J. Amer. Soc. Hort. Sci. 123(5):814–820. 1998.

Nitrate Uptake and Nitrogen Use Efficiency of Two Sweetpotato Genotypes during Early Stages of Storage Root Formation

Margarita R. Villagarcia[1] and Wanda W. Collins[2]
Department of Horticultural Science, North Carolina State University, Raleigh, NC 27695-7609

C. David Raper, Jr.[2]
Department of Soil Science, North Carolina State University, Raleigh, NC 27695-7619

Additional index words. carbohydrates, fibrous roots, growth rate, *Ipomoea batatas*, nitrogen accumulation, starch, storage roots

Abstract. **Soil N availability is an important component in storage root production of sweetpotato [*Ipomoea batata* (L.) Lam.]. A controlled-environment experiment was conducted to characterize effects of N availability on patterns of dry matter, nonstructural carbohydrates, and N accumulation, and to determine possible components of N use efficiency that vary between two genotypes of sweetpotato. Rooted cuttings of 'Jewel' and MD810 were transplanted into pots filled with sand and kept in a growth chamber for 72 days. Plants were watered during the first 30 days with a complete nutrient solution that contained 14 mM NO_3^- and then for the next 42 days with one of three complete nutrient solution that contained either 2, 8, or 14 mM NO_3^-. At 30, 44, 58, and 72 days after transplanting, three plants from each cultivar and treatment combination were sampled and separated into leaves, stems plus petioles, fibrous roots, and storage roots. Each plant fraction was freeze-dried, weighed, ground, and analyzed for total N, soluble sugars, and starch. Availability of N in the substrate, which limited dry matter accumulation at 2 mM NO_3^-, was nonlimiting at 8 and 14 mM NO_3^-. In both genotypes, net assimilation rate, efficiency of N use (i.e., increments of dry matter accumulated per increment of N taken up), and proportion of dry matter allocated to storage roots were greater for N-stressed (2 mM NO_3^-) than N-replete (8 and 14 mM NO_3^-) plants. For the N-stressed plants, however, efficiency of N use was greater in MD810 than in 'Jewel'. Although rate of NO_3^- uptake per unit fibrous root mass was similar in the two genotypes under the N stress treatment, MD810 had greater uptake rate than 'Jewel' under nonlimiting availability of NO^{3-} in the substrate. The increased rate of uptake under nonlimiting NO_3^- supplies apparently was related to enhanced rates of carbohydrate transport from shoots to roots. As tissue concentration of N declined in response to the lowest application of NO_3^-, shoot growth was limited prior to, and to a greater extent than, the photosynthetic rate. The resulting relative decline in sink activity of shoots thus presumably increased the availability of carbohydrates for transport to roots.**

Successful commercial production of storage roots by sweetpotato [*Ipomoea batatas* (L.) Lam.] requires careful management of soil N availability. As with other crop species, a certain amount of N is required to promote the shoot development and photosynthetic activity needed to provide the photoassimilates for growth of the storage roots (Kays, 1985). When excessive N is available to the crop, however, suppression of cambial activity and increased lignification of root tissue inhibits the formation of storage roots as sinks for photoassimilates (Togari, 1950). Furthermore, while enhance partitioning of photoassimilates to roots can result from a relatively low N status of plants, high rates of N assimilation repress partitioning to roots by promoting new shoot growth as a competitive sink (Raper et al., 1978).

The ideal sweetpotato plant thus would be one that is efficient in acquisition of N and its use to maintain photosynthetic activity when the substrate supply of N is low, yet one that retains its capacity to initiate storage roots and partition photoassimilates to them when substrate supply is high. Variations in soil properties, climatic conditions, and field management history, however, make an appropriate balance of N for optimum yield of storage roots difficult to achieve. Genotypic differences for N uptake and assimilation have been reported in crops such as maize (*Zea mays* L.) (Chevalier and Schrader, 1977; Mackay and Barber, 1986), wheat (*Triticum aestivum* L.) (Van Sanford and MacKown, 1986), and cotton (*Gossypium hirsutum* L.) (Jenkins et al., 1982). Genotypic variation also may exist in sweetpotato. In soil fertility experiments (Walker et al., 1989), a greater concentration of NO_3^- in petioles of 'Centennial' than in 'Jewel' in response to N fertilization indicated possible genotypic differences in either N uptake or assimilation. Morphological and yield responses among sweetpotato cultivars to N fertilization also indicate possible genotypic differences in N use. Cultivars that produce higher yields of storage roots at higher rates of N fertilization tend to have a smaller leaf area per plant than those adapted to lower N levels (Bouwkamp, 1985; Haynes et al., 1969).

Exploiting genetic variability in efficiency of N use is an important consideration in adapting crops to specific environments. The aspect of efficiency of N use explored in this experiment is physiological efficiency, which is the amount of dry matter or economic yield per unit of N in the plant and includes the efficiency with which plants can absorb N relative to the amount applied (Jackson et al., 1986; Moll et al., 1982). Selecting genotypes for differences in their efficiency of N use involves determination of yield response to N and such physiological phenomena as N uptake rate (mg of N in the plant/g of fibrous roots/d) and efficiency of N use (g of dry matter accumulated/g of N taken up). The rate of N uptake, which refers to the efficiency of acquisition and transport of N, and efficiency of N use, which refers to assimilation and redistribution of N, depend in turn on a number of physiological and morphological

Received for publication 27 May 1997. Accepted for publication 13 Mar. 1998. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.
[1]Graduate research assistant.
[2]Professor.

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features of the plant. Thus, it is worthwhile for breeders to identify which of these components of efficiency of N use (efficiency of N uptake or efficiency of N use) is the major contributor to yield response of sweetpotato to N availability.

An experiment was conducted in a controlled environment to gain a better understanding of which components of N use are involved in differential growth responses to concentrations of substrate N. Two sweetpotato cultivars were compared during early stages of vegetative growth and initiation of storage root. The objectives of the experiments were to a) characterize the effect of N availability in the substrate on patterns of accumulation of dry matter, N, soluble sugars, and starch within sweetpotato plants; and b) determine which components of efficiency of N use vary between the cultivars.

Materials and Methods

Sweetpotato plants were grown in a controlled-environment growth room of the phytotron of North Carolina State Univ. (Downs and Thomas, 1991). The growth room was maintained at day/night temperatures of 28/22 ± 0.25 °C with a 10-h day period and a 14-h night period. A photosynthetic photon flux density of 600 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and a photomorphogenic irradiance of 12 $W \cdot m^{-2}$ were provided during the day from a combination of cool white fluorescent and incandescent lamps. Ambient CO_2 concentration was maintained between 350 and 400 $\mu L \cdot L^{-1}$.

Treatments consisted of the sweetpotato genotypes 'Jewel' and MD810 and N at 2, 8, and 14 mM NO_3^- in a complete nutrient

Table 1. Coefficients of polynomial equations describing shoot dry mass (MS in g/plant), fibrous root dry mass (MFr in g/plant), storage root dry mass (MSr in g/plant), whole-plant mass (MT in g/plant), leaf area (LA in cm^2/plant), N content in leaves (N_L in mg/plant), and whole-plant N accumulation (N_{MT} in mg/plant) as a function of time for sweetpotato grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3^-.

Genotype	N concn (mM NO_3^-)	Functions	Regression coefficients b_o	b_1	R^2
MD810	2	*Ln*MS	0.878	0.042	0.95
		*Ln*MFr	0.040	0.018	0.60
		*Ln*MSr	–7.169	0.136	0.87
		*Ln*MT	0.981	0.044	0.96
		*Ln*LA	6.673	0.023	0.96
		LnN_L	4.849	0.014	0.96
		LnN_{MT}	5.303	0.017	0.98
	8	*Ln*MS	0.286	0.054	0.96
		*Ln*MFr	–0.464	0.024	0.66
		*Ln*MSr	–12.880	0.205	0.96
		*Ln*MT	0.454	0.054	0.97
		*Ln*LA	5.858	0.045	0.96
		LnN_L	3.877	0.041	0.98
		LnN_{MT}	4.418	0.043	0.97
	14	*Ln*MS	0.623	0.050	0.96
		*Ln*MFr	–0.237	0.019	0.78
		*Ln*Msr	–24.202	0.365	0.88
		*Ln*MT	0.857	0.048	0.98
		*Ln*LA	6.187	0.043	0.96
		LnN_L	4.163	0.040	0.98
		LnN_{MT}	4.690	0.042	0.97
Jewel	2	*Ln*MS	0.815	0.034	0.97
		*Ln*MFr	–0.178	0.021	0.75
		*Ln*MSr	–5.677	0.105	0.89
		*Ln*MT	0.879	0.038	0.99
		*Ln*LA	6.209	0.028	0.97
		LnN_L	4.630	0.017	0.84
		LnN_{MT}	5.075	0.019	0.90
	8	*Ln*MS	0.668	0.043	0.94
		*Ln*MFr	–0.356	0.028	0.90
		*Ln*MSr	–7.830	0.122	0.99
		*Ln*MT	0.916	0.042	0.96
		*Ln*LA	6.067	0.039	0.95
		LnN_L	4.198	0.035	0.95
		LnN_{MT}	4.804	0.035	0.93
	14	*Ln*MS	0.337	0.050	0.94
		*Ln*MFr	–0.003	0.018	0.88
		*Ln*MSr	–4.812	0.072	0.97
		*Ln*MT	0.705	0.046	0.95
		*Ln*LA	5.770	0.045	0.96
		LnN_L	3.811	0.044	0.93
		LnN_{MT}	4.380	0.043	0.93

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solution. Observations from field experiments (unpublished data) indicated that the two genotypes differed in their responses to N fertilization. The experimental design was a 2 × 3 × 3 factorial arranged as a split-split plot in a randomized complete block design with three replications and with genotype as the main plot, N concentration as the subplot, and harvesting time as the sub-subplot. The position of each replication in the growth chamber of the phytotron remained constant throughout the experiment. Growth chamber position was therefore used as blocks.

Vine cuttings, taken from plants grown in the greenhouse, were rooted in distilled water for 14 d. These plants then were transplanted into 7-L plastic pots (one plant per pot) that were filled with steam-sterilized river sand and placed in the growth room for 72 d. During the first 30 d of pretreatment, all pots in the growth room were watered with a complete nutrient solution that contained 14 mM NO_3^-, 1 mM $H_2PO_4^-$, 7 mM K^+, 5 mM Ca^{2+}, 2 mM Mg^{2+}, 3 mM SO_4^{2-}, 19 μM B, 7.4 mM Cl, 3.7 μM Mn, 0.3 μM Zn, 0.13 μM Cu, 0.05 μM Mo, and 10.0 μM Fe(II) as 330 Fe-Sequestrene (DTPA). The pH of the solution was between 5.5 and 6.0. The nutrient solution was applied three times daily to each pot as follows: 500 mL of the solution were applied within the first hour of the light period; 500 mL were applied during the middle of the light period; and 500 mL were applied during the final hour of the light period. The final 500 mL of nutrient solution, which followed application of 2000 mL of deionized water to leach out excess salts, were applied after the leaching water stopped draining from the pot.

The N treatments, which were initiated 30 d after transplanting (DAT), were continued for the next 42 d of exponential growth. The appropriate complete nutrient solution that contained either 2, 8, or 14 mM NO_3^- was applied daily to each pot in the same volumes and on the same schedule established during pretreatment. The 14-mM NO_3^- treatment was a continuation of the pretreatment nutrient solution. For the 2- and 8-mM NO_3^- treatments, the additional NO_3^- of the pretreatment–treatment solution was replaced by SO_4^{2-} (9 and 6 mM) with concentrations of other nutrient ions remaining the same.

At 30 (initiation of treatments), 44, 58, and 72 DAT, three plants were sampled from each treatment combination. Each plant was separated into leaf blades, stems-plus-petioles, and roots. Root systems were carefully washed from the sand and separated into fibrous roots and storage roots. The initiation of storage roots was assessed by the first appearance of a localized increase in storage root diameter. Roots greater than 0.7 cm in diameter were considered future storage roots. The plant parts were then freeze-dried, weighed, and ground for chemical analyses.

The ground tissues of all plant parts were analyzed for concentrations of total N, starch, and soluble sugars. Total N was determined by a micro Kjeldahl procedure (Association of Official Analytical Chemists, 1975). For determination of total soluble sugars and starch, 100-mg samples of freeze-dried ground tissue were extracted three times with 5 mL hot 80% ethanol. After each extraction, tubes were held in a water bath at 100 °C for 5 min and then centrifuged for 10 min at 85,000 g_n. Supernatants were pooled and assayed for total soluble sugars by using the phenol-sulfuric acid method (Hodge and Hofreiter, 1972). Starch in the remaining pellet was gelatinized with NaOH, hydrolyzed using amyloglucosidase from *Aspergillus niger* (Sigma Chemical Co., #A3042) according to the method of Pharr and Sox (1984), and then analyzed as glucose by the phenol-sulfuric acid method (Hodge and Hofreiter, 1972). These concentration data were multiplied by dry masses of the tissues to calculate the contents of total N, total soluble sugar, and total starch in each plant part. Total N for each of the plant parts was summed as total N accumulation in the whole plant, and the total N accumulation was used to calculate rates of N uptake (mg of N/g of fibrous roots/d) and efficiencies of N use.

All data were first analyzed by standard analysis of variance procedures for split-split plot designs (SAS, 1990). Changes in dry matter and nitrogen accumulation in relevant plant parts as a function of time were described by least squares regression techniques.

Results and Discussion

All main effects and time × treatment interactions were significant at $p \leq 0.05$ (data not shown). The principal effect of N treatments occurred between substrate concentrations of 2 and 8 mM NO_3^-. For all treatments, good fits were obtained with exponential growth models in the form $\text{Ln } Y = b_o + b_1 t$, where Y is shoot dry mass, fibrous root dry mass, storage root dry mass, total dry mass, leaf area, N content in leaves, or N content in plant; t is time in DAT; and b_o and b_1 are constants. Coefficients for all equations used in subsequent data summarization are given in Table 1.

Growth and dry matter accumulation. Responses for dry matter accumulation in leaves and stems-plus-petioles were similar for all treatments. Data for these plant parts thus were combined as shoot dry mass (Fig. 1 A and B). Plants that received 8 and 14 mM NO_3 accumulated more dry matter in their shoots than plants given 2 mM NO_3^-. Accumulation of dry matter did not differ for plants within the two higher N concentrations. MD810 accumulated more shoot dry matter than 'Jewel' at all concentrations of N supply (Table 2).

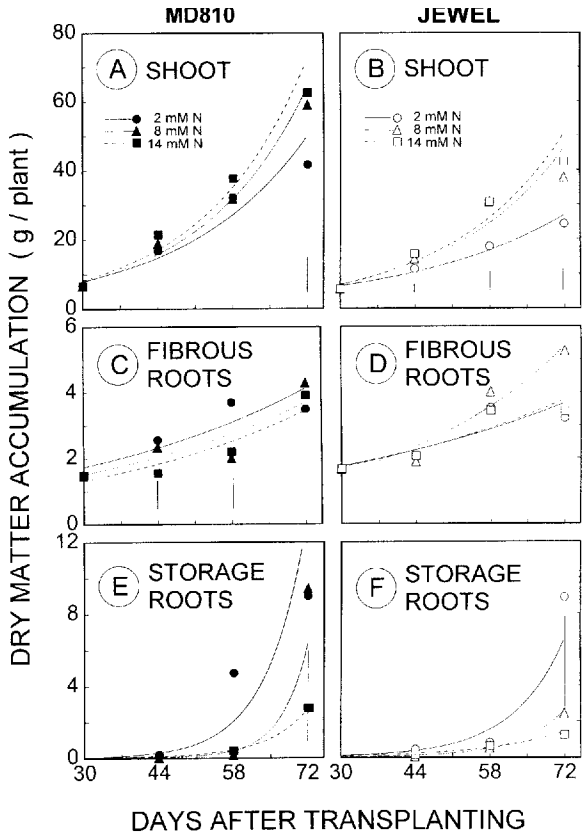

Fig. 1. Dry matter accumulation in shoots (**A** and **B**), fibrous roots (**C** and **D**), and storage roots (**E** and **F**) of MD810 and 'Jewel' sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3 initiated at 30 d after transplanting. Observed values are shown as symbols; values predicted by regression analysis are shown as lines (equations are given in Table 1); and values for LSD are shown as vertical bars when significant at the 5% level of probability.

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Table 2. Comparison of dry mass, leaf area, N content, and carbohydrate concentrations, dry mass basis, 72 d after transplanting between MD810 and 'Jewel' sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3^-.

Variable	Genotype	N concn (mM NO_3^-)		
		2	8	14
Shoot dry mass (g/plant)	MD810	41.8	59.0	62.6
	Jewel	24.5	37.9	42.5
	LSD(0.05)	9.2	6.5	18
Fibrous root dry mass (g/plant)	MD810	3.5	4.3	3.9
	Jewel	3.2	5.3	3.4
	LSD(0.05)	NS	NS	NS
Storage root dry mass (g/plant)	MD810	9.0	9.4	2.8
	Jewel	8.9	2.4	1.3
	LSD(0.05)	NS	4.5	NS
Leaf area (dm^2/plant)	MD810	39	80	95
	Jewel	35	60	72
	LSD(0.05)	NS	13	19
N content in plant (mmol/plant)	MD810	48	127	142
	Jewel	40	93	111
	LSD(0.05)	NS	16	NS
Shoot soluble sugars ($mg \cdot g^{-1}$)	MD810	114	108	101
	Jewel	102	85	75
	LSD(0.05)	NS	17	19
Shoot starch ($mg \cdot g^{-1}$)	MD810	174	98	94
	Jewel	81	62	49
	LSD(0.05)	43	31	21

Increases in leaf area (data not shown) in response to N concentration were similar to those for shoot dry mass with MD810 generating more leaf area than 'Jewel' at the two higher concentrations of N supply (Table 2). There was, however, no difference in leaf area between the two genotypes at the 2-mM NO_3^- supply.

Growth of fibrous roots had no consistently different response to concentrations of N application (Fig. 1 C and D). The differences between MD810 and 'Jewel' at 72 DAT also were not significant (Table 2).

It was anticipated that storage root initiation would be completed by ≈8 weeks after planting (Lowe and Wilson, 1974). The period of rapid bulking of storage roots in the experiment reported herein, however, began only shortly before the experiment was terminated at 72 DAT. It thus may be inappropriate in this experiment to compare yield responses of 'Jewel' and MD810 directly because initiation of the periods of rapid bulking may have been different for the genotypes. Although storage root growth of 'Jewel' apparently had obtained an exponential growth phase by 72 DAT, it is difficult to ascertain from the data at 8 and 14 mM NO_3^- whether storage root growth of 'Jewel' had attained an exponential growth phase by 72 DAT (Fig. 1 E and F). It is more apparent that by 72 DAT storage root growth of MD810 had attained exponential growth at 2 and 8 mM NO^3 and likely at 14 mM NO_3^-. Nevertheless, dry mass of storage roots at 72 DAT was least for both genotypes supplied with 14 mM NO_3^- and was not different between the genotypes at 2 mM NO_3^- (Table 2). Dry mass of storage roots at 72 DAT for MD810 with 8 mM NO_3^- was, however, the same as with 2 mM and was significantly greater than that for 'Jewel' with 8 mM NO_3 . It thus is apparent that supplying N at 14 mM NO_3^- retarded accumulation of dry matter in storage roots of both genotypes, which is a trend similar to that found among other genotypes in experiments by Walker et al. (1989). Growth of storage roots seemed less affected by the intermediate NO_3^- application of 8 mM for MD810 than for 'Jewel', which may indicate variable genotypic responses to N availability.

Nitrogen accumulation and growth responses. A greater N concentration was maintained in leaves of both genotypes as the N supply increased from 2 to 8 mM NO_3^-, and was ≈1.5 times greater for 8 mM NO_3^- at 72 DAT (Fig. 2 A and B). No further difference was detected as the N supply increased from 8 to 14 mM NO_3^-. The

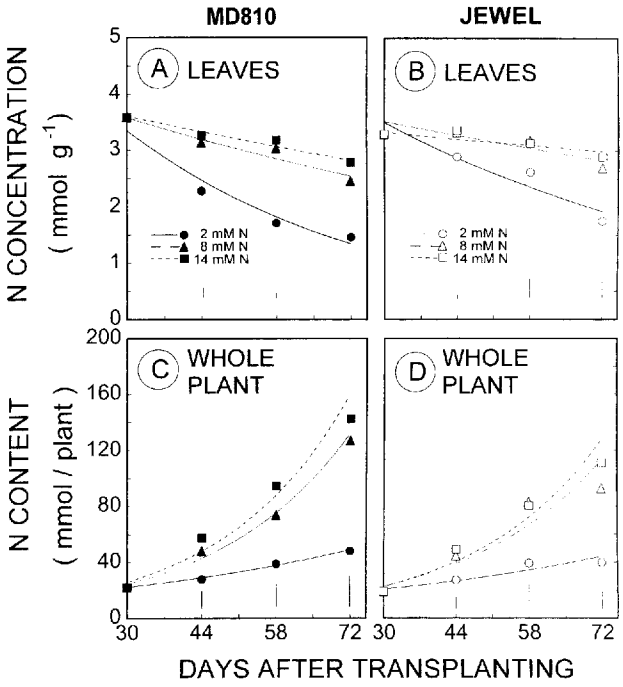

Fig. 2. Concentration on a dry mass basis of N in leaves (**A** and **B**) and accumulation of N in whole plants (**C** and **D**) of MD810 and 'Jewel' sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO^3 initiated at 30 d after transplanting. Observed values are shown as symbols; values predicted by regression analysis are shown as lines lines (equations are given in Table 1); and values for LSD are shown as vertical bars when significant at the 5% level of probability.

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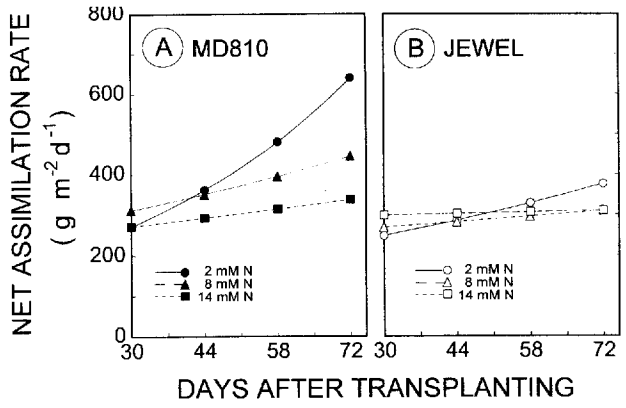

Fig. 3. Net assimilation rates on a dry mass basis of MD810 (**A**) and 'Jewel' (**B**) sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3^- initiated at 30 d after transplanting. Observed values are shown as symbols, and values predicted by regression analysis are shown as lines.

only difference between genotypes was the greater concentration at 2 mM NO_3^- for 'Jewel' than for MD810 (data not shown). The patterns of response for N concentration in stems and petioles and in fibrous roots (data not shown) to application of NO_3^- were similar to those observed in leaves, although concentrations both in stems and petioles and in roots at the end of the treatment period were only ≈40% of that in leaves at 2 mM NO_3^- and ≈60% of that in leaves at 8 and 14 mM NO_3^-.

Plants of both cultivars that were exposed to NO_3^- at 8 and 14 mM accumulated N exponentially throughout the treatment period with no statistical distinction between the two higher supplies within genotypes (Fig. 2 C and D). Together with observations of similar absence of differences in response between these two higher supplies of NO_3^- for N concentration and for exponential accumulation of dry matter (Fig. 1), it is evident that N availability did not limit growth at 8- and 14-mM supplies of exogenous NO_3^-. Plants with N at 8 and 14 mM thus will be referred to collectively as N-replete plants. Conversely, accumulation of N by plants of both genotypes exposed to 2 mM NO_3^- was essentially linear with a very small slope. The restricted accumulation of dry matter and leaf area, as well as the greater rate of decline in N concentration (Fig. 2 A and B), make it evident that 2 mM NO_3^- was growth limiting. Plants grown at this lower concentration of NO_3^- thus will be referred to as N stressed.

Genotype MD810 tended to accumulate more total N than 'Jewel' at all application concentrations of NO_3^-. The difference between genotypes, however, was significant only at 8 mM NO_3^- (Table 2).

Net assimilation rate. Net assimilation rate (NAR), defined as the rate of increase in whole plant dry matter (i.e., g/plant/day) per unit of leaf area (Radford, 1967), was derived by dividing the change in predicted plant dry matter during a day by predicted leaf area on that day (Table 1). Net assimilation rate was similar for the two genotypes at 14 mM NO_3^-, but became progressively greater during the treatment period for MD810 than for 'Jewel' when NO_3^- supply was limiting at 2 mM (Fig. 3). Under the 14-mM NO_3^- treatment, the concentration of N in leaves tended to decline slightly more rapidly for MD810 than for 'Jewel' (Fig. 2 A and B). For both genotypes, however, N in leaves at the end of the treatment period was still between 2.0% and 2.4%, which is about the threshold concentration of ≈2.2% that has been reported by Tsuno (1964) for N limitation of photosynthetic rate for sweetpotato leaves. It thus would appear that N concentration did not become a limiting factor for photosynthesis during the course of this experiment and, because NAR is an approximation of net photosynthesis, MD810 was more efficient than 'Jewel' in converting radiant energy to chemical energy under N-limiting conditions but not under nonlimiting N supply. This apparently enhanced light-use efficiency for N-limited MD810 perhaps is related to the effect of the N stress in increasing leaf thickness. The specific leaf mass of N-stressed MD810 increased during the treatment period from ≈3.1 mg cm^{-2} to ≈4.9 mg cm^{-2}, while for 'Jewel', the specific leaf mass did not increase in response to low N. Increased leaf thickness is associated with increased photosynthetic rates (Osmond et al., 1980). The specific leaf mass for N-replete plants of both cultivars remained at ≈3.0 mg cm^{-2}.

Growth responses to availability of soluble sugars and starch. Concentrations of soluble sugars in shoots of N-stressed plants generally were greater than those of N-replete plants (Fig. 4 A and B). Concentrations of sugars for the N-replete plants by 72 DAT were greater in shoots of MD810 than of 'Jewel' (Table 2). There was no difference in concentration of soluble sugars in shoots from 2 mM NO_3^- at 72 DAT (Table 2); however, the expected increase in concentrations of sugars (Henry and Raper, 1991) initially following imposition of the N stress was more rapid for MD810 than for 'Jewel' (Fig. 4 A and B). Although the initially higher rate of increase in concentrations of soluble sugars in shoots of N-stressed MD810 plants diminished as the storage roots began to develop after 44 DAT, the greater shoot mass of the N-stressed MD810 plants (Fig. 1 A) resulted in a greater availability of sugars for translocation to fibrous and storage roots than occurred in shoots of N-stressed 'Jewel'.

Concentrations of starch in response to NO_3^- supply in the substrate followed similar trends to those for soluble sugars. N-stressed plants accumulated a higher percentage of starch in shoots (Fig. 4 C and D), as well as other plant fractions (data not shown), than N-replete plants. Also, the concentration of starch in shoots

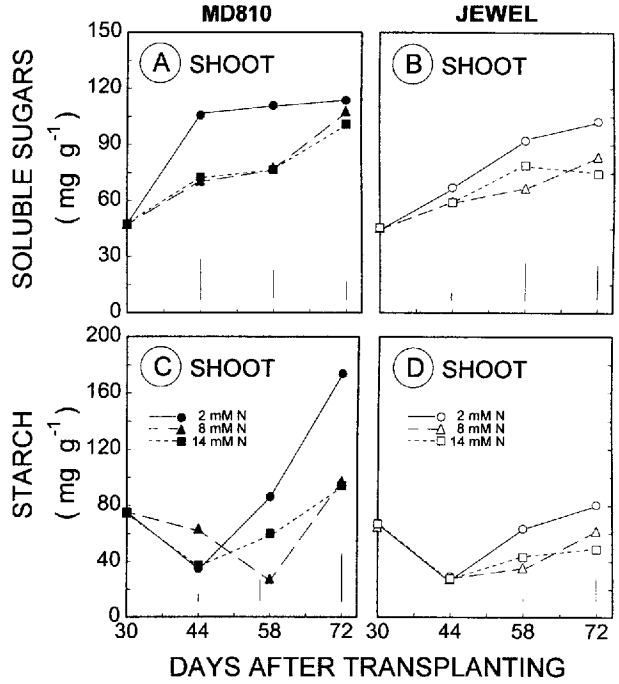

Fig. 4. Concentration on a dry mass basis of soluble sugars (**A** and **B**) and starch (**C** and **D**) in shoots of MD810 and 'Jewel' sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3^- initiated at 30 d after transplanting. Observed values are shown as symbols, and values for LSD are shown as vertical bars when significant at the 5% level of probability.

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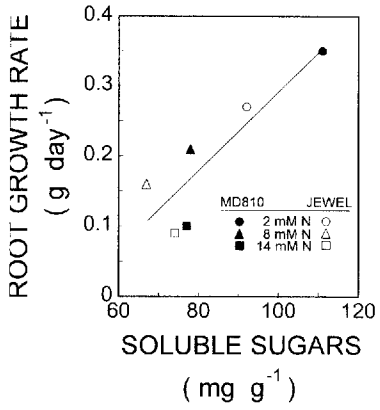

Fig. 5. Relationship at 58 d after transplanting between rates of root growth and concentration of soluble sugars on a dry mass basis in shoots of MD810 and 'Jewel' sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3 initiated at 30 d after transplanting ($Y = -0.406 + 0.080$, $R^2 = 0.77$).

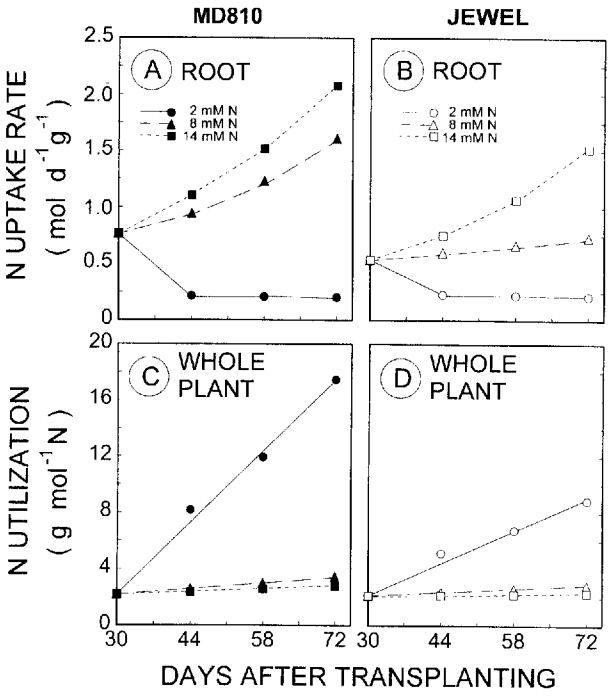

Fig. 6. Rates of N uptake (**A** and **B**) and use efficiency on a dry mass basis of N (**C** and **D**) of MD810 (**A** and **C**) and 'Jewel' (**B** and **D**) sweetpotato genotypes grown under controlled conditions with N treatments of 2, 8, and 14 mM NO_3^- initiated at 30 d after transplanting.

was greater under all N concentrations for MD810 than for 'Jewel' (Table 2). Although starch is not a transportable carbohydrate, the starch pool serves as a source for replenishment of sugars as they are utilized and transported out of the shoot.

Consistent with observations of Tsuno (1970), growth rates of roots (g dry matter/d/plant as calculated from the regression equation for accumulation of dry matter in fibrous and storage roots during the treatment period) were positively correlated with the concentration of soluble sugars in the shoots and negatively correlated with the supply of NO_3^- in the substrate. This is illustrated in Fig. 5 at 58 DAT. These results for sweetpotato support the supposition (Raper et al., 1978; Henry and Raper, 1991; Andrade, 1995) that, if N in leaves remains above the threshold concentration that restricts photosynthetic rate, N stress enhances the availability of carbohydrate for translocation to roots. Nitrogen stress constrains initiation and expansion of new leaves, which are net sinks for photoassimilates, to a greater extent than it restricts the rate of photosynthesis and thus, by lowering the relative sink demand of shoots makes more carbohydrate available for translocation to roots. These results also support the related supposition (Raper et al., 1978; Henry and Raper, 1991; Andrade, 1995) that, if the sink demand of shoots is increased by initiation and growth rates of new leaves, nonlimiting N nutrition restricts the availability of carbohydrates for partitioning to roots. It should be noted that a decline in growth rate of new shoot structures not only lessens the related carbohydrate demand of the shoot for synthesis of structural materials, but also reduces the related respiratory costs for maintenance of the shoot.

Nitrogen uptake rate. When NO_3^- was supplied at the growth-limiting concentration of 2 mM, the rate of N uptake (mmol N accumulated in the plant/d/g dry matter of fibrous roots) did not differ between the two genotypes (Fig. 6 A and B). Following an initial drop in uptake rate from between 0.5 and 0.7 to ≈0.2 mmol·d^{-1}·g^{-1} after initiation of the N-stress treatment, uptake rate remained at ≈0.2 mmol·d^{-1}·g^{-1}. The physiological capacity of each genotype for NO_3^- uptake thus appears to be similar when availability of exogenous N is limiting. Conversely, when the exogenous supply of NO_3^- was not at growth-limiting concentrations, uptake rates were greater for MD810 than for 'Jewel'. Because the dry masses of roots were not different between genotypes, MD810 apparently has a greater physiological capacity for NO_3^- uptake when the exogenous NO_3^- is available in non limiting concentrations.

The observed differences in rate of N uptake may be due to differing fluxes of C from shoots to roots. Raper et al. (1978), in a model for functional balance between the demands for C and N products between roots and shoots, proposed that N uptake depends on the flux of C from shoots to roots rather than on the characteristics of roots or the exogenous N concentration only. The model can be demonstrated by the relationship between the relative accumulation rate of N (RARN with units of N accumulated per unit of total plant N/d, or d^{-1}) and the relative growth rate of roots (RGR_r with units of root dry matter accumulated per unit of root dry matter/d, or d^{-1}). Values for RARN and RGR_r can be derived from regression equations for total N accumulation and root growth when N accumulation and root dry matter are expressed as natural logarithms (Henry and Raper, 1991; Raper et al., 1978).

Table 3. Relative growth rate of roots (RGR_r) and relative accumulation rate of N (RARN) by sweetpotato plants grown in sand culture with 2, 8, and 14 mM NO_3^- for 42 d (N treatments were initiated at 30 d after transplanting). Although expressed in units of d^{-1}, values for RGR_r are calculated as root dry matter accumualted per unit root dry matter per day and for RARN are calculated as N accumulated per unit total plant N per day.

N	RGR_r (d^{-1})			RARN (d^{-1})		
(mM NO_3^-)	MD810	Jewel	Mean	MD810	Jewel	Mean
2	0.053	0.050	0.052	0.017	0.019	0.018
8	0.049	0.037	0.043	0.043	0.035	0.039
14	0.033	0.026	0.030	0.042	0.043	0.043
Mean	0.045	0.038	0.041	0.034	0.032	0.033

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Several observations are relevant from the data for RGR_r and RARN (Table 3). First, when plants were supplied with NO_3^- at 2 mM, both genotypes had RARN of ≈0.02 d^{-1} that were much lower than their RGR_r of ≈0.05 d^{-1}. As the exogenous NO_3^- increased to nonlimiting concentrations, RGR_r decreased and RARN increased such that RGR_r approximately equaled RARN at 8 mM NO_3^-. This indicates that at 2 mM NO_3^- the external availability of NO_3^- rather than flux of C to the roots defined the limit to the rate of NO_3 uptake. Also, as the supply of NO_3^- was increased to nonlimiting concentrations of 8 and 14 mM, the decrease in RGR_r was more gradual for MD810 than for 'Jewel'. Assuming that RGR_r is proportional to net flow of C from shoot to roots, as exogenous supply of NO_3^- became nonlimiting a relatively enhanced capacity of MD810, compared to 'Jewel', for partitioning C to roots enhanced the capacity for NO_3^- uptake.

Nitrogen use efficiency. Efficiency of N use, or the proficiency of the plant to use increments of incoming N in concurrent production of dry matter, was estimated as the ratio of the calculated growth rate (calculated as change in g of dry matter accumulated per d per plant) to the calculated rate of N accumulation (calculated as the change in g of N accumulated per d per plant) at each sampling date (Fig. 6 C and D). Under nonlimiting supplies of N, efficiency of N use for both genotypes was low and almost constant throughout the treatment period, and both genotypes utilized N more efficiently when N supply was limited by providing NO_3^- at 2 mM than when it was not limiting. Under limiting supplies of N, however, MD810 was almost twice as efficient as 'Jewel' in using N to produce dry matter.

Literature Cited

Andrade, M.I. 1995. Physiological basis of yield stability in sweetpotato. PhD diss. (Diss. Abstr. AAI9525525). N.C. State Univ., Raleigh.

Association of Official Analytical Chemists. 1975. Official methods of analysis. 12th ed. Assn. Offic. Anal. Chem., Washington, D.C.

Bouwkamp, J.C. 1985. Production requirements, p. 9–34. In: J.C. Bouwkamp (ed.). Sweetpotato products: A natural resource for the tropics. CRC Press, Boca Raton, Fla.

Chevalier, P. and L.E. Schrader. 1977. Genotypic differences in nitrate absorption and partitioning of N among plant parts in maize. Crop Sci. 17:897–901.

Downs, R.J. and J.F. Thomas. 1991. Phytotron procedural manual for controlled environment research at the Southeastern Plant Environment Laboratories. N.C. Agr. Res. Ser. Tech. Bul. 244 (revised).

Haynes, P.H., J.A.J. Spence, and C.J. Walter. 1969. The use of physiological studies in the agronomy of root crops, p. 34–45. In: E.A. Tai (ed.). Proc. Intl. Symp. Trop. Root Crops. vol. 1. Univ. West Indies, Trinidad.

Henry, L.T. and C.D. Raper, Jr. 1991. Soluble carbohydrate allocation to roots, photosynthetic rate of leaves, and nitrate assimilation as affected by nitrogen stress and irradiance. Bot. Gaz. 152:23–33.

Hodge, J.E. and B.T. Hofreiter. 1972. Determination of the reducing sugars and carbohydrates, p. 380. In: R.L. Whistler and N.L.Wolfrom (eds.). Methods in carbohydrate chemistry. vol. 1. Academic Press, New York.

Jackson, W.A., W.L. Pan, R.H. Moll, and E.J. Kamprath. 1986. Uptake, translocation, and reduction of nitrate, p. 73–108. In: C.A. Neyra (ed.). Biochemical basis of plant breeding: Nitrogen metabolism. vol. 2. CRC Press, Boca Raton, Fla.

Jenkins, J.N., J.R. Nichols, Jr., J.C. McCarty, Jr., and W.L. Parrot. 1982. Nitrate in petioles of three cottons. Crop Sci. 22:1230–1233.

Kays, S.J. 1985. The physiology of yield in sweetpotato, p. 79–132. In J.C. Bouwkamp (ed.). Sweetpotato products: A natural resource for the tropics. CRC Press, Boca Raton, Fla.

Lowe, S.B. and L.A. Wilson. 1974. Comparative analysis of tuber development in six sweetpotato (*Ipomoea batatas* (L.) Lam) cultivars: I. Tuber initiation, tuber growth and partition of assimilates. Ann. Bot. 38:307–317.

Mackay, A.D. and S.A. Barber. 1986. Effects of nitrogen on root growth of two corn genotypes in the field. Agron. J. 78:699–703.

Moll, R.H., E.J. Kamprath, and W.A. Jackson. 1982. Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. Agron. J. 74:562–564.

Osmond, C.B., O. Björkman, and D.J. Anderson. 1980. Physiological processes in plant ecology. Springer-Verlag, New York.

Pharr, D.M. and H.N. Sox. 1984. Changes in carbohydrates and enzyme levels during the sink source translocations of leaves of *Cucumis sativus* L., a stachyose translocator. Plant Sci. Lett. 35:187–193.

Radford, P.J. 1967. Growth analysis formulae—Their use and abuse. Crop Sci. 7:171–175.

Raper, Jr., C.D., D.L. Osmond, M. Wann, and W.W. Weeks. 1978. Interdependence of root and shoot activities in determining nitrogen uptake rate of roots. Bot. Gaz. 139:289–294.

Togari, Y. 1950. A study of tuberous root formation in sweetpotato. Bul. Natl. Agr. Expt. Sta. Tokyo 68:1–96.

Tsuno, Y. 1964. Sweetpotato: Nutrient physiology and cultivation, p. 18–43. Intl. Potash Inst., Berne, Switzerland.

Tsuno, Y. 1970. Dry matter production of sweetpotato and yield increasing techniques. Fertilite 38:3.

Van Sanford, D.A. and C.T. MacKown. 1986. Variation in nitrogen use efficiency among soft red winter wheat genotypes. Theor. Appl. Genet. 72:158–163.

Walker, D.W., K.J. Poche, and E.M. Poche. 1989. Cultivar differences of N uptake and dry matter partitioning in hydroponically grown sweetpotato. Comm. Soil Sci. Plant Anal. 20:567–580.

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