

Genotypic Variation in Responses of Cassava (*Manihot esculenta* Crantz) to Drought and Rewatering: Root System Development

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Abstract : Soil moisture condition is a major factor that affects root system development and thus, crop production. This study aimed to evaluate genotypic variations of cassava in root system structures and their responses to different soil moisture conditions by examining various root traits including production and elongation of adventitious roots and their laterals. Four pot experiments were conducted and different genotypes of various backgrounds were grown under well-watered, droughted, droughted to rewatered conditions. One field experiment was also conducted with selected genotypes till maturity. Results showed that substantial genotypic variations exist in root system structure, and the effects of the soil moistures were significant for most of the root traits. The principal component analysis (PCA) showed that the lateral root development mainly accounted for the variations in root system structure regardless of soil moisture conditions. The PCA on the differences between droughted and well-watered control, and droughted-rewatered and the control further indicated that the branching ability of adventitious roots was mainly responsible for the root system responses to drought as well as rewatering. Genotypic ranking in root system responses to drought was almost consistent among the pots and field experiments. Genotypic variations in rooting depth were relatively small while those in horizontal spread were apparent in the field experiment. The ability to maintain adventitious root elongation under drought, resulting in relatively large horizontal spread of root system and to recover sharply from drought by lateral root branching may be related to good growth and yield performance under field.

Key words : Cassava, Drought, Drought recovery, Lateral roots, Plasticity, Principal component analysis.

We have accumulated experimental evidence that a root system of an individual plant is an integration of several kinds of component roots with dissimilar morphology, anatomy, and physiological functions (Yamauchi et al., 1996) and genetic control (Wang et al., 2005). They also differ in developmental responses to various environments (Wang and Yamauchi, 2006). Zobel (2005) also presented the identical view that a plant root system is composed of a coordinated set of genetically and functionally distinct classes of roots. Consequently, these facts indicate that the traits of each component root need to be determined to understand the characteristics in development and function of the entire root system of the crop species.

O'Toole and Bland (1987) extensively and intensively reviewed the literature to show that substantial genotypic variations exist in root system development, and first pointed out the importance of phenotypic plasticity that is defined as the ability of a plant to alter its phenotype in response to changing environment, for the root system function of agricultural crops.

In fact, roots exhibit distinct adaptive responses to adverse conditions, including developmental changes in root structure and various physiological characteristics (Wang and Yamauchi, 2006). Yamauchi et al. (1996) indicated that such phenotypic plasticity in root system development is the key trait for stress tolerance and can be effectively understood as integrated consequences of plastic responses of each component root.

Quantitative information is fundamental and thus indispensable to understand the functional significance of root system structure and development, and their plasticity. In this aspect, with special attention to the differences among the component roots, we have quantified root system structures and their responses to various soil conditions for food crop species like cereals (Yamauchi et al., 1987; Yamauchi et al., 1996; Bañoc et al., 2000; Suralta and Yamauchi, 2008; Suralta et al., 2008a, 2008b) and legume species (Kono et al., 1987; Mia et al., 1996a, 1996b), and examined the physiological (Ogawa et al., 2005)

and genetic (Wang et al., 2005) bases for such root plasticity.

On the other hand, a cassava root system is relatively simple as compared with those of cereals and legume species. It consists of adventitious roots initiating from the cut end and nodes of the stem cutting and their concomitant lateral roots of different branching orders. However, detailed quantitative study on cassava root system development and its responses to various environments is quite limited. Besides, most cassava studies dealt with shoot growth (Okogbenin et al., 2003) and tuber production (De Pinho et al., 1995; El-Sharkawy and Cadavid, 2002) as an organ to be harvested. Among them, Pardales and Esquibel (1996) found out that cassava root development during the early establishment period was substantially affected by the moisture content of the soil. Pardales and Yamauchi (2003) quantified the root development of cassava and sweet potato as a function of moisture treatments in the soil, varieties and changing soil moisture conditions by a series of pot experiments. Results showed that both root production and elongation were generally suppressed by deficient soil moisture condition, and the plants showed recovery responses especially in the branching of lateral roots after rewatering. Likewise, genotypic variations existed in root response to various soil moisture conditions but these findings still have to be validated further as variations in genotypes and growing conditions were rather limited in their studies.

In this study, we therefore used different cassava genotypes of varying agronomic and genetic backgrounds to maximize genotypic variations and conducted a series of pot experiments to evaluate the responses of plants of different ages to various soil moisture conditions including different intensities and durations of drought, and rewatering. They were conducted under different agro-climatic conditions, locations and years. A field experiment was then conducted using some of the selected genotypes to evaluate the responses in plant growth and yield under field conditions to the different soil moisture conditions, and to evaluate the role of root responses.

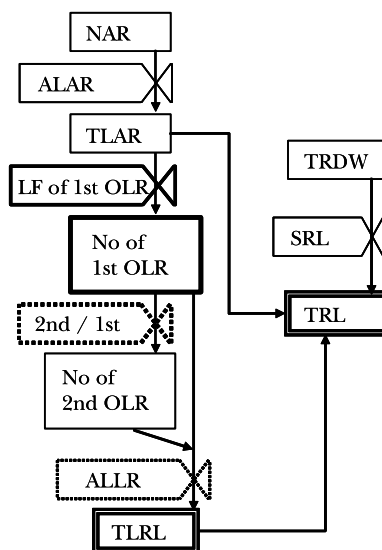


Fig. 1. Relationship among root traits. Doubled (TRL and TLRL) and thicker bold line (No of 1st OLR) indicates the major factor in PC 1 and PC 2, respectively, for root system structure, and thinner bold (LF) and doubled (TRL and TLRL) line indicates the major factor in PC 1 and PC 2, respectively for the root responses (D/W, D-RW/W). TRL was mostly determined by TLRL. Dashed lines indicate the traits that were not determined in this study. NAR, number of adventitious roots; ALAR, average length of adventitious roots, TLAR, total length of adventitious roots, LF, linear frequency; OLR, order lateral root; ALLR, average length of lateral roots; TLRL, total lateral root length; TRL, total root length; SRL, specific root length; TRDW, total root dry weight.

Our methodology in this study was to evaluate the root system structure principally based on the total root length that is of key functional significance because it determines the size of contact with soil (Yamauchi, 2004). Additional traits were examined to analyze how the entire root system structure that was quantified based on the total root length was constituted by the production (number) and elongation (length) of component roots; adventitious and lateral roots of different branching orders (Fig. 1).

This paper reports the results of 1) the quantitative analysis of the genotypic variations in the root system

Table 1. Location, type and duration of experiments, average daily maximum and minimum temperatures and relative humidity, soil moisture content and duration of drought and rewatering treatments.

Exp	Location	Type of Exp	Duration of Exp	Temperature (°C)		RH (%)	SMC (%)			Duration (d)	
				Max	Min		W	D	RW	D	RW
1	VSU, Philippines	pot	16 Aug-10 Nov '01	33.8	25.9	62.1	25	10	–	55	–
2	VSU, Philippines	pot	01 Mar-30 Apr '03	31.5	28.2	74.1	25	15	–	30	–
3	Nagoya University, Japan	pot	15 Jun -24 Oct '03	38.5	24.9	71.8	20	4	20	16	14
4	Nagoya University, Japan	pot	24 Jul -08 Nov '04	35.5	19.5	61.8	20	4	20	30	14
5	VSU, Philippines	field	04 Feb -31 Oct '03	31.5	23.6	80.8	R	D	–	207	–

Exp, experiment; Max, maximum; Min, minimum; RH, relative humidity; SMC, soil moisture content; W, well-watered; D, droughted; RW, droughted-rewatered; R, rainfed conditions; VSU, Visayas State University.

structures and their developmental processes, 2) the evaluation on the effects of different soil moisture conditions (i.e., well-watered, droughted, droughted and then rewatered conditions) on the root system structure, and 3) the identification of root traits that are consistently and mainly responsible among the genotypes examined for characterizing the entire root system structure under the different soil moisture conditions, and their plastic responses to those changing moisture conditions. The genotypic variations in the root system structures and their responses were then related to those in plant growth under different soil moisture conditions to understand the importance of root system development for plant adaptation.

Materials and Methods

1. Pot experiment

(1) Experiment 1

This experiment was conducted in Philippine Root Crop Research and Training Center (PhilRootcrops), Visayas State University (VSU), Baybay, Leyte, Philippines (136° 56' 57" E, 35° 9' 47" N) from 16 August to 10 November, 2001 (Table 1). Twenty-eight different cassava genotypes originating from various places with diverse characteristics were used (Table 2).

A rigid rain shelter of 9.5 m wide, 16.0 m long, and 2.5 m high with transparent acetate (0.08 mm thick) roof was constructed to protect the experimental pots against precipitation. Uniform cassava stem cuttings of about 20 cm in length of each genotype were planted in vertical position at one cutting per polyethylene pot (25 cm wide; 25 cm high). The pots were filled with 9 kg of air-dried sandy loam soil mixed with 1.6 g of powdered complete fertilizer (14% N, P₂O₅, K₂O). Two days prior to planting, the soil in each pot was saturated with tap water and allowed to drain for a day, which resulted in 25% soil moisture content (SMC). This SMC was maintained in all pots from planting till harvest for well-watered control pots. For drought treatment, watering was withheld starting from 30 days after planting (DAP) until the SMC dropped to 10%, which was maintained thereafter. The SMC of each pot was checked every other day using the soil moisture sensor (Hydrosense, Decagon Devices, USA). The target SMC for each treatment was maintained by adding water of the amount decreased after the previous measurement. At 85 DAP (55 days after the start of drought treatment), plants were sampled in both treatments. Three pots were prepared for each treatment of all 28 genotypes.

In the course of the entire experiment, air temperature and relative humidity were recorded daily (Table 1).

(2) Experiment 2

This experiment was conducted to examine the effects of drought on the developmental processes

of the root systems in the following three selected genotypes; VC-4 that formed the longest root system, PSB cv-19 that produced a medium size of root system, and Vassourinha that formed the smallest root system among the 28 genotypes under well watered condition in Exp. 1. This experiment was conducted from 1 March to 30 April, 2003 under the rain shelter that was used in Exp. 1.

All the plants were established for one month at 25% SMC, after which drought imposition began. At 30 DAP, a half of total number of pots which no longer received water (drought treatment) dropped SMC to 15%, and was then maintained under the same condition while the other half was continuously maintained at 25% SMC (well-watered control) (Table 1). All the other cultural practices including maintenance of SMC followed those of Exp. 1. Staggered samplings were performed at 10, 20 and 30 days after the onset of drought treatment (40, 50 and 60 DAP). Maximum and minimum temperatures and relative humidity were recorded daily (Table 1).

(3) Experiment 3

To evaluate the root responses to drought and the recovery processes by rewatering, we conducted this experiment from 15 June to 24 October, 2003 in a vinyl house at the experimental field of Nagoya University, Japan (136° 56' 57" E, 35° 9' 47" N). The average daily air temperature and relative humidity were recorded during the experiment (Table 1). Six genotypes were used in this experiment. They were selected among the 28 genotypes so as to maximize the genotypic variation in response to drought based on the ratios of stressed plants to well-watered control in total root length, which were determined in Exp. 1 where Rayong 5 showed the highest ratio (0.34), followed by PSB cv-19 (0.31), Vassourinha (0.30), PSB cv-11 (0.18), Zapote (0.14), and VC-4 (0.13) which showed the lowest.

About 20 cm cassava stem cuttings of each variety were obtained from PhilRootcrops, VSU and planted uprightly in 5-L plastic pots filled with 4 kg of air-dried sandy loam soil properly mixed with complete fertilizer (14-16-16). SMC of 20% was maintained throughout the establishment stage, which lasted for 100 days. At the end of the establishment stage, water was withheld and SMC was allowed to drop to 4% in half of the total pots (108 pots in total) to stimulate drought while the rest of the pots continued to be watered to maintain 20% SMC till the end of experiment (control). This was maintained for 16 days. At the end of the drought treatment (116 DAP), the droughted plants were rewatered for 14 d (Table 1). This was done by adding water to raise the SMC to 20%, which was the same as that of the well-watered control and maintained for 14 days up to 130 DAP.

In well-watered control plants, SMC was maintained at 20% throughout the experiment by such gravimetric method. The duration and intensity of water treat-

Table 2. List of the 28 cassava genotypes and their characteristics used in Exp. 1.

Genotype	Origin	Method of breeding	Developing Institution	Root yield (t ha ⁻¹)	Maturity (months)	Plant Type ^a
Golden Yellow	Philippines	Local selection		20–30	8–10	MTE
Indang 2	Philippines	Local selection		15–25	10–12	MTMB
Kadabao	Philippines	Local selection		20–30	10–12	TE
Kaplutan	Philippines	Local selection		15–25	8–10	MTE
Namaya	Philippines	Local selection		15–25	10–12	MTSB
Nito-nito	Philippines	Local selection		15–25	10–12	MTSB
Pintuyan 3	Philippines	Local selection		15–25	10–12	MTMB
Siasi	Philippines	Local selection		15–25	10–12	MTE
Tandang 2	Philippines	Local selection		15–25	10–12	TE
Zapote	Philippines	Local selection		20–30	10–12	MTMB
Datu 1	USA	Introduction of Hawaiian 4	IPB, UPLB	30–40	10–12	MTMB
Lakan 1	Indonesia	Local selection	IPB, UPLB	35–45	8–10	MTE
Sultan 1	Philippines	Selection from F1 population (Bogor 397×Sip 242-2)	IPB, UPLB	35–45	9–11	MTSB
Sultan 2	Philippines	Selection from F1 population (Mcol 1684×Bogor)	IPB, UPLB	25–35	10–12	TSB
Vassourinha	Brazil	Local selection	IPB, UPLB	25–35	10–12	SDE
PSB cv-11	Colombia, CIAT	Selection from CM3419 F1 population	IPB, UPLB	30–40	10–12	MTMB
PSB cv-12	Colombia, CIAT	Selection from SM972 F1 population	IPB, UPLB	25–35	10–12	MTMB
VC-1	Colombia, CIAT	Selection from CM 323 F1 population	IPB, UPLB	25–35	9–11	MTSB
VC-2	Colombia, CIAT	Introduction of CMC40	IPB, UPLB	35–45	8–10	MTMB
VC-4	Colombia, CIAT	Selection from F1 population (CM 728-3×CM 681-2)	IPB, UPLB	35–45	9–12	MTE
PSB cv-13	Colombia, CIAT	Selection from F1 population (CMC 40×Branca de Santa Catalina)	Philrootcrops, VSU	25–35	10–12	MTMB
PSB cv-14	Colombia, CIAT	Selection from F1 population (CM 323-52×Java Brown)	Philrootcrops, VSU	30–40	8–10	TSE
PSB cv-15	Colombia, CIAT	Selection from F1 population (CM 630-122×CM 728-2)	Philrootcrops, VSU	25–35	10–12	MTSB
PSB cv-16	Colombia, CIAT	Selection from F1 population (Kadabao×Branca de Santa Catalina)	Philrootcrops, VSU	25–35	10–12	MTMB
PSB cv-19	Colombia, CIAT	Selection from open pollinated seeds of CM 523-7	Philrootcrops, VSU	25–35	10–12	MTSB
KU-50	Thailand	Selection from F1 population (Rayong 1×Rayong 90)	RFCRC, DA	25–35	10–12	MTE
Rayong 5	Thailand	Selection from F1 population (MR27-77-10×Rayong 3)	RFCRC, DA	25–35	10–12	MTSB
Rayong 60	Thailand	Selection from F1 population (Mcol 1684×Rayong 1)	RFCRC, DA	20–30	10–12	SDE

^aMTE : medium tall and erect, MTMB:medium tall and moderately branching, MTSB:medium tall and slightly branching, SDE:semi-dwarf and erect, TE:tall and erect, TSE:tall and slightly erect and TSB:tall and slightly branching; IPB, Institute of Plant Breeding, University of the Philippines, Los Banos; Philrootcrops, Philippine Root Crops Research and Training Center; VSU, Visayas State University; RFCRC, Rayong Field Crops Research Center; DA, Department of Agriculture.

Source: adapted from Philrootcrops data base.

ments are summarized in Table 1. Destructive sampling was performed before withholding water (100 DAP) at the end of the drought treatment (116 DAP) for both continuously well-watered, and the well-watered and then droughted plants, as well as at the end of

rewatering period (130 DAP) for both continuously well-watered, and the well-watered, droughted, and then rewatered plants.

(4) Experiment 4

To verify the results of Exp. 3, we conducted this

Table 3. Root traits of genotypes that were grown under well-watered (W) and droughted (D) conditions and the maximum and minimum values, average, and the result of ANOVA in Exp. 1.

Root trait	Soil moisture treatment						ANOVA		
	W		D/W		Average		SM	G	SM X G
	Max	Min	Max	Min	W	D/W			
TRL (cm plant ⁻¹)	30028	5960	0.48	0.13	12708	0.26	**	**	**
TRDW (g plant ⁻¹)	4.40	1.73	0.31	0.07	3.01	0.16	**	**	**
SRL (cm g ⁻¹ plant ⁻¹)	7866	2541	4.02	0.71	4374	1.74	*	*	**
TLAR (cm plant ⁻¹)	1450	534	0.97	0.25	889	0.56	**	**	**
ALAR (cm plant ⁻¹)	21	10	3.20	0.65	14	1.08	**	**	ns
NAR (no. plant ⁻¹)	108	38	0.99	0.17	63	0.57	**	**	**
TLRL (cm plant ⁻¹)	28578	5426	0.45	0.14	11818	0.24	**	**	**
LF (no. cm ⁻¹)	1.90	0.90	1.88	0.52	1.25	1.04	**	**	**
No. of 1st OLR (no. plant ⁻¹)	1723	499	1.22	0.22	1118	0.58	**	**	**
No. of 2nd OLR (no. plant ⁻¹)	5423	795	0.61	0.10	2211	0.32	*	**	*

TLR, total root length; TRDW, total root dry weight; SRL, specific root length; AR, adventitious root; TLAR, total length of AR; ALAR, average length of AR; NAR, number of AR; TLRL, total lateral root length; LF, linear frequency (number of 1st order lateral roots per cm of adventitious root); OLR, order of lateral root; W, well-watered treatment; D, droughted treatment; D/W, droughted to well-watered control ratio; ANOVA, analysis of variance; SM, soil moisture; G, genotype.

*, **, ns, indicates at the 5%, 1% and no significant difference, respectively (Duncan Multiple Range Test, n = 3).

experiment from 24 July to 8 November, 2004. The same cultural management practices and experimental design were adopted, including experimental location and intensity of soil moisture treatments. However, the age of plants were younger and the duration of drought treatment was longer than those of Exp. 3. The same genotypes as Exp. 3 were used except that Golden yellow, which is widely accepted by the local farmers in the Philippines, was added while Vassourinha and Zapote were excluded. Drought treatment lasted for 30 days. At the end of the drought treatment (90 DAP), the droughted plants were rewatered for 14 days as in Exp. 3 (Table 1). The timing and procedures of sampling followed those in Exp. 3.

2. Field experiment

(1) Experiment 5

An area of 864 m² was prepared and ridges were formed right after the last harrowing width of 0.75 m apart in PhilRootcrops, VSU. Plot size with a dimension of 9 m² was prepared. The planting distance was set to 0.75 m between ridges and 0.75 m between hills making 4 rows per subplot and 4 hills per row, 16 plants per plot, respectively. Alleyways measuring 1 m were provided between replications and 2 m between treatment plots to facilitate data gathering. Five diverse cassava genotypes were used; Golden Yellow, Rayong 5, PSB cv-11, PSB cv-19 and VC-4.

One 20-cm long stem cutting was planted per hill on 4 February, 2003. A total of 640 plants were utilized to accommodate all entries (16 plants per plot with

40 plots (5 genotypes×2 treatments×4 replications). At 34 DAP, one half of the total number of plants for each genotype (320 plants) was covered with plastic rain shelter with a dimension of 18 m×24 m to impose drought condition. The other half of the plants was continuously grown under rainfed conditions. The plants for both treatments were harvested at 259 DAP (31 October, 2003).

3. Root sampling and measurements

After each sampling, the belowground parts were carefully washed with tap water and preserved in FAA (formalin-acetic acid-alcohol) for further analysis. In Exps. 1 and 2, we manually counted the number of adventitious roots, and their 1st order and 2nd order lateral roots separately. The length of the adventitious roots was measured using a ruler. From these data, the linear frequency of lateral roots was calculated as the number of lateral roots per unit length of adventitious root axis (Ito et al., 2006). In Exps. 1 and 2, the total root length including the adventitious roots and their laterals roots was then determined following the line intersection method developed by Tennant (1975). Then roots were oven dried for 72 h at 80°C and weighed. Total lateral root length was calculated as a difference between the total root length and the sum of adventitious root length. Total root length was divided by the total root dry weight to obtain specific root length.

In Exps. 3 and 4, the same traits with those in Exps. 1 and 2 were measured except the number of 2nd order laterals. For total root length measurement, root

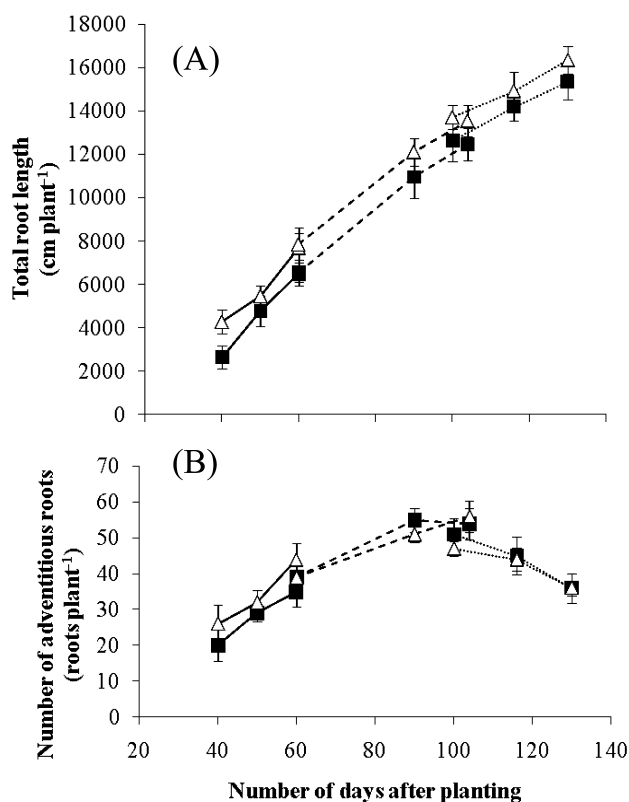


Fig. 2. Changes with growth in total root length (A) and number of adventitious roots of plants grown under well-watered conditions in VC-4 (■) and PSB cv-19 (△) in Exps. 2 (40 to 60 DAP), 3 (100 to 130 DAP) and 4 (60 to 104 DAP).

images were digitized by scanning and the root length was measured using NIH image analysis program (a public-domain program) following the method developed by Kimura et al. (1999), and Kimura and Yamasaki (2001).

In Exp. 5, the belowground parts including tubers were carefully excavated from all of the 16 plants in every plot, and the tip of the deepest root was recorded as the vertical maximum rooting depth. Each of the harvested belowground parts was classified into marketable tuber (diameter >5 cm) and the rest as adventitious roots whose lengths were manually measured and the numbers were counted, and then oven dried for 72 h at 80°C and weighed to obtain total root dry weight.

4. Experimental design and statistical analysis

Exps. 1, 2 and 5 were laid in a split plot design arranged in a randomized complete block design. There were three replications for Exp. 1, and four for Exps. 2 and 5. For Exp. 5, the two water treatments (with and without rain shelter) served as main plots, while the cassava genotypes as subplots. Analysis of variance was done using the General Linear Model following SAS program. Similarly, Exps. 3 and 4 were arranged

in a randomized complete block design with three replications. Comparison among treatment means was done using the Duncan Multiple Range Test at 1% and 5% significance level. To identify traits mainly responsible for determining the root system structures and their plastic responses to drought and rewatering treatments, principal component analysis (PCA) was performed using the mean values of three replications of the roots parameters in all experiments (Exps. 1 to 4), as suggested by Iezzoni and Pritts (1991) with EXCEL STATISTICS 2006.

Results

1. Quantitative analysis on root system structure and their developmental processes

Table 3 shows the ten different root traits of the 85-day-old plants for the 28 genotypes examined in Exp. 1. Under well-watered conditions, the total root length averaged about 127 m ranging from 60 to 300 m per plant. Most of the length was accounted for by lateral roots, which was 118 m accounting for 93% of the total root length in average, and the rest by that of adventitious roots. The 85-day-old plants that had not yet started tuber formation weighed 3 g per plant for root dry matter in average, which was converted into length of 44 m per g as expressed by specific root length. The entire root system consisted of 63 adventitious roots that produced 1.3 lateral roots on 1 cm of the axes as expressed by the linear frequency (Ito et al., 2006), which totaled to 1,118 of the first order laterals, which then branched into 2,211 second order laterals per plant. Fig. 1 shows the relationship among the root traits that were determined in this study, which will be described more in details later.

We then examined the processes of those root system development by utilizing the data collected in different experiments although the data themselves are not present unless otherwise specified. The results of Exp. 2 that dealt with the developmental processes of root systems of PSB cv-19, Vassourinha and VC-4 showed that the well-watered plants continued to increase the total root length at least up to the end of the experiment (60 DAP) (Fig. 2 shows the results of PSB cv-19 and VC-4 only). The data for non-stressed plants in Exp. 4 which collected data on 60, 90 and 104 DAP, and Exp. 3 on 100, 116 and 130 DAP (Table 1) show that the total root length continued to increase even at 130 DAP for all the genotypes examined although the rate of increase slightly slowed down thereafter (Fig. 2 (A)). In contrast, formation of new adventitious roots peaked between 90 to 104 DAP at 50 to 60 roots per plant for these genotypes (Fig. 2 (B) for PSB cv-19 and VC-4). In the plants that were grown under rainfed field conditions for about nine months in Exp. 5, the number of adventitious roots ranged from 13 for VC-4 to 21 for PSB cv-19 (Table 4). Out of them, about 30% for PSB cv-19 to 64% for VC-4 were

Table 4. Root traits of genotypes grown with (droughted conditions) and without (rainfed conditions) rain shelter under field conditions in Exp. 5.

Genotype	TRDW (g plant ⁻¹)		NAR				VMRD (cm plant ⁻¹)	
			marketable tubers (no. plant ⁻¹)		total number (no. plant ⁻¹)		R	D/R
	R	D/R	R	D/R	R	D/R		
Golden Yellow	705 c	0.48 a	8.1 a	0.51	15 b	0.75	60 a	0.82
Rayong 5	1167 a	0.40 c	7.5 a	0.46	16 b	0.60	46 b	0.78
PSB cv-19	573 c	0.19 c	6.4 b	0.62	21 c	0.46	50 b	0.66
PSB cv-11	775 b	0.27 c	6.2 a	0.40	13 c	0.56	47 a	0.74
VC-4	851 d	0.10 b	8.5 b	0.31	13 a	0.58	56 b	0.49
Average	838	0.29	7.34	0.46	16	0.59	51	0.75
SM	**		**		*		*	
G	**		**		*		*	
SM×G	**		ns		ns		*	

TRDW, total root dry weight; R, rainfed; D, droughted; D/R, ratio of droughted to rainfed control; NAR, number of adventitious root; VMRD; vertical maximum rooting depth; SM, soil moisture treatment; G, genotype. In column, means followed by the same letter are not significantly different at 5% level by DMRT. The order of genotypes was based on the ranking of D/W ratios of total root length.

*, **, ns, indicates at the 5%, 1% and no significant difference, respectively (Duncan Multiple Range Test, n=16).

marketable tubers while the others were non tuberous roots. This means that many of the adventitious roots were shed off as plants matured. The average length of adventitious roots also followed the same pattern, and the values peaked at around 90 DAP while genotypic variation was relatively small.

As pointed out earlier, based on the results of Exp. 1 on 85-day-old plants, lateral roots were shown to be the major component of the entire root system. Integration of results from other experiments indicates that the laterals continued to be the major component not only 85 days after planting but throughout the growth regardless of genotypes because the lateral roots accounted for at least 86% of the total root length. The number of first order lateral roots continued to increase even at 130 DAP while the rate of increase was slowed down especially after 60 DAP for almost all the genotypes. Thereafter, the laterals also shed off as plants matured and only few were observed to remain on the adventitious roots about nine months after planting in the field for all the genotypes (Exp. 5)

2. Effects of soil moisture condition and genotype on the root system development

(1) Pot experiment (Exps. 1, 2, 3 and 4)

ANOVA in Table 3 shows that the soil moisture conditions (drought) significantly affected the root traits in Exp. 1. The significant interactions between genotypes and soil moisture for almost all the traits mean that the intensities of the soil moisture effects on the root traits also significantly differed with the genotypes. Specifically, the drought treatment reduced total root length to 26% of well-watered

control in average, ranging from 48% (Golden yellow) to 13% (VC-4 and VC-2). The reduction was mainly attributable to that in the total lateral root length, which was 24% of control. Total lateral root length is determined by the following three parameters; total length of adventitious roots that produce laterals on their axes, linear frequency of laterals on the adventitious roots, and the length (elongation) of each individual lateral root. In this experiment, we measured the former two parameters but not the third one because it is almost impossible to measure each length. Examinations on the relationship between drought/well-watered (D/W) ratios in linear frequency and those in total lateral root length, and the D/W ratios in total length of adventitious roots and total lateral root length showed no correlation for both parameters (data not shown). This fact means that the reduction in the length of each lateral due to drought, which was not measured in this study, might have the major cause for the reduction in the total lateral root length, while the linear frequency of lateral roots was scarcely affected by the drought.

The reductions in adventitious root development were in turn attributed to the reduced total length of adventitious roots, which was 56% of control, especially the initiation of roots, which was 57% of control as expressed by the number of adventitious roots but not elongation of each root, which was 108% of control as expressed by the average length of adventitious roots. The number of first order laterals was reduced to 58% of control and that of the second order laterals was reduced to 32% of control accordingly.

The results shown in Exps. 3 and 4 also show

Table 5. Root traits of genotypes that were grown under well-watered (W) and droughted (D) conditions in Exp. 1, and well-watered (W) and droughted-rewatered (D-RW) conditions in Exps. 3 and 4, and the eigen vectors of each trait in the first two principal components (PC) for W, D, D/W and D-RW.

Root trait	Exp. 1						Exp. 3		Exp. 4	
	W		D		D/W		D-RW/W		D-RW/W	
	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2	PC 1	PC 2
TRL (cm plant ⁻¹)	0.706	0.056	0.625	0.076	0.05	0.53	0.54	0.61	0.61	0.72
TRDW (g plant ⁻¹)	3×10 ⁻⁴	6×10 ⁻⁴	5×10 ⁻⁴	8×10 ⁻⁴	-0.04	0.03	-0.13	-0.11	-0.23	-0.15
SRL (cm g ⁻¹ plant ⁻¹)	0.115	-0.009	-0.064	-0.003	0.02	0.04	-0.21	-0.10	-0.22	-0.31
TLAR (cm plant ⁻¹)	0.015	0.038	0.028	0.036	-0.01	-0.03	-0.10	0.13	-0.12	0.11
ALAR (cm plant ⁻¹)	0.005	-0.001	0.003	-0.001	0.26	0.12	0.20	0.13	0.33	0.13
NAR (no. plant ⁻¹)	-0.007	0.004	-0.001	0.004	-0.06	-0.04	-0.05	-0.05	-0.03	-0.04
TLRL (cm plant ⁻¹)	0.691	0.071	0.710	0.075	0.33	0.71	0.05	0.63	0.10	0.62
LF (no. cm ⁻¹)	0.005	-0.005	0.003	3×10 ⁻⁴	0.81	-0.13	0.91	0.11	0.84	0.17
No. of 1st OLR (no. plant ⁻¹)	0.022	0.752	0.017	0.643	0.06	0.04	0.16	0.11	0.01	0.10

TLR, total root length; TRDW, total root dry weight; SRL, specific root length; AR, adventitious root; TLAR, total length of AR; ALAR, average length of AR; NAR, number of AR; TLRL, total lateral root length; LF, linear frequency (number of 1st order lateral roots per cm of adventitious root); OLR, order of lateral root; W, well-watered treatment; D, droughted treatment.

that drought significantly reduced root system development. Furthermore, rewatering caused significantly different responses from continuously well-watered control, and such responses differed among genotypes as indicated by the significant interaction between genotypes and soil moisture treatments (data not shown).

(2) Field experiment (Exp. 5)

Table 4 shows the total root dry weight, number of adventitious roots and vertical maximum rooting depth for the plants grown in the field under drought (D) with rain shelter and rainfed (R) conditions without the shelter while the length of adventitious roots will be shown later in Table 6. The genotypes are arranged in the same order in Table 6, in which they were ranked according to the order of D/W ratios in total root length in Exp. 1. Drought significantly inhibited root growth as compared with rainfed conditions (Table 4). Significant genotypic variations existed and the effects of the growing conditions were also significant in all the traits examined. As expressed by D/R ratios, on average, the total root dry weight was reduced by 71%, the total length of adventitious roots by 44% (Table 6), number of adventitious roots including tubers by 41%, and the vertical maximum rooting depth by 25%. Furthermore, soil moisture x genotype interaction was significant for root dry weight, adventitious root length and maximum root depth.

3. Identification of key root traits that characterize the root system structure and their plastic responses to drought and rewatering by principal component analysis

To identify root traits that mainly characterize

the entire root system structure of 28 genotypes, we performed principal component analysis (PCA) by using the values of well-watered, droughted, and droughted then rewatered plants in Exps. 1, 3 and 4. The results of only Exp. 1 are shown in Table 5 (Exp. 1, W (well-watered treatment) and D (droughted treatment)).

The eigen values indicated that the first two PCs accounted for 82% of the total variations observed in Exp. 1 (data not shown). The eigen vectors shown in Table 5 indicate that most of the root traits in Exp. 1 had positive weight for PC 1, which accounted for 46% of the total variations among the genotypes (data not shown). Important root traits were length factors, such as total root length and total lateral root length, which were consistent with the three experiments (data for Exps. 3 and 4 not shown) whether plants were grown either under well-watered, droughted, or droughted then rewatered conditions. These results suggest that PC 1 provided the measure of the root system size. Since lateral roots accounted for the major portion of the entire root system, and the total length of the root system was highly correlated with the total lateral root length ($r=0.82^{**}$, significant at 1% level), the results further show that the PC 1 measured mainly the total lateral root length. PC 2 accounted for 36% of the total variations in Exp. 1 (data not shown). Among the root traits, the number of first order laterals was the most important one in all the experiments under the three conditions for PC 2 (only the data for well-watered and droughted plants in Exp. 1 are shown in Table 5). In summary, the root system structure of the genotypes that were grown either under well-watered, droughted or droughted then rewatered condition were primarily characterized by the lateral root development based on

Table 6. Genotypic comparison of root responses in total root length to soil moisture treatments in Exps. 1, 2, 3, 4 and 5.

Genotype	Total root length							Total length of adventitious roots
	Exp. 1		Exp. 2	Exp. 3	Exp. 4	Exp. 3	Exp. 4	Exp. 5
	W (cm plant ⁻¹)	D/W	D/W	D/W	D/W	D-RW/W	D-RW/W	D/R
Golden yellow	11087	0.48	—	—	0.80	—	1.14	0.76
PSB cv-14	11322	0.41	—	—	—	—	—	—
Kaplutan	9910	0.40	—	—	—	—	—	—
Rayong 60	12527	0.38	—	—	—	—	—	—
Sultan 1	10423	0.37	—	—	—	—	—	—
Rayong 5	11354	0.34	—	0.95	0.76	0.82	0.79	0.59
PSB cv-13	7536	0.34	—	—	—	—	—	—
Kadabao	11387	0.32	—	—	—	—	—	—
PSB cv-19	13920	0.31	0.82	0.95	0.73	0.85	0.88	0.52
Vassourinha	5960	0.30	0.72	0.71	—	1.22	—	—
PSB cv-16	13135	0.28	—	—	—	—	—	—
Tandang 2	12265	0.27	—	—	—	—	—	—
Pintuyan 3	12300	0.24	—	—	—	—	—	—
Lakan 1	15870	0.24	—	—	—	—	—	—
PSB cv-15	10407	0.23	—	—	—	—	—	—
VC-1	15547	0.23	—	—	—	—	—	—
Siasi	10817	0.22	—	—	—	—	—	—
Sultan 2	13519	0.21	—	—	—	—	—	—
Nito-nito	10294	0.21	—	—	—	—	—	—
KU-50	14580	0.19	—	—	—	—	—	—
Indang 2	12720	0.19	—	—	—	—	—	—
PSB cv-11	10798	0.18	—	0.77	0.68	0.88	0.93	0.55
Datu 1	9934	0.17	—	—	—	—	—	—
Namaya	13608	0.16	—	—	—	—	—	—
PSB cv-12	15683	0.14	—	—	—	—	—	—
Zapote	13437	0.14	—	0.73	—	1.77	—	—
VC-4	30028	0.13	0.58	0.59	0.58	1.18	0.95	0.39
VC-2	15452	0.13	—	—	—	—	—	—
Average	12708	0.26	0.71	0.78	0.71	1.02	0.94	0.56
SM		**	**	**	**	**	*	*
G		**	**	*	*	*	*	*
SM×G		**	**	*	*	ns	*	*

W: well-watered treatment; D/W: droughted to well-watered control ratio; D-RW/W: droughted-rewatered to well-watered ratio; (corresponding to drought treatment period) and 116 to 130 DAP (rewatering) in Exp. 3, and 60 to 90 DAP (drought) and 90 to 106 DAP (rewatering) in Exp. 4. D/R: droughted to rainfed control ratio in Exp. 5. SM, soil moisture; G, genotype; SM X G, soil moisture and genotype. The order of genotypes was based on the ranking of D/W ratios of total root length.

*, **, and ns indicates the difference at 5%, 1% level and no significance, respectively (Duncan Multiple Range Test n=3).

the results in PCs 1 and 2. (Fig. 1).

To determine the traits that were responsible for the changes in root system development in response to changing soil moisture, we used the D/W ratios for each trait during the droughted period in Exps. 1, 3 and 4, and the D-RW/W ratios during rewatered period in Exps. 3 and 4 were used to perform PCA.

Results revealed that for D/W ratios, the first two PCs explained 82% of the total variations in Exp. 1, and for RW/W ratio, they explained 86% in Exp. 3 and 88% in Exp. 4 (data not shown). Among the root traits examined, as shown in Table 5, the linear frequency of lateral roots showed the highest eigen vector in PC 1 in Exp. 1. In PC 2, the length factor, total root length

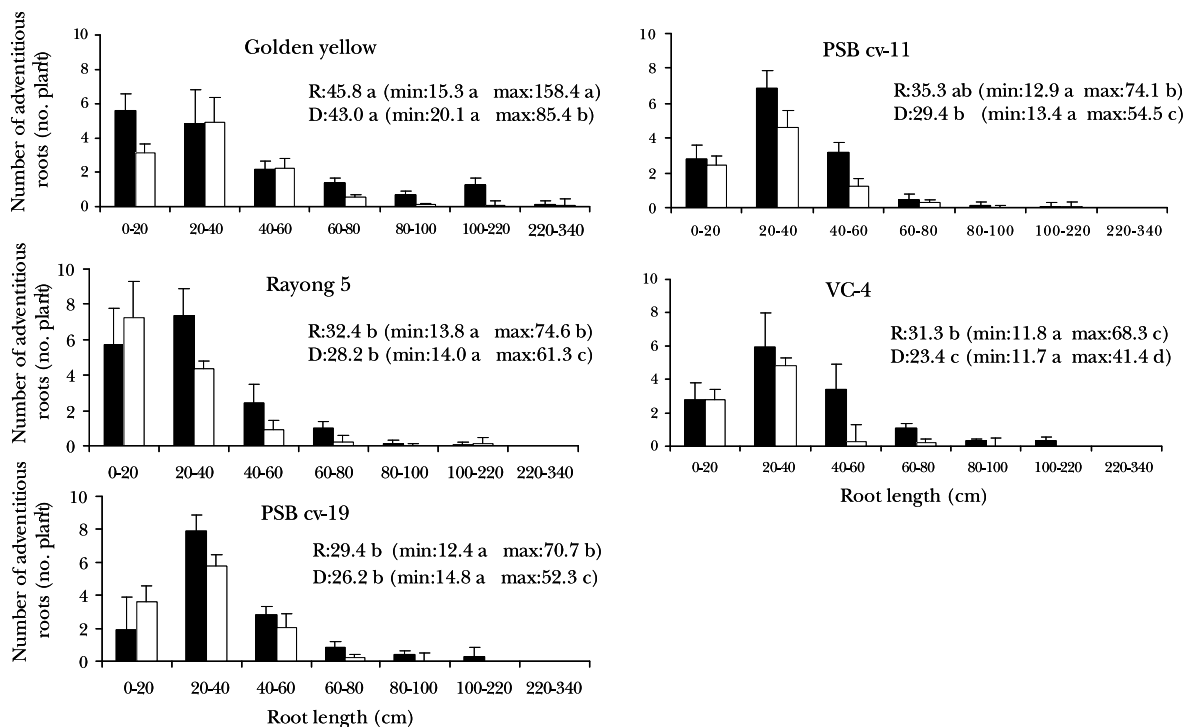


Fig. 3. Genotypic variation in frequency distribution of adventitious root length in a root system of an individual plant grown without (rainfed ■) and with (droughted □) rain shelter under field condition in Exp. 5. Frequency distribution was obtained from average of 15 plants in the number of adventitious roots that fell in the length class ranging in 0-20, 20-40, 40-60, 60-80, 80-100, 100-220 and 220-340 cm. Entries at the upper right side corner of every graph indicate the average length of adventitious roots (cm) under rainfed (R) and droughted (D) conditions. Numbers enclosed in parentheses are the averages of the minimum and maximum lengths of adventitious roots of 15 plants. Numbers followed by the same letter in each average adventitious root, minimum and maximum adventitious roots are not different significantly at 5% level of probability (Duncan Multiple Range Test, $n=15$).

and total lateral root length were the two important traits. Such trends were all consistent in Exps. 3 and 4 including both D/W and D-RW/W ratios (data not shown) (Fig. 1).

4. Genotypic variation in root responses to various soil moisture conditions

To compare root responses to drought and rewatering among the genotypes examined in the five experiments, Table 6 summarizes the D/W ratios in total root length for Exps. 1 to 4 and the D/R ratios in total length of adventitious roots in Exp. 5, and ranks the genotypes according to the D/W ratios in Exp. 1. The genotypic ranking was almost the same in all the experiments. The genotypes with relatively high D/W ratios in Exp. 1 such as Golden yellow, Rayong 5 and PSB cv-19 showed higher ratios also in the other experiments while VC-4 showed the lowest ratio in all the experiments. Golden yellow in Exp. 4 showed the highest ratio in response to both drought (D/W) and rewatering (D-RW/W). Rayong 5 showed the highest D/W ratio in Exp. 3 and the second highest ratio following Golden yellow in Exp. 4.

Under field conditions (Exp. 5), Golden yellow

showed the highest ratio in total adventitious root length in droughted to rainfed plants (D/R), followed by Rayong 5, PSB cv-19, PSB cv-11 and VC-4 (Table 6). Genotypic ranking by other root traits such as total root dry weight, number of adventitious roots and vertical maximum rooting depth almost followed the ranking by the D/R ratio in adventitious root length, and were almost consistent with the rankings by the D/W ratio in total root length observed in pot experiments (Table 4). When the genotypes are compared by using absolute value, Golden yellow also produced the greatest total length of adventitious roots (data not shown), and the deepest roots among the genotypes under both soil moisture conditions (Table 4).

Fig. 3 shows the frequency distribution of the length of adventitious roots of the plants that were grown under droughted and rainfed conditions in the field (Exp. 5). The genotypic difference in average length was not very large, but that in the distributions of the length in each genotype was pronounced. Golden yellow had significantly longer roots on average as well as maximum length under both conditions as compared with the other genotypes. Rayong 5 tended to show the second maximum length in

both conditions. Drought significantly reduced the development of the longest roots in each genotype.

Discussion

1. Root system structure and developmental processes

Cassava plant forms a relatively simple root system consisting of adventitious roots and their concomitant lateral roots of different branching orders. A series of experiments was conducted in this study using different genotypes, which quantified the root system development principally based on the total root length together with the traits related with the production (number) and elongation (length) of component roots.

The key feature of the root system structure found in cassava which was common to that of other food crop species like cereals (Yamauchi et al., 1987; Bañoc et al. 2000; Ito et al. 2006; Wang et al., 2009) and legumes (Kono et al., 1987; Krauss and Deacon, 1994; Mia et al., 1996a) so far reported was that the lateral root is the major component in a root system.

On the other hand, those studies including the ones on cassava (Pardales and Esquibel, 1996; Izumi et al., 1999; Pardales and Yamauchi, 2003; Iijima et al., 2004) rarely examined the developmental processes but investigated with only one or a few samplings. By contrast, this study examined the root system developmental processes and showed that although there were slight differences among the genotypes, production of adventitious roots in general peaked around three months after planting, and thereafter the numbers and average length of adventitious roots continued to decrease. Although the peak of lateral root production lagged behind that of adventitious roots, their number also drastically decreased toward the maturity. Fitter et al. (1996) found no change in root turnover in CO₂ enriched wheat because there was little or no mortality of wheat roots until they all died synchronically at the end of the life cycle, and thus concluded that root turnover is not an important issue with annual crop plants, while there were some reports that showed turnover of the roots for a few food crop species (Gibbs and Reid, 1992).

We generally agree with the views presented by Fitter et al. (1996) based on our observations on a number of different crop species. Thus the fast root turnover found in cassava in this study appears to be unique to this root crop as pointed out by Izumi et al. (1999). We observed that the tuber formation started also around 90 DAP in most of the genotypes. This indicates that the tuber formation may trigger the senescence of other non-tuberous roots by demanding more photosynthate, which is the subject for further study.

2. Effects of soil moisture regimes and genotype on the root system development

Drought generally inhibited the root development

of cassava, and the degree of inhibition expressed by the ratio of the drought to well-watered control, differed among the genotypes. We used this ratio in such a way that the genotype that showed higher ratio (less inhibition) has the ability to better adapt to water-deficient conditions. The rankings of genotypes based on the ratios were almost consistent among the pots (Exps. 1, 2, 3 and 4), and field experiments (Exp. 5) (Table 6) as indicated earlier. In particular, Golden yellow showed the least suppression in root development by water deficit in all the experiments. All the traits that are related with lateral root branching of this genotype showed every sign of sharp responses to drought conditions. For example, in Exp. 1, specific root length increased by 127% and linear frequency of the first order laterals by 35%. Their number was decreased by 15%, which was one of the least affected among the 28 genotypes examined (data not shown).

In addition, we found that only Golden yellow exceptionally showed both the least suppression under drought and the sharpest recovery upon rewatering (Table 6). Such wide adaptability may most probably be related with the least suppression by drought treatment in all the root traits examined in the field experiment (Exp. 5) (Tables 4, 6).

3. Key root traits that determined the response to drought and rewatering

The results of PCA showed that it was consistently the size factor such as the length of the entire root system, which mainly characterized the root system structure of the genotypes examined (Table 5, Fig. 1), and the length of the entire root system was primarily determined by the total laterals roots length (the product of production and elongation of laterals). On the other hand, it was the production of laterals, i.e., the branching ability of adventitious roots expressed by linear frequency that was mainly responsible for the root system responses to drought as well as rewatering (Table 5, Fig. 1).

This fact clearly suggests that the branching plays the key role when the entire root system shows the plastic responses in development. Yamauchi et al. (1996), and Wang and Yamauchi (2006) proposed that such plasticity might be closely related to the adaptability of the crop plants to soil moisture stress conditions including fluctuation. Bañoc et al. (2000) and Suralta et al. (2008a) presented very clear examples showing the important roles of lateral root plasticity in rice. This study revealed that such plasticity is also one of the key traits of cassava plants to adapt to conditions where soil moisture continues to decline or suddenly increases, which mimics occasional rains under rainfed conditions.

4. Genotypic variations in the root system structures in relation to the plant growth under different soil moisture conditions

As indicated earlier, there have been only very limited number of studies that quantified cassava root system structure. Many of the studies showed that cassava is a relatively shallow rooted species, whose root systems were confined within about 60 cm in depth (Tscherning et al., 1995; Pardales and Esquibel, 1996; Izumi et al. 1999; Pardales and Yamauchi, 2003). The results obtained in this study also showed that the root systems penetrated only to 0.51 m under rainfed and 0.38 m under drought condition in average (Table 4).

In contrast, some of the studies showed that cassava extended its fibrous roots into deeper strata of soil profile. For example, the deepest cassava roots penetrated to 2.6 m (Connor et al., 1981) and to 1.3 m under field conditions (El-Sharkawy et al. 1992), and to 1.8 m within 3 months of planting in a root box (Izumi and Iijima, 2002). However, as pointed by Aresta and Fukai (1984), soil strength greatly affects root distribution in general, and thus the genotypic variations seem to be masked. The high drought tolerance of cassava has not been clearly attributed to its deep roots.

On the other hand, the information on horizontal spread of cassava root system is also quite limited. Iijima et al. (2004) observed that adventitious roots extended 1 to 2 m horizontally from the base of the plants. In our study, differences in the horizontal spread of root system could be evaluated and compared between the genotypes and the growth conditions based on the adventitious root length because the rooting depths were generally shallow in this experiment (Table 4). The results showed that significant genotypic variations existed and Golden yellow showed the greatest adventitious root length among the five genotypes examined in the field, which developed the adventitious root of about 1.6 m in length at maximum (Fig. 3). As stated above, drought generally inhibited horizontal spread of root system, but Golden yellow was able to retain greater root elongation than the other genotypes under drought. Rayong 5 also showed a similar root response. It is worthy to note that Rayong 5 was also the genotype whose root system development was less affected by drought in Exps. 1, 3 and 4 (Table 6). These facts indicate that such ability of roots to maintain elongation growth under drought may be one of the mechanisms ensuring water collection under fluctuating soil moisture conditions including drought (Ogawa et al., 2005). Elongation of long roots horizontally may therefore be beneficial to catch occasional rainfall on the surface of the soil.

Golden Yellow is a local variety in the Philippines (Table 2), which was released by the Philippine Root Crop Research and Training Center as a high yielding

one for cultivation in early 80's, and has been widely planted by farmers (Mariscal et al., 2001). Rayong 5 is a variety developed at Rayong Field Crop Research Center in Thailand for high dry matter content and relatively high yield (Table 2) (Sarakarn et al., 2001) and has been one of the most widely planted varieties (Rajanaridpiched et al., 2007). The popularity of these varieties is at least partially due to their outstanding performance in the field in terms of yield and most probably its stability under rainfed conditions where soil moisture tends to drastically fluctuate. Such good performance may be attributable to the integrated abilities of maintaining adventitious root elongation which results in wide horizontal spread of root system and responding of lateral roots development to drought, and sharp recovery in root system development from drought upon rewatering.

Acknowledgements

We thank Dr. Editha Cedicol of Southeast Asian Regional Center for Graduate Study and Research in Agriculture (SEAMEO SEARCA) for her technical editing of English.

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