

Plant Productivity and Water Use Efficiency of Sweetpotato (*Ipomoea batatas*) as Affected by Nitrogen Supply

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A pot experiment was conducted in a tropical mid-elevation environment (861 m altitude) to evaluate sweetpotato (*Ipomoea batatas* (L.) Lam.) clones of different origin and breeding intensity for traits related to growth phenomena, nitrogen-use efficiency, and transpirational water-use efficiency (WUE) as affected by different levels of N fertilization. Genotypes with small canopies were associated with a consistently positive response in their final storage root dry matter (DM) yields to increasing N supply, and with efficient allocation of DM and N to storage roots. Genotypes with high canopy net assimilation rates (NARs) had a high proportion of leaves exposed to the sun and high chlorophyll content in leaves. Nitrogen stress led to increased transpiration per unit leaf area and decreasing WUE. Decreasing WUE under N stress was due to lower total plant DM production rather than to increased total water transpiration per plant.

As do most other field crops, sweetpotato responds well to improved management practices, among which N fertilization plays an important role in producing satisfactory yields. Previous investigations did not indicate an optimum range of N fertilization because the response of sweetpotato to N fertilization depends highly on genotypic and environmental variation (Villagarcia, 1996). Jones and Bouwkamp (1992) reported that an application of 60 kg N/ha increased yields of three USA varieties, but decreased yields of three African varieties. Hill et al. (1990) showed that total biomass, storage root yields, and foliage weight were not significantly affected by the addition of fertilizer N. But there is general agreement

that high N supply leads to excessive shoot growth, even though that does not always reduce storage root yields (Villagarcia, 1996).

So far, there have been no detailed studies on water use efficiency (WUE) of sweetpotato. Larenas de la F. and Accatino (1994) suggest that sweetpotato requires a continuous water supply throughout the growing season. Others (Hahn and Hozyo, 1984; Rehm and Espig, 1996) reported that sweetpotato plants were relatively drought tolerant. However, physiological reactions of sweetpotato plants to N or drought stress have not been reported. Furthermore, interactions between N supply and WUE deserve more attention to increase our understanding of the physiological regulation of WUE.

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Therefore, the objectives of the research reported here were to:

- evaluate the effect of N fertilization on final storage root yields of sweetpotato clones,
- describe varietal differences in growth phenomena such as leaf area index, specific leaf area (SLA), root:shoot ratio, net assimilation rate (NAR), and relative growth rate (RGR),
- determine genotype and N effects on nitrogen use efficiency (NUE), and
- determine if WUE is affected by N supply, and if so, how.

Materials and Methods

Pot experiment

Two sweetpotato genotypes (Jewel and Tanzania) were grown in an inert substrate with six levels of N supply (0.0, 0.4, 0.8, 1.2, 1.6, and 2.0 g N/pot) at CIP's experiment station in San Ramón, Peru, (861 m above sea level) under an open glass roof. The experimental unit was arranged as a 2 by 6 factorial treatment combination using a randomized complete block design with four replicates treating genotypes as main plots, with N levels as subplots. Each treatment combination consisted of 12 plants with one plant/pot. Water supply was held at 80% of field capacity throughout the entire growing period. All mineral nutrients except N were supplied in sufficient amounts to avoid nutrient deficiencies. Once a week the amount of transpired water/plant was estimated. At three sampling dates, 42, 84, and 126 days after transplanting (DAT), four plants of each treatment combination, representing four replicates, were harvested to determine fresh and dry weights of plant fractions (stems, leaves, petioles, fibrous roots, and storage roots), SLA (m^2 leaf area/kg leaf dry matter (DM)), and pigment concentration in leaves. SLA was determined by sampling 30 leaf disks of 1.2 cm diameter of each treatment combination. To derive SLA, fresh weight

and dry weight of these 30 leaf disks, which represented a leaf area of 33.9 cm^2 , were determined. Leaf area per plant was derived from SLA and leaf DM production per plant. The extinction coefficient of leaves (the angle of leaf inclination relative to the soil surface) was estimated with a simple plastic triangle. Morphophysiological traits such as NAR, RGR, and leaf area ratio were calculated according to Radford (1967). Pigment contents were measured by a Norsk Hydro N-Tester (Norsk Hydro ASA, Oslo, Norway) in the field and related to photometrically determined chlorophyll and carotene concentrations in plant tissue, according to the method for pigment extraction proposed by Lichtenthaler and Wellburn (1983). Concentrations of nitrogen, potassium, calcium, magnesium, and phosphorus in plant tissue were determined by the Kjeldahl method according to Novozamsky et al. (1983). Discrimination against $^{13}\text{CO}_2$ in leaves and carbon (C) concentrations in shoot parts were determined by a Finnigan Delta mass spectrometer (Thermo Finnigan, San Jose, CA, USA). To derive NAR, C concentrations in fibrous and storage roots were assumed to be 39%. Carbon isotope discrimination ($\delta^{13}\text{C}$ [‰]) has been shown to relate closely to WUE for a range of crop species, e.g., for sunflower (Virgona and Farquhar, 1996), potato (Jefferies, 1995), and wheat (Farquhar and Richards, 1984). This is commonly explained by differences in stomatal opening, which affects the internal partial pressure of CO_2 inside the leaf. Since the enzyme Rubisco reacts more readily with $^{12}\text{CO}_2$ than it does with $^{13}\text{CO}_2$, Rubisco discriminates against the heavy isotope (Lambers et al., 1998).

Analysis of data

All data sets were analyzed by standard ANOVA procedures for a randomized complete block design, using the PROC UNIVARIATE procedure of SAS software (SAS, 1990).

Results and Discussion

The two genotypes grown in the pot experiment differed in their habit and growth characteristics. Jewel was characterized by a shallow canopy and almost horizontal leaves (extinction coefficient approximately 1.0), whereas Tanzania had a more or less erect growth and an extinction coefficient of approximately 0.5 to 0.6. Jewel initiated storage root growth earlier than Tanzania. For both genotypes, storage root initiation was delayed with high N supply.

Dry matter accumulation of the two genotypes grown in the pot experiment (Jewel and Tanzania) was characterized by higher shoot and fibrous root DM production in Tanzania (Table 1). Storage root DM production, averaged across N levels, was not significantly different between genotypes at the final sampling date (126 DAT), but Jewel had initiated storage root growth earlier than Tanzania. Tanzania yielded higher with low and moderate N supply, whereas Jewel produced more storage root DM than Tanzania at high N levels. Shoot growth and shoot:root ratio were increased with each increment in N

supply. High N levels (1.6 and 2.0 g N/plant) led to declining storage root DM production. Plants that did not receive any fertilizer N generated very low amounts of DM in both shoots and roots.

Patterns of N accumulation (data not shown) varied between genotypes. Tanzania accumulated more total N/plant compared to Jewel. Fertilizer N was almost completely absorbed by sweetpotato plants. Therefore, N concentrations in plant DM increased significantly with each increment in N supply. The amount of N present in zero-N plants is assumed to be the quantity of N that was in the vine cuttings the day of transplanting. Large shoot growth of Tanzania was reflected in the relatively lower amounts of N allocated to storage roots. N concentration in storage roots was significantly higher for Jewel.

Chlorophyll a + b content per unit leaf area and specific leaf N (SLN) [g N/m² leaf area] were significantly higher for Tanzania (Figure 1). Chlorophyll content per unit leaf area increased slightly with increasing N supply, whereas SLN showed a pronounced increase when N supply was altered.

Table 1. Shoot dry matter, fibrous root dry matter, and storage root dry matter accumulation of two sweetpotato genotypes at 126 DAT grown in pots with six N levels. Values followed by common letters do not differ significantly (capital letters refer to N levels; lowercase letters to genotypes).

N ¹	0.0	0.4	0.8	1.2	1.6	2.0	Mean*
Shoot dry matter (g/plant)							
Jewel	5.97 a D	11.04 b C	13.81 b B	14.73 b B	25.93 b A	27.69 b A	16.53 b
Tanzania	10.31 a F	21.21 a E	39.88 a D	47.26 a C	52.94 a B	71.84 a A	40.58 a
Mean**	8.14 F	16.12 E	26.85 D	30.99 C	39.44 B	49.78 A	
CV [%]				14.80			
R ²				0.97			
Jewel	5.50 a BC	7.27 b A	4.52 b C	5.61 b BC	6.81 b AB	6.28 b AB	6.00 b
Tanzania	9.19 a E	14.67 a D	16.25 a C	13.91 a D	21.58 a A	17.88 a B	15.58 a
Mean**	7.35 D	10.97 BC	10.39 C	9.76 C	14.20 A	12.08 B	
CV [%]				24.05			
R ²				0.86			
Jewel	12.99 b C	56.09 b A	58.98 b A	56.51 b A	31.87 b B	36.94 a B	42.23 b
Tanzania	14.22 a E	67.08 a B	63.72 a B	75.20 a A	34.90 a C	22.02 b D	46.19 a
Mean**	13.60 C	61.59 A	61.35 A	65.86 A	33.38 B	29.48 B	
CV [%]				25.07			
R ²				0.82			

¹ Application of N (g/plant).

Differences between genotypes and N levels in NAR and genotype by N interactions on NAR were highly significant ($P < 0.01$). Throughout the entire growing period, Tanzania showed the highest NAR compared with Jewel (Figure 2). Highest net photosynthetic rates were obtained with 0.4 g N/plant for both genotypes, with a significant decrease when N supply exceeded that amount. Zero-N Tanzania plants had increasing NAR toward maturity, whereas NAR of N-stressed Jewel plants declined with time and was nearly zero toward the final

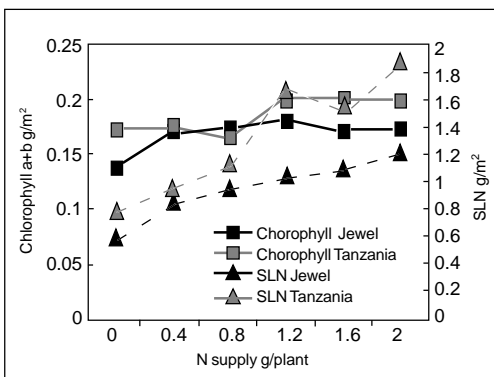


Figure 1. Specific leaf N (SLN) and chlorophyll content in leaves at 42 DAT of two sweetpotato genotypes grown in pots at six N levels.

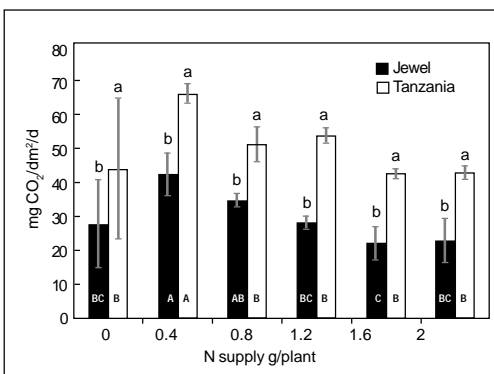


Figure 2. Mean net assimilation rate (NAR) over 126 days of two sweetpotato genotypes grown in pots at six N levels. Capital letters indicate significant differences between N levels within each genotype ($P = 0.05$). Significant differences between genotypes within N levels are indicated by lowercase letters ($p = 0.05$). Mean SE is indicated by grey bars.

sampling date. With N levels between 0.4 and 2.0 g N/plant, NAR of Jewel remained almost constant with time, whereas fertilized Tanzania treatments showed decreased NAR toward maturity.

In N-fertilized treatments, SLN and chlorophyll content per unit leaf area increased with increasing N supply, whereas NAR decreased with increasing N supply. NAR of plants that did not receive fertilizer N could not be related to SLN or chlorophyll content in leaves inasmuch as SLN and chlorophyll content remained almost constant during ontogeny in N-stressed plants, whereas NAR changed significantly with time, as mentioned above.

Differences in discrimination against $^{13}\text{CO}_2$ ($\delta^{13}\text{C}$) in leaves were highly significant between genotypes and N levels ($P < 0.01$). Table 2 shows C isotope discrimination in leaves at the final sampling date (126 DAT). Lower negative values for $\delta^{13}\text{C}$ were observed for Tanzania at all N levels. With increasing N fertilization, discrimination against $^{13}\text{CO}_2$ declined significantly.

There was a significant positive correlation between $\delta^{13}\text{C}$ and SLN, which remained almost constant throughout the entire growing period. There was also a significant positive relationship between $\delta^{13}\text{C}$ and total plant DM production, which was strongest during early growth ($r = 0.86$ for the period between 0 and 42 DAT).

If transpiration from leaves is assumed to increase linearly with stomatal conductance, data for transpiration rates per unit leaf area should relate closely to stomatal opening. No significant differences were found between genotypes in mean transpiration rates across all N levels. However, differences between N levels were highly significant ($P < 0.01$) (Figure 3). In the zero-N treatment, transpiration per unit leaf area was significantly higher for both genotypes. At the 0.4 g N/plant treatment, transpiration rate per unit leaf area was

Table 2. Discrimination against $^{13}\text{CO}_2$ [‰] at 126 DAT in leaves of two sweetpotato genotypes grown in pots with six N levels. Values followed by common letters do not differ significantly (capital letters refer to N levels; lowercase letters to genotypes).

N ¹	C Isotope in leaves						
	0.0	0.4	0.8	1.2	1.6	2	Mean *
Jewel	-31.71 b C	-32.07 b D	-31.47 b C	-30.83 b B	-30.12 b A	-30.03 b A	-30.97 b
Tanzania	-30.95 a E	-30.88 a E	-30.40 a D	-29.52 a C	-29.01 a B	-28.71 a A	-29.84 a
Mean**	-31.26 D	-31.44 D	-30.83 C	-30.09 B	-29.52 A	-29.30 A	
CV [%]				-0.36			
R ²				0.99			

Note: a = Mean separation within rows for genotypes by MSD = 0.0971; P = 0.05; b = Mean separation within columns for N levels by MSD = 0.26; P = 0.05.

¹ fertilization (g N/plant).

slightly higher compared to treatments that received between 0.8 and 2.0 g N/plant. Therefore, it can be concluded that stomatal opening increased significantly under N stress. Increasing internal CO_2 partial pressure under N stress is reflected in more negative discrimination against $^{13}\text{CO}_2$. There was a significant negative correlation between C isotope discrimination and transpiration rate per unit leaf area. During early growth this correlation was strongest ($r = -0.63$ between 0 and 42 DAT).

Total water transpiration was significantly higher for Jewel across all N levels (data not shown). This was mainly due to higher total transpiration of Jewel when N supply was at a high level. WUE was significantly higher for Tanzania at all N levels (Figure 4) and throughout the entire growing period. For both genotypes, WUE was significantly lower under zero-N conditions. This was due to very low total DM production and higher stomatal opening under N stress, which was reflected in the observed higher transpiration rate. Jewel had maximum WUE when N supply was 0.4 g N/plant, whereas Tanzania had maximum WUE with 1.2 g N/plant.

WUE declined significantly over time in all treatments, which coincided with higher discrimination against $^{13}\text{CO}_2$ toward maturity. Responses in WUE to N supply did not change over time.

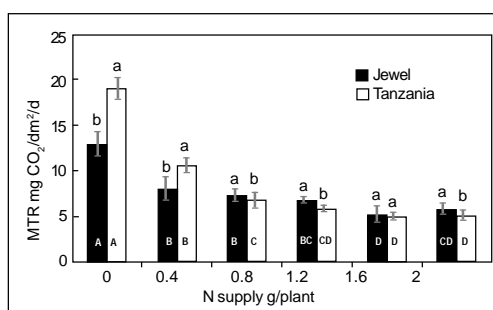


Figure 3. Mean transpiration rate (MTR) over 126 days of two sweetpotato genotypes grown in pots at six N levels. Capital letters indicate significant differences between N levels within each genotype (P = 0.05). Significant differences between genotypes within N levels are indicated by lowercase letters (p = 0.05). Mean standard error (SE) is indicated by grey bars.

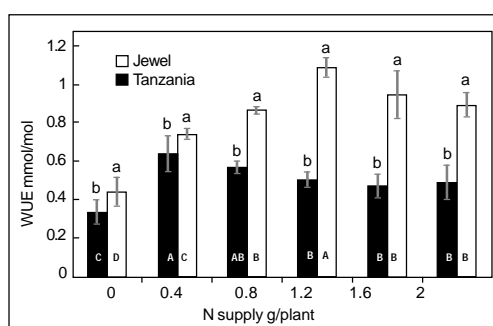


Figure 4. Transpiration water use efficiency (WUE) of two sweetpotato genotypes grown in pots with six N levels. Capital letters indicate significant differences between N levels within each genotype (P = 0.05). Significant differences between genotypes within N levels are indicated by lowercase letters (p = 0.05). Mean SE is indicated by grey bars.

There was a close relationship between C isotope discrimination and WUE. The linear correlation between $\delta^{13}\text{C}$ and WUE was highly significant and positive, with higher WUE obtained when discrimination against $^{13}\text{CO}_2$ was less negative. This correlation was highest during early growth. Until 42 DAT, 85% of the observed variation in WUE was explained by $\delta^{13}\text{C}$. Until 84 or 126 DAT, variation in $\delta^{13}\text{C}$ explained 80% or 64% of variation in WUE, respectively.

Conclusion

Results of the pot experiment showed that both storage root initiation and storage root growth are delayed with high N supply, confirming observations of earlier investigators (Lowe and Wilson, 1974; Villagarcia, 1996). High NAR of Tanzania confirms the assumption that varietal differences in photosynthetic efficiency may depend on both leaf inclination and chlorophyll content in leaves. A low extinction coefficient allows more efficient light transfer through canopies. More vertically inclined leaves might be advantageous, particularly under high light conditions by minimizing the probability of photoinhibition and increasing light penetration to lower leaves, thereby maximizing whole-canopy photosynthesis (Lambers et al., 1998). Consistently higher NAR values of Tanzania as compared with Jewel could be attributed to more efficient light interception of this genotype due to its more erect leaves. Tanzania also had higher chlorophyll content per unit leaf area, which is characteristic for crop species or varieties adapted to high irradiance (Lambers et al., 1998). Ideotypes such as Tanzania may therefore be more efficient in total plant biomass production under conditions of high irradiance, which was the case in San Ramón.

Concerning the N effect on WUE, it has been shown that N stress leads to increased stomatal opening, thereby reducing WUE. Varietal differences in

WUE were due to variation in total plant DM production, because total water transpiration did not differ significantly between genotypes. Tanzania had higher NAR and showed less discrimination against $^{13}\text{CO}_2$ than did Jewel. This indicates that carboxylation rates, rather than stomatal opening, predominantly accounted for variation between genotypes in WUE and $\delta^{13}\text{C}$. Thus, a higher plant productivity (i.e., a higher total plant DM production) due to increased N supply, or due to inherently higher total plant DM production of a genotype, is associated with higher WUE and less negative discrimination against $^{13}\text{CO}_2$. A significant positive correlation between RGR and discrimination against $^{13}\text{CO}_2$ was found by Virgona and Farquhar (1996) for sunflower, supporting this hypothesis. Faster growing genotypes, such as Tanzania, which have higher N contents in plant tissue, have higher NAR and use water more efficiently. Since WUE was significantly affected by genotype by N interactions, selection for high WUE with regard to soil fertility or N input intensity seems possible. Significant genotype effects and genotype by N interactions also occurred for fibrous root DM production. A larger root system may be advantageous in case of drought stress to reach water in deeper soil layers. Selection for genotypes that have a larger root system may be an approach in breeding for increased drought tolerance.

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