An Anomalous, High External Phosphorus Requirement for Young Cassava Plants in Solution Culture. V. Int. Symp. Tropical Root Crops

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Abstract

Twelve cassava cultivars and one cultivar each of soybean, cotton and maize were grown for 28 days at eight constant solution phosphorus concentrations ranging from 0.05 to 1021 μM. The cassava cultivars required solution phosphorus concentrations from 28 to 78 μM to achieve 95% of maximum whole plant yield whereas soybean, cotton and maize required 0.6, 0.6 and 1.0 μM, respectively.

The young cassava plants exhibited a higher internal phosphorus requirement than the other species. However, the major reason for the higher external phosphorus requirement of cassava was the low physiological efficiency of its root system in absorbing phosphorus. Rates of phosphorus absorption associated with 95% of maximum yield were similar in all species; the physiologically inferior root system of cassava required a much higher external phosphorus concentration than the other species to achieve these rates.

The results are discussed with reference to the reputation that cassava enjoys as a plant well-adapted to low fertility situations.

Introduction

Cassava (*Manihot esculenta* Crantz) has gained a reputation for being well adapted to soils of low fertility. This reputation is partly based on the results of agronomic trials which often have shown little or no response to fertilizer application and partly on the plant's ability to grow in situations where other agricultural plants fail. However, a dearth of information exists on quantitative external nutrient requirements for the growth of cassava.

In a paper presented at the Fourth Symposium of the International Society for Tropical Root Crops, we briefly presented data showing that the external concentrations of potassium, calcium and ammonium nitrogen needed for maximal early growth of cassava were roughly comparable to those required for maximal growth of other agricultural species (Edwards *et al.*, 1977). However, we also indicated that higher external nitrate nitrogen and phosphorus concentrations were needed to achieve maximal growth of cassava than for the other crop species. In this paper, we report on an experiment in which 12 cassava cultivars and one cultivar each of soybean (*Glycine max* (L.) Merr.), cotton (*Gossypium hirsutum* L.) and maize (*Zea mays* L.) were grown in flowing solution culture at phosphorus concentrations from 0.05 to 1021 μM.

Methods

Twelve cassava cultivars (Table 1) and one cultivar each of soybean, cotton and maize were grown for 28 days in eight flowing solution culture units (Asher and Edwards, 1978) in which the solution phosphorus concentrations were maintained at 0.05 ± 0.014, 0.70 ± 0.05, 3.0 ± 0.4, 12 ± 0.6, 50 ± 2, 127 ± 6, 313 ± 11, and 1021 ± 37 μM, respectively.

Cassava stem tip cuttings were propagated in mist chambers as described by Forno *et al.* (1976) and after 18 days they were transferred to the flowing solution culture units which at this time contained basal nutrients only. Soybean, cotton and maize plants were raised from seed in a germination cabinet at 31°C and transferred into the solution culture system when the radicles were 5 to 10 mm long. Phosphorus was applied three days after all plants were established in the units.

All nutrient solutions were maintained at 25± 0.5°C and at pH 6.0 ± 0.2. Basal nutrient elements were supplied at the following concentrations (μM): Ca 1000, N (as NO_3^-) 1000, S 825, K 250 to 1270, Mg 200, Na 35, Fe (as sequestrene-138), 20, Cl 15, Si 10, B 3, Zn 0.5, Mn 0.25, Cu 0.1, Co 0.04, and Mo 0.02. The basal nutrients were renewed completely every seven days after draining off the old solution. Solution phosphorus analyses were conducted daily using the method of Jintakanon *et al.* (1975) for the two lowest concentrations and that of Truog and Meyer (1929) for the higher concentrations.

An initial harvest, immediately before imposing the phosphorus treatments and a final harvest, 28 days later, were taken. Fresh and dry weights of tops and roots were obtained. Following digestion of sub-samples in concentrated H_2SO_4 containing 2.5% salicylic acid, phosphorus concentrations in the plant material were determined using a Technicon Autoanalyzer (O'Neill and Webb, 1970).

Results

All cassava cultivars grew poorly and exhibited symptoms of phosphorus deficiency when grown at the lowest solution phosphorus concentration of 0.05 μM. The mean dry matter yield of the 12 cassava cultivars at this concentration was 18% of maximum and the range 12 to 26%. Increasing the solution phosphorus concentration to 0.7 μM significantly increased yield in seven cultivars (Fig. 1) and alleviated to a considerable degree the occurrence and intensity of phosphorus deficiency symptoms.

Dry matter yield of all cassava cultivars increased with further increases in solution phosphorus concentration with all cultivars reaching maximum yield at either 50 or 127 μM phosphorus (Fig. 1). Solution phosphorus concentrations required to achieve 95% relative yield of whole plants ranged from a low of 28 μM for M Aus 7 to a high of 78 μM for Ceiba (Table 1). The 12 cassava cultivars appear to fall into two groups with respect to solution phosphorus requirement, the first group requiring 28 to 32 μM and the second group requiring 62 to 78 μM.

The solution phosphorus concentrations necessary to achieve 95% of the maximum whole plant yield of cassava were very much higher than those required to achieve a comparable yield in soybean (0.6 μM), cotton (0.6 μM) or maize (1.0 μM) grown concurrently in the same nutrient solutions. The solution phosphorus requirements of all cassava cultivars are also greater than those of eight temperate pasture species which ranged from 0.9 μM for silver grass (*Vulpia myuros*) to 16 μM for flatweed (*Hypochoeris glabra*) (Asher and Loneragan, 1967). Chantkam (1978) reported that six out of seven tropical pasture legumes which he studied achieved 90% of maximum yield at solution phosphorus concentrations below 3 μM. The high solution phosphorus requirement of cassava is greater than that of all other species reported from studies with good control of solution phosphorus concentration with the exception of potato (Houghland, 1947) and *Desmodium intortum* (Chantkam, 1978).

The much higher external phosphorus requirement of young cassava plants than of other species (Table 1) suggests that cassava either has a higher internal phosphorus requirement or that, as a species, it is physiologically inefficient in its acquisition of phosphorus from the root environment. At the lowest solution phosphorus concentration (0.05 μM) the concentration of phosphorus in the tops of cassava was similar to that in the tops of soybean, cotton and maize (Table 2). At 0.7 μM, the phosphorus concentration in the tops of all cassava cultivars was much lower than in the tops of the other three species (Table 2). At this solution concentration, both soybean and cotton had exceeded 95% of maximum yield.

The critical phosphorus concentrations in the tops of cotton, maize and soybean corresponding to 95% of maximum yield were 0.19, 0.38 and 0.40%, respectively. Cassava not only reached 95% of maximum yield at much higher solution phosphorus concentrations (Table 1) but also had a higher critical phosphorus concentration in the tops (Table 3). The mean critical phosphorus concentration in the tops of the cassava cultivars was 0.59%. The higher critical phosphorus concentration of cassava does not fully account for the higher external requirement of this species; the other species exceeded or approached 0.59% phosphorus in their tops at a solution phosphorus concentration of 3.0 μM (Table 2).

The higher solution phosphorus requirement of cassava does not appear to be associated with a different root weight ratio to that of the other species. In all species and cultivars the relative size of the root system decreased with increasing solution phosphorus concentration (Table 4). In cotton and maize, the root weight ratio was still high (0.25 and 0.32, respectively) as maximum yield was approached at 0.7 μM phosphorus, but in soybean and cassava the root weight ratio associated with maximum yield were less than 0.20 (0.7 μM treatment for soybean, 50-127 μM for cassava). The ability of plant species to increase the size of the root system relative to that of the tops under conditions of nutrient stress has been proposed as a mechanism by which some species may grow better than others in low soil fertility conditions (Asher and Ozanne, 1967; Spear *et al.*, 1978a). However, it would appear from the comparatively modest increases in root weight ratio of cassava at low solution phosphorus concentrations that this ability would be of lesser importance in cassava than in the other species when grown in phosphorus deficient soils.

Approximate mean rates of phosphorus absorption over the 28-day experimental period were calculated using the equation of Williams (1948). Rates of phosphorus absorption by all species and cassava cultivars increased with increasing solution phosphorus concentration (Table 5). A relative whole plant yield of 95% corresponded with mean phosphorus absorption rates varying from 6.3 μmol/g fr. wt. roots/day (Seda) to 11.0 μmol/g fr. wt. roots/day (M Aus 14). Mean phosphorus absorption rates of soybean and maize corresponding to 95% of maximum yield were of similar magnitude (Table 6), but achieved at much lower solution phosphorus concentrations.

The root system of cassava is thus physiologically much less efficient than that of soybean and maize in its ability to absorb phosphorus from solutions of the same external concentration. Cotton appeared to differ from the other species by reaching near-maximal yield at a much lower rate of phosphorus absorption per unit root weight. This was associated with a low critical phosphorus concentration in plant tops (Table 3) and a moderately high-root weight ratio (0.26) (Table 4). Cassava requires a solution phosphorus concentration of one to two orders of magnitude greater than the other species to absorb phosphorus at rates which do not limit growth. The rates of phosphorus absorption associated with near-maximal growth of cassava, soybean and maize are similar to those associated with near-maximal growth of eight temperate pasture species (Loneragan and Asher, 1967) and with near-maximal growth of the tropical pasture legumes *Stylosanthes humilis, Stylosanthes guianensis* and *Macroptilium lathyroides* (Chantkam, 1978).

At all solution phosphorus concentrations, including both those which were limiting for plant growth and those which were supraoptimal, cassava absorbed phosphorus at much lower rates than the other species (Table 5). The lower phosphorus absorption efficiency of cassava would be expected to render it less susceptible to phosphorus toxicity than the other species. However, at the highest solution phosphorus concentration (1021 μM), the mean relative yield of the 12 cassava cultivars (69%) was similar to that of soybean (67%) and cotton (78%) but much greater than that of maize (40%). Although the internal phosphorus requirement of cassava is higher than that of the other species, it may also have a low internal threshold concentration above which growth is restricted by phosphorus toxicity.

GENERAL DISCUSSION

The very high external phosphorus requirement exhibited by cassava when grown in solution culture at constant phosphorus concentrations suggests that for maximum growth in field situations it may require higher phosphorus fertility levels than other species. This result is paradoxical in the sense that cassava has gained a reputation as a species which can exploit low fertility conditions in the field better than most other agricultural species. Subsequent work in which cassava, soybean and maize were grown in a krasnozem (oxisol) with a high capacity for phosphorus fixation at a wide range of equilibrium soil solution phosphorus concentrations ($<$ 0.01 to 197 μM) showed that cassava grew relatively much better at the low soil solution phosphorus concentrations than predicted on the basis of its performance in the flowing solution culture experiment (S. Jintakanon, unpublished). The mechanism responsible for the improved performance of cassava when grown in soil at low soil solution phosphorus concentrations remains to be elucidated. The possible role of mycorrhizae in the improved performance of cassava at low solution phosphorus concentrations in the soil experiment is currently under investigation at this laboratory.

Although no microbiological examination of the root systems of cassava grown in the present flowing solution culture experiment was undertaken, it is to be expected that mycorrhizal infection was either nil, or at the most minimal. The omission of any deliberate inoculation step, the use of rooted stem tip cuttings as the experimental material, and the relatively short duration of the experiment (28 days) would be expected to minimize the development of any mycorrhizal association on the plant roots: The present results therefore almost certainly describe the poor physiological activity in phosphorus absorption of non-mycorrhizal root systems of cassava. This inefficiency in absorption by cassava root systems is not uniquely confined to phosphorus; rates of potassium absorption by young cassava plants are also much less than those by sunflower and maize over a wide range of solution potassium concentrations (Spear *et al.*, 1978b).

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Table 1. Solution phosphorus concentrations required for 95% relative yield of whole plants of cassava (12 cultivars), soybean, cotton and maize grown in flowing nutrient solution for 28 days.

Species	Cultivar	Solution P. concn. for 95% relative yield of whole plants
		(μM)
Cassava	M Aus 7	28
	Seda	29
	M Aus 3	30
	M Aus 14	31
	M Aus 12	32
	Amarillo	32
	Mameya	62
	M Aus 17	64
	Nina	66
	Pata de Paloma	68
	M Aus 10	72
	Ceiba	78
Soybean		0.6
Cotton		0.6
Maize		1.0

Table 2. **Phosphorus concentrations in the tops (a) and roots (b) of cassava (12 cultivars), soybean, cotton and maize grown in flowing nutrient solution at eight constant phosphorus concentrations for 28 days**

Species	Solution phosphorus concentration (μ M)								Solution phosphorus concentration (μ M)							
	0.05	0.70	3.0	12	50	127	313	1021	0.05	0.70	3.0	12	50	127	313	1021
	(a) TOPS				% P				(b) ROOTS				% P			
Cassava																
M Aus 7	0.09	0.15	0.47	0.46	0.69	0.68	0.69	0.59	0.08	0.12	0.36	0.57	0.95	1.13	1.26	1.06
Seda	0.08	0.09	0.35	0.43	0.57	0.57	0.61	0.59	0.08	0.12	0.32	0.44	0.73	0.83	0.87	0.81
M Aus 3	0.07	0.13	0.50	0.47	0.64	0.64	0.72	0.62	0.08	0.13	0.35	0.51	0.79	0.84	1.09	0.94
M Aus 14	0.08	0.10	0.44	0.52	0.69	0.69	0.73	0.66	0.07	0.10	0.27	0.45	0.71	0.71	0.96	0.83
M Aus 12	0.09	0.11	0.48	0.54	0.67	0.71	0.75	0.66	0.07	0.12	0.29	0.49	0.68	0.75	0.84	0.87
Amarillo	0.07	0.10	0.38	0.45	0.49	0.49	0.59	0.53	0.07	0.13	0.31	0.48	0.77	0.66	0.85	0.74
Mameya	0.09	0.12	0.34	0.41	0.65	0.64	0.66	0.57	0.08	0.10	0.26	0.45	0.63	0.77	0.75	0.66
M Aus 17	0.09	0.13	0.39	0.46	0.69	0.65	0.67	0.58	0.08	0.12	0.29	0.53	0.77	0.86	0.91	0.96
Nina	0.08	0.09	0.35	0.43	0.60	0.58	0.58	0.57	0.08	0.13	0.33	0.48	0.72	0.87	0.88	0.81
Pata de Paloma	0.09	0.10	0.37	0.43	0.57	0.59	0.67	0.55	0.08	0.12	0.28	0.55	0.70	0.86	1.01	0.78
M Aus 10	0.07	0.09	0.35	0.53	0.58	0.58	0.61	0.60	0.09	0.12	0.26	0.43	0.50	0.53	0.66	0.64
Ceiba	0.11	0.14	0.41	0.47	0.62	0.65	0.68	0.65	0.08	0.12	0.31	0.49	0.68	0.85	0.81	0.78
Mean of 12 cv.	0.08	0.11	0.40	0.47	0.62	0.62	0.66	0.60	0.08	0.12	0.30	0.49	0.72	0.81	0.91	0.82
Soybean	0.13	0.42	0.55	0.52	0.58	0.60	0.66	0.88	0.13	0.42	0.76	0.84	1.09	1.35	1.38	1.31
Cotton	0.09	0.21	0.58	0.77	0.88	0.92	1.02	1.02	0.14	0.20	0.37	0.62	0.54	0.60	0.76	0.82
Maize	0.10	0.22	0.82	0.76	1.10	0.93	1.18	1.17	0.08	0.21	0.78	0.92	1.16	1.28	1.33	1.22

Table 3. Critical phosphorus concentrations in the tops of cassava (12 cultivars), soybean, cotton and maize grown in flowing nutrient solution for 28 days

Species	Cultivar	Critical P concn[1]
		% P in dry matter
Cassava	M Aus 7	0.59
	Seda	0.53
	M Aus 3	0.61
	M Aus 14	0.66
	M Aus 12	0.64
	Amarillo	0.47
	Mameya	0.60
	M Aus 17	0.62
	Nina	0.55
	Pata de Paloma	0.56
	M Aus 10	0.57
	Ceiba	0.62
Soybean		0.40
Cotton		0.19
Maize		0.38

[1]Critical P concentration corresponding to 95% relative whole plant yield.

Table 4. Root weight ratios[1] of cassava (12 cultivars), soybean, cotton and maize grown in flowing nutrient solution at eight constant phosphorus concentrations for 28 days

Species	Solution phosphorus concentration (μM)							
	0.05	0.70	3.0	12	50	127	313	1021
Cassava								
M Aus 7	0.33	0.31	0.23	0.21	0.19	0.18	0.21	0.18
Seda	0.22	0.22	0.23	0.20	0.16	0.16	0.20	0.18
M Aus 3	0.26	0.25	0.26	0.22	0.19	0.19	0.22	0.22
M Aus 14	0.20	0.19	0.22	0.20	0.16	0.16	0.19	0.16
M Aus 12	0.22	0.21	0.24	0.22	0.18	0.18	0.19	0.19
Amarillo	0.20	0.23	0.18	0.16	0.14	0.13	0.16	0.15
Mameya	0.22	0.27	0.21	0.20	0.18	0.16	0.17	0.17
M Aus 17	0.28	0.29	0.24	0.21	0.19	0.17	0.19	0.20
Niná	0.21	0.21	0.20	0.19	0.17	0.18	0.19	0.18
Pata de Paloma	0.18	0.16	0.21	0.16	0.16	0.16	0.19	0.17
M Aus 10	0.18	0.24	0.25	0.23	0.18	0.19	0.19	0.18
Céiba	0.25	0.25	0.21	0.19	0.16	0.16	0.20	0.19
Mean of 12 cv	0.23	0.24	0.22	0.20	0.17	0.17	0.19	0.18
Soybean	0.35	0.16	0.14	0.20	0.13	0.14	0.18	0.19
Cotton	0.25	0.26	0.15	0.15	0.10	0.12	0.14	0.16
Maize	0.47	0.32	0.22	0.21	0.20	0.17	0.21	0.22

[1] Root weight ratios claculated on a dry weight basis.

Table 5. Mean rates of phosphorus absoprtion by cassava (12 cultivars), soybean cotton and maize grown in flowing nutrient solution at eight constant solution phosphorus concentrations for 28 days

Species	Solution phosphorus concentration (μ M)							
	0.05	0.70	3.0	12	50	127	313	1021
	μmol/g fresh wt. roots/day							
Cassava								
M Aus 7	0.22	0.85	4.90	6.41	9.19	10.09	10.40	9.94
Seda	0.08	0.57	3.58	5.31	6.94	7.45	7.76	8.58
M Aus 3	0.19	0.87	4.98	6.34	9.23	10.03	9.57	9.89
M Aus 14	0.13	0.68	5.01	7.15	11.70	10.78	10.34	11.78
M Aus 12	0.16	0.92	4.74	7.65	10.78	12.84	11.66	10.30
Amarillo	−0.18	0.84	4.46	6.69	8.87	9.16	7.94	9.66
Mameya	0.21	0.69	3.70	6.39	9.10	10.23	9.35	10.42
M Aus 17	0.04	0.68	3.51	5.56	8.59	9.36	8.27	8.01
Nina	0.01	0.57	4.15	6.43	8.00	8.83	8.32	9.24
Pata de Paloma	0.15	0.49	4.17	6.45	7.62	8.52	8.14	8.93
M Aus 10	0.14	0.63	2.64	6.47	8.13	8.43	9.08	7.81
Ceiba	0.15	0.80	5.33	7.20	8.99	10.60	9.12	9.93
Mean of 12 cv	0.11	0.72	4.26	6.50	8.93	9.69	9.16	9.54
Soybean	0.61	9.27	12.74	11.12	14.35	15.48	16.34	20.17
Cotton	0.05	1.99	9.84	14.42	17.84	16.83	20.17	18.43
Maize	0.46	3.20	13.70	16.19	18.52	19.40	19.45	18.04

Table 6. Approximate rates of phosphorus absorption corresponding with 95% of maximum whole plant yield of cassava (12 cultivars), soybean, cotton and maize grown in flowing nutrient solution for 28 days

Species	Cultivar	Rate of P absoprtion for 95% of maximum yield
		μmol/g fresh wt. roots/day
Cassava	M Aus 7	7.3
	Seda	6.3
	M Aus 3	8.7
	M Aus 14	11.0
	M Aus 12	10.1
	Amarillo	8.6
	Mameya	9.2
	M Aus 17	8.8
	Nina	8.3
	Pata de Paloma	8.0
	M Aus 10	8.3
	Ceiba	10.0
Soybean		8.6
Cotton		1.7
Maize		7.2

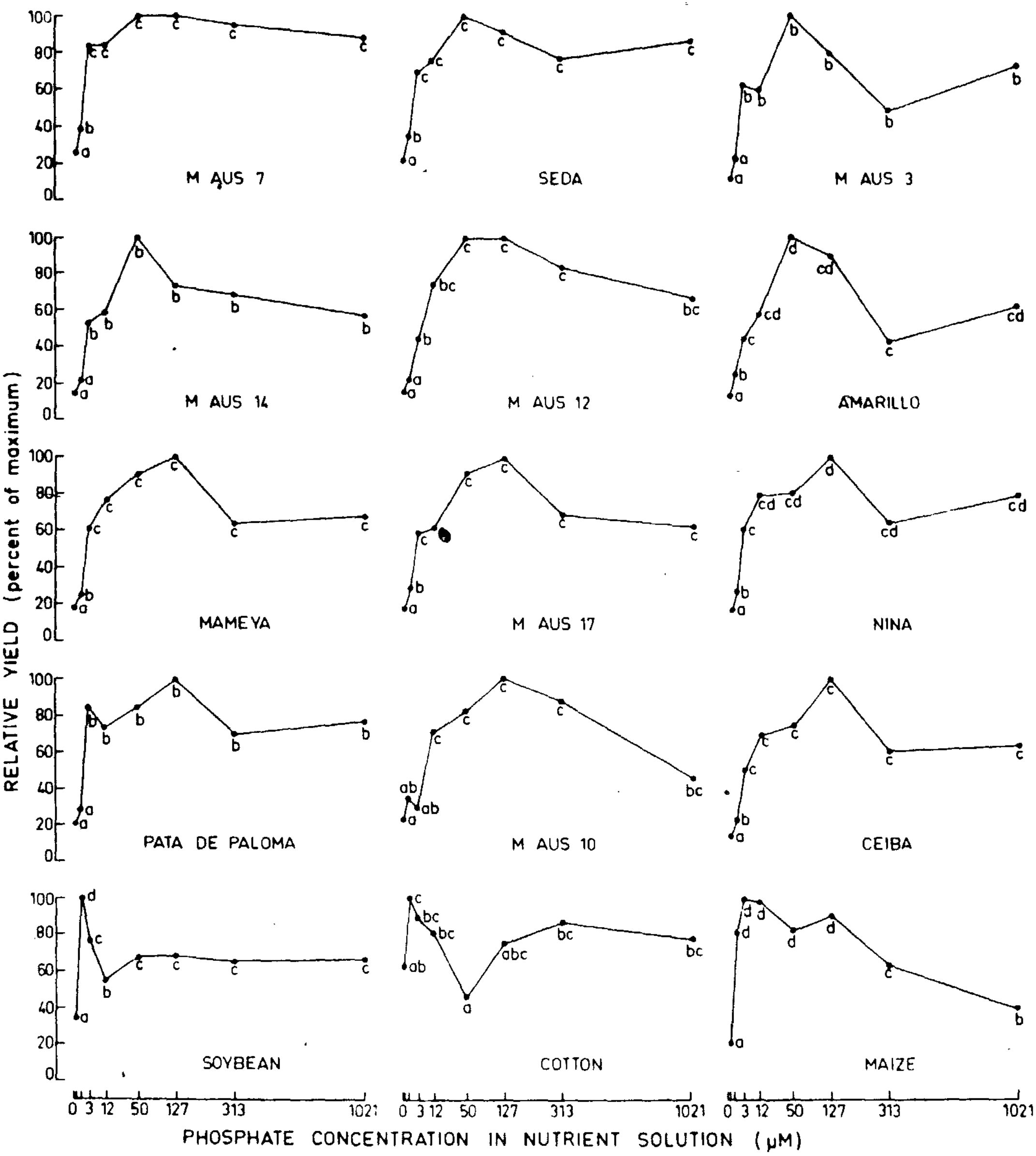

Figure 1. Effect of solution phosphate concentration on relative yields of whole plants of cassava (12 cultivars), soybean, cotton and maize: means of four replicates; values with same letter are not significantly different ($P < 0.05$) by Duncan's range test.

Maximum dry weights (g/plant) were as follows:

M Aus 7 8.57, Seda 7.93, M Aus 3 10,00, M Aus 14 6.91, M Aus 12 6.67, Amarillo 6.15, Mameya 8.28, M Aus 17 10.00, Nina 8.87, Pata de Paloma 6.72, M Aus 10 3.57, Ceiba 10.47, Soybean 4.45, Cotton 0.93, Maize 8.06.