 reduction in the shoot controls NO_3 uptake by roots. This process incorporates the recirculation of K^+ within the plant and is as follows: K^+ and NO_3^-, the ions taken up in largest amounts by the root, are translocated in the xylem to the shoot, where for every NO_3^- ion reduced an equivalent of malate is formed (3). Some of the K^+ originally accompanying this NO_3^- is then transferred together with malate via the phloem to the root system. Here the malate is oxidized and decarboxylated, and the HCO_3^- produced is released stoichiometrically in exchange for further uptake of NO_3^-. The K^+ remaining in the root, together with this NO_3^-, is transported upwards and the cycle repeated. This mechanism necessitates an excess uptake of anions over cations by the plant, in accordance with the net HCO_3^- excretion from the roots. The often observed increase in the pH in NO_3 cultures is a reflection of this phenomenon (14, 17).

Findings consistent with the above mechanism have been presented by a number of authors (4–6, 9). However, unequivocal proof is lacking that the products of NO_3 reduction in upper plant parts can control NO_3 uptake by roots. Evidence is needed that charge from NO_3 assimilation in the tops is effluxed as HCO_3^- from the roots, concomitant with K recirculation in the plant. To demonstrate this was the purpose of the present study.

In previous publications investigating ionic balance in tomato plants (15, 16) we concluded that in this particular species the control mechanism outlined above was relatively unimportant. This conclusion was reached from studies in which the fate of anion charge arising from the assimilation of NO_3^- and SO_4^{2-} in NO_3-fed plants was followed in its distribution between organic anion accumulation in the plant and HCO_3^- efflux into the nutrient medium (as measured by excess anion over cation uptake). Increasing the level of NO_3 nutrition, compensating with SO_4^{2-}, stimulated organic acid anion accumulation in the plant tops, whereas HCO_3^- efflux from the roots represented only a small percentage—at most 20%—of the assimilated charge. The cation/anion uptake ratios were therefore close to unity and the amount of NO_3^- taken up by exchange for HCO_3^- derived from NO_3^- reduction (as OH^-) was relatively small. It was also inferred from this investigation that the extensive K recirculation as necessitated by the control model did not occur. This was confirmed by subsequent investigations of tomato plants in this laboratory (1). The same pattern of behavior is probably true for other plant species which reduce NO_3^- in the tops and in which the cation/anion uptake ratio is close to unity, *i.e.* sugar beet (22), tobacco (21).

We suggest that the NO_3 transport model might be more applicable to plant species in which HCO_3^- root efflux is dominant with an associated high excess anion over cation uptake. In order to test this idea further we extended our investigations to another plant species. *Ricinus communis* var. Gibsonii was chosen as it offered the considerable advantage that both xylem and phloem saps can be obtained from mature plants. The analyses of these saps provide an indication of the upward and downward movements of ions which can be applied to the model. Furthermore, since this species is a C_3 plant, the problems of differentiating between the direct effects of NO_3 metabolism on malate accumulation and malate levels associated with C_4 metabolism are avoided. As in our previous investigation with tomato, ion uptake and assimilation and organic acid anion accumulation were determined for individual plant parts, and for entire plants in relation to plant age and the level of NO_3 nutrition. We were therefore able to follow the fate of assimilated NO_3^- and SO_4^{2-} between organic acid anion accumulation and HCO_3^- excretion.

MATERIALS AND METHODS

Castor oil seeds (*R. communis* var. Gibsonii) were germinated in a 1:1 sand soil mixture maintained at 30 C in the dark. On the appearance of the first leaves, the seedlings were transferred to aerated nutrient solutions held in six 52-liter containers, each container supporting 10 plants.

The composition of the nutrient solution was as follows: $Ca(NO_3)_2$ (2 meq/l), KH_2PO_4 (1 meq/l), $MgSO_4$ (2 meq/l). The micronutrients were supplied as: Fe-EDTA (2.80 μg Fe/ml), $MnSO_4 \cdot 4H_2O$ (0.43 μg Mn/ml), H_3BO_3 (0.33 μg B/ml), $ZnSO_4 \cdot 7H_2O$ (0.06 μg Zn/ml), $CuSO_4 \cdot 5H_2O$ (0.08 μg Cu/ml) and $Na_2MoO_4 \cdot 2H_2O$ (0.04 μg Mo/ml). The nutrient solutions were completely renewed every 4 days. The initial solution pH was 5.5.

The plants were grown in a growth chamber at a light intensity of 80 w m^{-2} provided by warm-white fluorescent tubes. A relative humidity of 80% was maintained and a 16-h light, 8-h dark cycle employed at 27 C and 19 C respectively. Harvests were taken after 12, 18, 26, 32 and 42 days of growth, plants being thinned out from the containers as the experiment progressed. For each of the first 4 harvests, 10 plants were removed, and individual fresh and dry weights (85 C) of leaves, stems and roots recorded. After the fourth harvest the remaining plants were subjected to two NO_3 treatments each comprising 10 plants. In one treatment the NO_3 level was depressed to 1 meq/l whereas in the other it was raised to 10 meq/l supplied as $Ca(NO_3)_2$. The Ca^{2+} concentration in the lower NO_3 treatment was maintained by the addition of $CaSO_4$. Sulfate was thus the compensating ion in the nutrient medium. This ion was chosen as it is known to have little influence on the uptake of other ion species (19).

After a further 10 days of growth (42 days), during which period the solutions were not renewed, phloem and xylem saps were collected for analysis from the plants of the two NO_3 treatments. Phloem sap was obtained from diagonally cut incisions in the bark of the plants as described by Hall *et al.* (11). The total sample was collected over a 3-h period for each plant. After each sample collection during the 3-h period, the sap was stored in plastic vials held in ice to restrict evaporation. The sap was weighed and stored in a deep freeze at −20 C prior to analysis. Xylem sap was collected after decapitating the plants 1 cm above the root system. A suitable length of polyvinyl chloride tubing was attached to the cut stump to allow the exudate to collect. This was then removed using a syringe. Sap exuded during the first 15 min after decapitation was discarded because of possible phloem contamination. The sample collected during the period between 15 and 60 min after decapitation was weighed and stored for analysis in plastic vials at −20 C. After sap collection the plants were harvested and divided into leaves, stems and roots, and fresh and dry weights were taken as in the previous harvests.

Dried plant material obtained from all of the harvests was analyzed for total nitrogen, nitrate, total sulfur, inorganic sulfur, phosphate, chloride, calcium, magnesium, potassium, sodium, and the alkalinity of ash (total organic anions) as referred to in previous publications (16, 17). Cations and anions in the phloem and xylem saps were also estimated by the above techniques. Total organic acids in the saps were determined by a modified method of Hiatt and Hendricks (13). Three-tenths ml of exudate was mixed with 10 ml 80% ethanol and insoluble material removed by centrifugation. The supernatant was evaporated to dryness at 50 C using a rotary evaporator and the residue dissolved in 10 ml warm distilled H_2O. This solution was passed through a Zerolit 325 (H^+) resin to remove the basic fraction and then through an Amberlite 1R-45 (formate) resin to remove the organic acid fraction. This fraction was eluted with 10 ml 20% and 10 ml 50% formic acid, evaporated to dryness at 50 C and the residue redissolved in 5 ml warm distilled H_2O. Total organic acids were determined in the sample by titrating with 0.02 N NaOH.

The statistical analyses of the plant saps refer to analysis from each of the 10 plants of both NO_3 treatments. Student's *t* test was used.

RESULTS

Table I shows the influence of age (harvests 1–4) on cumulative yields and ion uptake by whole castor oil plants. At all four harvests the uptake of anions was in the order of twice that of the cation uptake, thus indicating a considerable HCO_3^- efflux from the roots at the stages in this growth period. The slight increase in cation to anion uptake ratio from harvest 1 to 4 largely reflects the corresponding fall in N concentration.

The fate of the negative charge resulting from NO_3^- and SO_4^{2-} assimilation in its distribution between organic acid anion accumulation and HCO_3^- efflux (excess anion over caption uptake) is given for the same plants (Table II). The values for assimilated (N + S) are all balanced within 10% by the totals of organic acid anion accumulated plus HCO_3^- efflux. In all treatments the largest fraction of the negative charge was directed toward HCO_3^- excretion (between 58 and 63%). This fraction was greatest in the youngest plants. The values for assimilated (N + S), HCO_3^- excretion and organic acid anion accumulation fell with increasing age. This again probably reflects the falling rates of NO_3 uptake and utilization as the plants aged.

A more detailed survey of the influence of the level of NO_3 nutrition on the total anion charge from assimilated NO_3^- and SO_4^{2-} and its distribution between organic acid anion accumulation and HCO_3^- excretion can be seen in Table III. The table compares the uptake and assimilation of ions over a 10-day period (between harvests 4 and 5) by whole castor oil plants growing at the two different levels of NO_3 nutrition. In agreement with the data in Table II assimilated (N + S) values at both NO_3 levels are fairly well balanced by the sums of organic acid anion accumulation and HCO_3^- excretion. However, the absolute values of assimilated (N + S) charge and their distribution differ between the NO_3 treatments. At the higher NO_3 level, the pattern was similar to that already observed in the four previous harvests (Table II) with HCO_3^- accounting for a high proportion (56%) of the assimilated anion charge. At the lower level of NO_3 nutrition, however, the assimilated (N + S) was only half that of the high NO_3 treatment, and of this charge only a small fraction (23%) was directed toward HCO_3^- excretion. This is in accordance with the high cation to anion uptake ratio (about 0.85) for this treatment.

The difference in ion uptake between treatments largely results from a disparity in N uptake. The N uptake from the higher level of NO_3 nutrition was almost three times greater than that from the lower NO_3 treatment. The uptake of Ca^{2+} and Mg^{2+} was also stimulated at the higher level of NO_3 nutrition whereas Cl^- uptake was enhanced at the lower NO_3 level. These synergistic and antagonistic effects on ionic balance have often been observed in plants grown under different NO_3^- regimes (16). The uptake of K^+ was the same in both treatments.

From the N uptake data we calculated that in the low NO_3 treatment only 27% of the applied NO_3^- was still in the solution at the end of the experiment. The rest had been taken up by the plants. The comparative value for the higher NO_3 level was 80%. These findings indicate the much more marked differences between the two NO_3 treatments at the end of the experiment and strongly suggest that the plants in the low NO_3 regime were subjected to N stress conditions. This also implies that despite the small net HCO_3^- efflux over the 10-day period it seems likely that there must have been a shift from HCO_3^- to H^+ efflux towards the end of the experiment as previously observed by ourselves and other workers studying N stress (14, 16).

Table I. *Influence of Age on Yield and Cation and Anion Uptake by Castor Oil Plants*

Harvest	Yield	Cations					Anions					Cation/Anion Uptake Ratio
		K	Ca	Mg	Na	Total	N	S	P	Cl	Total	
	g/10 plants	*meq/100 g dry weight*										
1	10.3	108	66	50	2	226	377	30	33	20	460	0.49
2	30.1	97	62	49	2	210	319	31	24	18	392	0.54
3	69.8	94	49	40	2	185	277	30	18	15	340	0.54
4	134.4	102	52	50	2	206	293	30	25	18	366	0.56

The cation-anion balances of leaves, stems, and roots of plants grown at the two levels of NO_3 nutrition are given in Table IV. The sums of the total cations (K^+, Ca^{2+}, Mg^{2+}, Na^+) closely balanced (within 10%) the total respective anion sums (NO_3^-, SO_4^{2-}, Cl^-, $H_2PO_4^-$, and organic acid anions). It may be supposed that the most important charges have been taken into account. Regardless of the level of NO_3 nutrition at which the plants were grown the total cation and anion concentrations were lowest in the leaves. Other trends were similar in both treatments. Highest levels of K^+ and NO_3^- were present in the stems, Ca^{2+} in the leaves, and Mg^{2+} in the roots. Organic acid anion concentrations were lowest in the leaves and in all tissues balanced from 49 to 65% of the total cation charge. At the higher level of NO_3 nutrition the total cation and anion levels were raised by about 10 to 15% in all tissues. In particular, the concentrations of Ca^{2+}, Mg^{2+}, and NO_3^- were higher. Chloride, on the other hand, was depressed.

The weights and ionic composition of xylem sap collected from plants of the two NO_3 treatments are shown in Table V. In agreement with previous work on root pressure exudation, much greater sap weights were obtained from the higher NO_3 treatment (23).

A very close balance between cations and anions was obtained in sap from plants grown at the higher NO_3 level. The major anion charge was NO_3^- and this was largely balanced by K^+ and Ca^{2+}. Organic acid anions were detected in only trace amounts. In the low NO_3 treatment such a close balance between cations and anions was not obtained and an anion deficit reported. The total cation concentration and composition were rather similar to that of the higher NO_3 treatment. However, the anion composition differed markedly. The NO_3^- concentration was considerably lower and a significant proportion of the anion fraction was made up by organic acid anions. Chloride too was increased 3-fold. The anion charge not accounted for was probably made up by HCO_3^- which was not estimated. This may be inferred from the much higher pH of the sap from the low NO_3 plants (7.3 as compared with 5.6 from the high NO_3 treatment).

The weights and ion composition of phloem sap obtained from

Table II. *Influence of Age on Organic Anion Accumulation, HCO_3 Excretion and Total Levels of Assimilated (N + S) by Whole Castor Oil Plants*

Harvest	HCO_3 Excreted[a]	Organic Acid Anions	Organic Anions Accumulated + HCO_3 Excreted	Assimilated (N + S)
	meq/100 g dry weight			
1	234 (63)[b]	139	373	352
2	182 (58)	130	312	295
3	155 (58)	112	267	268
4	160 (59)	112	272	260

[a] Excess anion over cation uptake: (N + S + P + Cl) − (K + Ca + Mg + Na).

[b] Figures in parentheses indicate the % HCO_3 excretion of the total anion charge (organic acid anions + HCO_3 excreted).

Table III. *Influence of Level of NO_3 Nutrition between Harvests 4 and 5 on Ion Uptake, Nitrate and Sulfate Assimilation, and Organic Acid Accumulation*

1 meq/l NO_3 solution							
Uptake					Assimilation and Accumulation		
Cations					Excess anion uptake (HCO_3 excretion)	Organic acid anions	Organic (N + S)
meq/plant					*meq/plant*		
K	Ca	Mg	Na	Total	3.1 (23)[a]	10.4 (77)	12.8
7.2	8.0	1.5	0.2	16.9	13.5		
Anions							
N	S	P	Cl	Total			
11.4	2.8	3.0	2.8	20.0			

10 meq/l NO_3 solution							
Uptake					Assimilation and Accumulation		
Cations					Excess anion uptake (HCO_3 excretion)	Organic acid anions	Organic (N + S)
meq/plant					*meq/plant*		
K	Ca	Mg	Na	Total	16.2 (56)	12.6 (44)	26.1
7.2	11.9	2.9	0.2	22.2	28.8		
Anions							
N	S	P	Cl	Total			
31.5	2.3	3.6	1.0	38.4			

[a] Figures in parenthesis indicate the % HCO_3 excretion and organic acid anions of the total assimilated (N + S) charge.

Table IV. *Influence of Level of NO_3 Nutrition (Harvest 5) on Yields and Cation-Anion Balance of Leaves, Stems, and Roots of Castor Oil Plants*

	Yield	Cations					Anions					
		K	Ca	Mg	Na	Total	NO_3	SO_4	H_2PO_4	Cl	Org. Anions	Total
1 meq/l NO_3 solution												
	g/plant	*meq/100 g dry weight*										
Leaves	9.9	56	79	35	1	171	2	24	28	10	107	171
Stems	8.9	126	58	23	2	209	38	11	20	32	129	230
Roots	4.0	108	51	68	2	229	13	21	43	35	126	238
10 meq/l NO_3 solution												
Leaves	10.4	55	98	37	1	191	14	21	36	8	125	204
Stems	8.1	146	67	30	2	245	96	13	21	23	121	274
Roots	3.9	84	82	85	3	254	78	17	36	16	122	269

Table V. *Influence of Level of NO_3 Nutrition on Weight (g/Plant) and Ionic Composition of Xylem Sap Collected between 15 and 60 min after Decapitation (meq/l)*[a]

	1.0 meq NO_3/l	10 meq NO_3/l
Sap weight	0.44	1.68***
Potassium	12.4	10.6 NS[b]
Calcium	7.4	9.4*
Magnesium	2.7	3.5**
Sodium	2.0	1.6*
Total cations	24.5	25.1 NS
Nitrate	6.2	19.0***
Sulfate	2.8	2.7 NS
Phosphate	2.0	3.0**
Chloride	3.3	1.3***
Organic Acids	5.8	Tr.***
Total anions	20.1	26.0***

[a] Significant differences: * $P < 5\%$; ** $P < 1\%$; *** $P < 0.1\%$.

[b] NS: not significant.

Table VI. *Influence of Level of NO_3 Nutrition on Weight (g/Plant) and Ionic Composition of Phloem Sap (meq/l)*[a]

	1.0 meq NO_3/l	10 meq NO_3/l
Sap weight	0.85	0.89 NS[b]
Potassium	68.1	79.6***
Calcium	0.8	0.8 NS
Magnesium	6.6	8.5***
Sodium	3.0	1.4***
Total cations	78.5	90.3***
Nitrate	0.0	0.0
Sulfate	2.4	1.8**
Phosphate	5.3	6.9**
Chloride	11.9	7.9***
Organic Acids	53.4	65.7*
Total anions	73.0	82.3 NS

[a] Significant differences: * $P < 5\%$; ** $P < 1\%$; *** $P < 0.1\%$.

[b] NS: not significant.

plants grown in the two NO_3 treatments are shown in Table VI. Similar weights were obtained and the balance between cations and anions observed in both treatments were within 10%. In both samples the ionic constituents present in highest concentrations were K^+ and organic acid anions. At the higher level of NO_3 nutrition the concentration of both these constituents was increased. The concentrations of Mg^{2+} and $H_2PO_4^-$ were also slightly higher and those of Na^+ and Cl^- lower in sap from the high NO_3 plants. In agreement with other workers we did not detect NO_3^- in the phloem and found only very low concentrations of Ca^{2+} (10, 18).

DISCUSSION

For the Ben Zioni-Dijkshoorn model to play a significant role as a NO_3 uptake control mechanism two conditions must be satisfied: (*a*) that NO_3 reduction occurs primarily in the upper plant parts; (*b*) that a considerable proportion of the anion charge arising from the assimilation of NO_3^- and SO_4^{2-} is directed toward HCO_3^- efflux, *i.e.* that anion uptake is much in excess of cation uptake. The data presented in this paper show that in castor oil plants both these criteria are met.

In plants abundantly supplied with NO_3^- (10 meq/l) the major anion transported from the roots to the tops in the xylem stream was NO_3^- and the two dominant cations Ca^{2+} and K^+ (Table V). This composition is consistent with the findings of other workers using different plant species well supplied with NO_3^- as is also the total xylem sap ionic charge (23). This high supply of NO_3^- to the shoots indicates that NO_3^- is mainly assimilated in the leaves. This view is further supported by the much lower levels of NO_3^- observed in the leaves than in the stems or roots of the plants (Table IV) and by independent observations which have shown that NO_3^- is the major form of nitrogen within *Ricinus* xylem sap (2).

The second criterion is also satisfied since at all stages in the growth of castor oil plants adequately supplied with NO_3 nutrition, anion uptake was considerably in excess of cation uptake (Tables I and III). This excess anion uptake or HCO_3^- excretion represented between 56 and 63% of the total charge from assimilated NO_3^- and SO_4^{2-} (Tables II and III).

Further evidence in support of the significant role of the model can be seen from the phloem sap analysis. In agreement with the concepts of Ben Zioni *et al.* (4), the two principal charge constituents were K^+ and organic acid anions. Ben Zioni *et al.* (4) suggested that the organic acid accompanying the K^+ may be malate and indeed Hall and Baker (10) reported this as the only organic acid anion in *Ricinus* phloem sap. More recent findings suggest, however, that malate may not be present in such large amounts as was formerly believed (18, 20). In our experiment the organic acid fraction was not separated. The phloem sap analyses, however, indicate the presence of a pathway capable of considerable charge transfer, irrespective of the makeup of the negatively charged organic constituents, and this is further borne out by the ion uptake data.

The mechanism by which the negative charge from malate or other organic acid anions in the phloem is transferred to the nutrient solution as HCO_3^- is still not completely clear. It has been established that synthesis and decarboxylation of organic acid anions are controlled by pH shifts in the root (12), a lowering in pH favoring enzymic decarboxylation. Roots taking up a large excess of anions over cations, and which do not reduce NO_3^- to any great extent, should have a considerably lower pH than phloem sap (pH 7–8). It may be supposed that the pH fall as phloem sap enters the root is conducive to the breakdown of organic acid anions transferred from the tops. When NO_3^- is adequately supplied, anion uptake is in considerable excess of cation uptake (Tables I and III) so that the mechanism for organic acid anion breakdown should be favored. On the other hand, when NO_3^- supply becomes limiting, cation uptake exceeds anion uptake with a resulting H^+ efflux from the root with an increase in root pH (12). This pH increase should be conducive to organic acid anion accumulation.

The concept of pH-controlled organic acid anion accumulation in the root is consistent with the xylem sap analysis for plants grown at different levels of NO_3 nutrition. When NO_3^- was adequately supplied, organic acids were present in only trace amounts in the xylem sap and the sap pH was 5.6. Under the NO_3 stress conditions, however, the pH of the sap rose to 7.3 and considerable amounts of organic acid anions were present (Table V). Similar observations in maize have been made by Dijkshoorn (8).

An important feature incorporated in the Ben Zioni-Dijkshoorn model is the recirculation of K^+ within the plant. The considerable amounts of K^+ in both xylem and phloem saps (Tables V and VI) clearly indicate its occurrence. The extent of its importance, however, is best demonstrated in Table III in which plants grown at high and low levels of NO_3^- were compared. At the higher level of NO_3 nutrition, NO_3 uptake was about three times greater (31.5 meq compared with 11.4 meq), whereas K^+ uptake was unaltered. The greater uptake of 20.1 meq NO_3^- was accompanied by an increase of 3.9 meq Ca^{2+} and 1.4 meq Mg^{2+} (total 5.3 meq). Ca^{2+} is almost absent in the phloem and Mg^{2+} is present in much lower concentrations than K^+ (Table VI). We therefore conclude that this additional uptake and transport of approximately 20.1 to 5.3 meq NO_3^- (14.8 meq NO_3^-) in the high NO_3 treatment was facilitated by 7.2 meq K^+. This result demonstrates the importance of K recirculation in this species. It also indicates the errors which can arise in attempting to use xylem sap exudate from decapitated *Ricinus* plants in K uptake studies. In the normal functioning plant a high proportion of the K^+ in the xylem appears to originate from the plant tops via the roots and not directly from the external solution.

The results reported here for castor oil plants contrast markedly to those we obtained previously for tomato (1, 15, 16). In both species NO_3^- is reduced in the tops but the distribution of charge is different. In castor oil plants a considerable proportion of the negative charge is transferred to the nutrient solution as HCO_3^- whereas in tomato it is mainly retained *in situ* as organic acid anions. This difference in behavior is reflected by differences in cation and anion distribution between plant tissues. In castor oil plants in complete contrast to tomato, the levels of cations and organic acid anions are relatively lower in the leaves and higher in the roots (Table IV). Increasing the level of NO_3 nutrition results only in a slight increase in cation and organic acid anion concentrations in the tops because of the large HCO_3^- efflux from the roots.

Why plant species should behave differently in this respect is uncertain. The greater movement of ionic constitutents in the phloem in the castor oil plant allows this species a better regulation of NO_3 uptake and a more efficient utilization of K^+. It is tempting to speculate that this may be an important factor in the growth of this species in its natural habitat.

LITERATURE CITED

1. Armstrong MJ, EA Kirkby 1979 Estimation of potassium recirculation in tomato plants by comparison of the rates of potassium and calcium accumulation in the tops with their fluxes in the xylem stream. Plant Physiol 63: 1143–1148
2. Baker DA 1978 Transport Phenomena in Plants. Outline Studies in Biology. Chapman and Hall, London
3. Ben Zioni A, Y Vaadia, SH Lips 1970 Correlations between nitrate reduction, protein synthesis and malate accumulation. Physiol Plant 23: 1039–1047
4. Ben Zioni A, Y Vaadia, SH Lips 1971 Nitrate uptake by roots as regulated by nitrate reduction products in the shoot. Physiol Plant 24: 288–290
5. Blevins DG, AJ Hiatt, RH Lowe, JE Leggett 1978 Influence of K on the uptake, translocation, and reduction of nitrate by barley seedlings. Agron J 70: 393–396
6. Breteler H, CH Hänisch Ten Cate 1978 Ionic balance of root-shoot nitrate transfer in dwarf bean. Physiol Plant 42: 53–56
7. Dijkshoorn W 1958 Nitrate accumulation, nitrogen balance and cation-anion ratio during the regrowth of perennial rye grass. Neth J Agric Sci 6: 211–221
8. Dijkshoorn W 1971 Partition of ionic constituents between organs. *In* RM Samish, ed, Recent Advances in Plant Nutrition. Gordon and Breach Science Publishers, New York, pp 447–476
9. Frost WB, DG Blevins, NM Barnett 1978 Cation pretreatment effects on nitrate uptake, xylem exudate and malate levels in wheat seedlings. Plant Physiol 61: 323–326
10. Hall SM, DA Baker 1972 The chemical composition of *Ricinus* phloem exudate. Planta 106: 131–140
11. Hall SM, DA Baker, JA Milburn 1971 Phloem transport of ^{14}C-labelled assimilates in *Ricinus*. Planta 100: 200–207
12. Hiatt AJ 1966 Reactions *in vitro* of enzymes involved in CO_2 fixation accompanying salt uptake by barley roots. Z Pflanzenphysiol 56: 233–245
13. Hiatt AJ, SB Hendricks 1967 The role of CO_2 fixation in accumulation of ions by barley roots. Z Pflanzenphysiol 56: 220–232
14. Houba VJG, F Van Egmond, EM Wittich 1971 Changes in production of organic nitrogen and carboxylates (C-A) in young sugar-beet plants grown in nutrient solutions of different nitrogen composition. Neth J Agric Sci 19: 39–47
15. Kirkby EA 1974 Recycling of potassium in plants considered in relation to ion uptake and organic acid accumulation. *In* Plant Analysis and Fertilizer Problems. Proc 7th Int Colloquium, Hanover, Federal Republic of Germany, pp 557–568
16. Kirkby EA, AH Knight 1977 Influence of the level of nitrate nutrition on ion uptake and assimilation, organic acid accumulation, and cation-anion balance in whole tomato plants. Plant Physiol 60: 349–353
17. Kirkby EA, K Mengel 1967 Ionic balance in different tissues of the tomato plant in relation to nitrate, urea or ammonium nutrition. Plant Physiol 42: 6–14
18. Mengel K, H-E Haeder 1977 Effect of potassium supply on the rate of phloem sap exudation and the composition of phloem sap of *Ricinus communis*. Plant Physiol 59: 282–284
19. Mengel K, EA Kirkby 1978 Principles of Plant Nutrition, p. 331. International Potash Institute, Berne, Switzerland
20. Smith, JAC 1978 Phloem loading and the control of solute transport in *Ricinus communis*. PhD thesis. Univ of Glasgow
21. Tejwani KG, KV Venkatramen 1958 Nutritional balance in flue-cured tobacco. Soil Sci 86: 310–312
22. Van Egmond F, VJG Houba 1970 Production of carboxylates (C-A) by young sugar-beet plants grown in nutrient solution. Neth J Agric Sci 18: 182–187
23. Wallace A, AM Abou-Zamzam, E Motoyama 1971 Cation and anion balance in the xylem exudate of tobacco roots. Plant Soil 35: 433–438