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Varietal Differences of Dry Matter Accumulation and Related Characters in Cassava (*Manihot esculenta* Crantz)

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ABSTRACT: This study was carried out to investigate the patterns of dry matter (DM) production and accumulation, and to screen the relationships between related major growth characters and DM accumulation in four cassava varieties in Bogor (6°19'-6°47'S, 106°21'-107°13' E), West Java, Indonesia. Gading and Adira1 developed an enough source and canopy in short at the early growth phase and then translocated assimilates to storage roots with a higher partitioning rate, even these varieties were considered as early-bulking varieties, which have superior source and sink potentials in increasing yield and DM of tubers. The root/shoot ratio (R/SR), total dry weight (TDW), leaf area duration, leaf area index (LAI), and number of tubers showed higher positive correlations with the dry weight of roots (DWR), and the direct effects of TDW, R/SR, and LAI on the DWR were higher. These characters were considered to be useful target characters to screen cassava varieties with high yield potential and high DM in aspect of tuber production.

***Keywords*: Cassava, source to sink relationship, dry matter, path coefficient**

Cassava is the third to forth important staple crop in Indonesia after rice, maize or soybeans (Dimyati & Manwan, 1992; MOA, 1996; Onwueme, 2002; Suprapti, 2002). Indonesia produced approximately 18.5 million MT of cassava, harvested from 1.24 million ha in 2003 and, consequently, Indonesia became the third biggest cassava producer in the world (FAOSTAT, 2004). However, even if the production in Indonesia has increased markedly since 2000, the planting area has decreased steeply from year to year In contrast, the specific consumption structures, which about 70 - 77% of the cassava production is used as food, 25% is to starch industries, and only 2% is used as feed, incited the domestic needs for cassava to increase tremendously. The domestic demand of cassava for food and industries in Indonesia has increased by 1 - 2 million MT every 5 years during 1990 - 2000 (Dimyati & Manwan, 1992; Wargiono *et al.*, 1995; DIKTU, 2001; FAOSTAT, 2004). As a consequence of these domestic situations, the import quantities of cassava products have increased rapidly within last decades and the result put Indonesia into major cassava importing countries in 2003, importing about 1.0 million MT (FAOSTAT, 2003, 2004). Under these situations, improving cassava to obtain varieties with high yield potential, high dry matter (DM) or high starch content continues to be a priority of breeding programs in Indonesia (Dimyati & Manwan, 1992; Hartojo *et al.*, 2001; Wargiono *et al.*, 2001).

Also, the improvement trials to obtain early-bulking or early-maturing cassava varieties, which can be harvested at less than 8 months after planting (MAP), have been a major issue for a long time in many countries (Duke, 1983; O'Hair, 1990; Ekanayake *et al.*, 1997) as well as in Indonesia (Dimyati & Manwan, 1992, Suprapti, 2002) because of its long maturing time of more than 10 months; most cassava varieties in Nigeria attain optimum weight at about 18 MAP when starch accumulation is highest (Ekanayake *et al.*, 1997), and an optimum age of 18-20 MAP was found in experiments with certain strains of the variety São Pedro Preto (SPP) in Java (Grace, 1977) or when it is 18-24 MAP, cassava production nearly doubles (Duke, 1983). However, improved varieties selected for early-bulking may be harvested at 6 MAP, attaining maximum yield at 9-12 MAP (Ekanayake *et al*, 1997; Onwueme, 2002), and early-maturing varieties are ready for harvesting at 7 MAP, while late-maturing varieties are ready at 12 MAP (Grace, 1977; Duke, 1983; O'Hair, 1990; Alves, 2002).

This study was conducted to analyze varietal differences on the patterns of DM production and accumulation, and to screen the relationships between major growth characters and DM accumulation of storage roots in cassava.

MATERIALS AND METHODS

Plant materials and collection

Gading (*sweet & local variety*, Clone no : BIC10), Adira1 (*sweet & hybrid variety*, BIC30), Pucuk Biru (*bitter & local*

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variety), and Adira4 (*bitter & hybrid variety,* BIC136) were tested in this study as the major varieties, which are widely cultivated in Bogor area, West Java. Gading and Adira1 were collected from Nanggewer village, Pucuk Biru from Cadasngampar village, and Adira4 from Cijujung village in Bogor, respectively. Adira1 (Mangi × Ambon) was released in 1978, and Adira4 crossed naturally with Muara (BIC528) was released in 1987 (Zuraida, 1993; Hartojo *et al.* 2001).

Experimental field and cultural practices

This study was carried out in the experimental field of Bogor Education Center, Education Office of Bogor district located in Karadenan (lowland, 141 - 163 m above sea level), Cibinong, Bogor, from May 2001 to January 2002. The soil pH of the field ranged 4.30 to 5.04 with an average of 4.60. During the period, the maximum, minimum, and mean temperature fluctuated between 29.2 - 32.3 °C, 20.1 - 22.0 °C, and 25.0 - 26.6 °C. Monthly rainfall ranged between 63.8 mm in December 2001 and 559.6 mm in January 2002. The dry season lasted from May to August.

The experimental field was laid out using a randomized block design with 4 replications for a plot size of 74.4 m^2 with a planting density of 90 plants per plot. Cultivation was carried out modifying the standard cultural practices recommended by The Indonesian Ministry of Agriculture (MOA, 2000) and other related literatures (Grace, 1977; Zuraida, 1993; Ekanayake *et al.*, 1997): twice plowing and ridging with a height of 15-20 cm before planting; no basal fertilization and twice top dressing based on N (urea) 200 kg, P (triple superphosphate, TSP) 150 kg, K (KCl) 150 kg per ha; the first top dressing was applied with the ratio of N (1/3) + P (All) + K (1/2) at one week after planting, and then the second top dressing with the ratio of N (2/3) + P (0) + K (1/2) at 2 MAP; 20 cm long stem-cuttings (stakes) were taken from the lower about 75 cm from the apex of more than 10 month-old plant stems after the first 20 cm had been discarded, and then planted vertically in 3 rows per plot with a planting space of 100 cm × 60 cm and a depth of 5 - 10 cm below the soil surface; weeding was done until 6 MAP. The number of nodes per stem-cutting was 13.8 in Gading, 10.5 in Adira1, 13.9 in Pucuk Biru, and 16.2 in Adira4, on average.

Growth characteristics of shoot and root

Number of leaves (NL), total leaf area (m^2, TLA), dry weight of leaves (g, DWL), and dry weight of stem (g, DWS) were measured as the parameters of shoot. Three plants in each variety and replication were harvested and investigated every month after planting for 8 months. The TLA per plant was examined by the length-breadth method using specific leaf area (SLA) (Yoshida *et al.*, 1976; Wani *et al.*, 2001) (Table 1). The DWL and DWS were examined using the dry method (Hidayat, 1978, Bradbury & Warren, 1988) at Indonesian Center for Agricultural Biotechnology and Genetic Resources Research and Development (BBBIOGEN).

Table 1. Estimation of calibration factor for cassava leaf area (n = 80).

Model	a	S.D	R-square	CV (%)
Y = aX	0.3957	±0 05	0 9534	12 8

The parameters of root such as number of tubers (NT) and dry weight of roots (tubers) (g, DWR) were examined with three plants in each variety and replication harvested every MAP. The DWR were examined using the same method as for the DWL and DWS. In addition, dry weight of shoot part (g, DWSP) and total dry weight (g, TDW) were also examined to compare biomass increase between the two parts and to estimate total biomass increase among the test varieties.

Matter production and accumulation characteristics of the plants

To analyze the changes of source characters and DM accumulation patterns, the following parameters were determined by the methods described by Kim (1992), O'Hair (1995), Sung & Lee (1997), and Ekanayake *et al.* (1998).

Root/shoot ratio (g/g, R/SR) = DWR/DWSP
Leaf area index (m^2/m^2, LAI) = L_A/S
Leaf growth rate (m^2/m^2/day, LGR) = $(L_{A2} - L_{A1})/(t_2 - t_1)$
Leaf weight ratio (g/g, LWR) = L_W/W
Leaf area duration ($m^2 \cdot$ day, LAD) = $(L_{A1}+L_{A2})(t_2 - t_1)/2$
Crop growth rate (g/m^2/day, CGR) = $(W_2 - W_1)/(t_2 - t_1)$
Tuber growth rate (g/m^2/day, TGR) = $(T_2 - T_1)/(t_2 - t_1)$
Partitioning coefficient (PC) = TGR/CGR

Relationship among leading characters

Phenotypic correlation coefficient (Mather, 1964), multiple regression equation (Gomez & Gomez, 1976), and path-coefficient (Li, 1966) were investigated to compare mutual relationship among the major growth characters.

RESULTS AND DISCUSSION

Growth characteristics of shoot and root

In general, the cassava canopy consists of leaves and

Table 2. Comparison of changes of dry weight of leaves (DWL) and stem (DWS) by growth phases in cassava varieties.

Varieties	Month after planting (MAP)							
	1	2	3	4	5	6	7	8
	Dry weight of leaves (g/plant)							
Gading	2.69	11.96	35.37	53.47	34.65	78.59	64.43	36.57
Adira1	3.21	8.64	24.68	41.76	36.29	69.63	55.41	35.38
Pucuk Biru	1.13	3.31	28.21	47.26	23.87	72.52	67.12	43.82
Adira4	1.12	3.42	20.29	39.83	32.05	39.13	42.08	46.64
F-value	11.80**	3.56^{ns}	0.71^{ns}	0.35^{ns}	0.71^{ns}	1.08^{ns}	0.72^{ns}	0.18^{ns}
Sweet[1)]	2.95	10.30	30.02	47.62	35.47	74.11	59.92	35.98
Bitter[2)]	1.12	3.36	24.25	43.54	27.96	55.82	54.60	45.23
F-value	16.68*	11.71*	0.34^{ns}	0.18^{ns}	11.44*	1.75^{ns}	0.26^{ns}	1.70^{ns}
	Dry weight of stem (g/plant)							
Gading	0.43	2.43	13.69	57.47	49.18	84.33	133.73	212.21
Adira1	0.52	1.92	9.81	35.83	41.54	122.93	160.86	304.08
Pucuk Biru	0.23	0.83	14.14	52.24	57.18	130.51	201.73	278.33
Adira4	0.21	0.78	7.90	35.38	59.77	87.88	147.31	226.65
F-value	7.20**	2.56^{ns}	0.84^{ns}	0.59^{ns}	0.35^{ns}	2.74^{ns}	0.39^{ns}	0.29^{ns}
Sweet	0.48	2.17	11.75	46.65	45.36	103.63	147.30	258.15
Bitter	0.22	0.80	11.02	43.81	58.48	109.20	174.52	252.49
F-value	11.60*	14.22*	0.03^{ns}	0.04^{ns}	2.80^{ns}	0.41^{ns}	0.70^{ns}	0.03^{ns}

[1)] Mean value of sweet varieties (Gading and Adira1)
[2)] Mean value of bitter varieties (Pucuk Biru and Adira4).
* Significant at P = 0.05 (LSD), ** Significant at P = 0.01 (LSD), ^{ns}Not significant

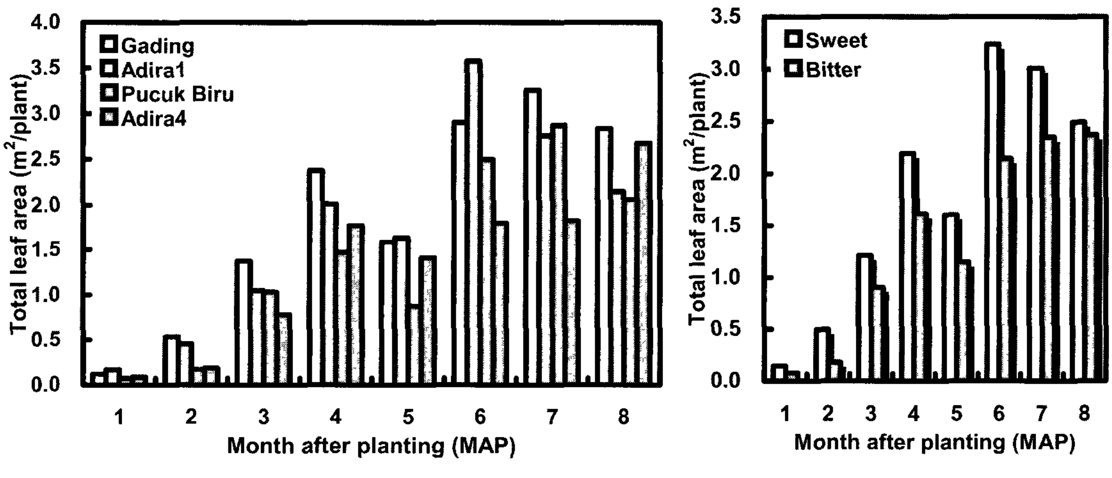

Fig. 1. Changes of total leaf area (TLA) by growth phases in cassava varieties.

stem. The DWL, DWS, and TLA per plant were significantly higher in Adira1, followed by Gading, at 1 MAP and, as a whole, these sweet varieties showed significantly higher values than the bitter varieties until 2 MAP. Moreover, the TLA and DWL of these sweet varieties tended to be much higher during the whole growing period, showing a peak at 6 MAP and then decreasing steeply. In the bitter varieties, on the contrary, the TLA continued to increase until 8 MAP, and DM accumulation in leaves began to reduce slowly after 6 MAP. Particularly, the TLA of Adira4 at 6 - 7 MAP showed the lowest values among the varieties because this variety produced less NL after 5 MAP compared with other varieties (Table 2 & Fig. 1).

These results indicated that Pucuk Biru and Adira4 as bit-

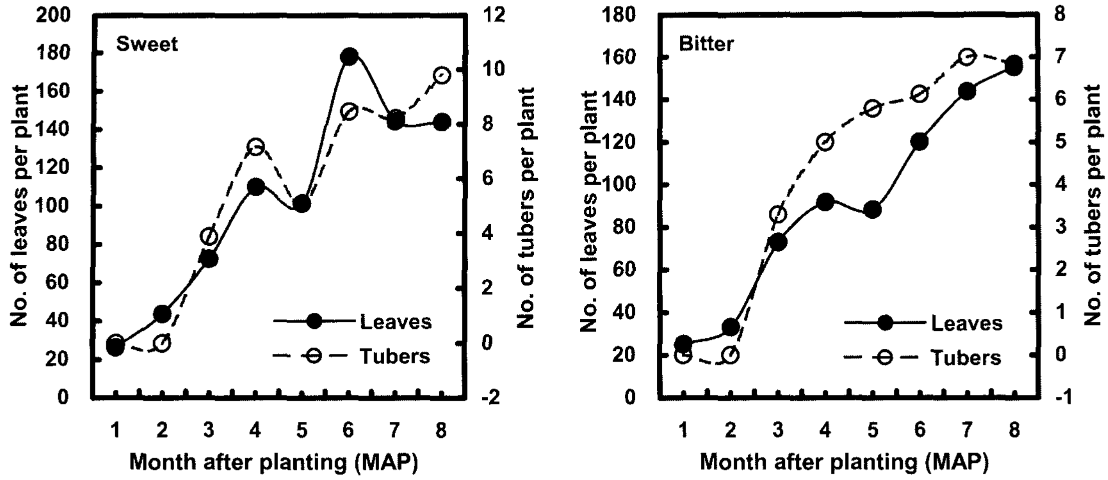

Fig. 2. Comparison of growth patterns of leaves and tubers by phases in cassava varieties.

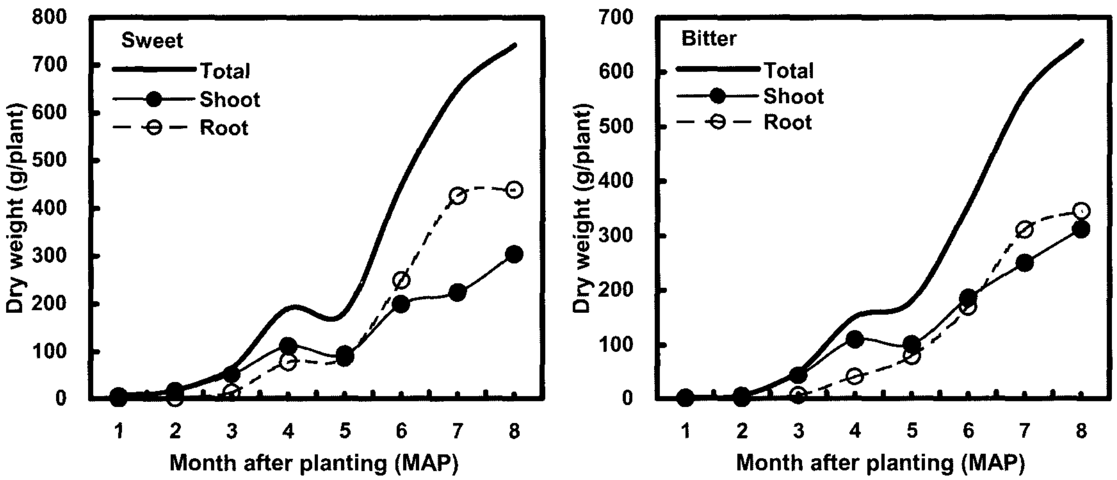

Fig. 3. Comparison of changes of dry weight of shoot and root part by growth phases in cassava varieties

ter varieties had a poor ability of canopy development at the early developmental phase and continued to accumulate DM in canopy until the latter part of storage roots bulking phase, causing a prolonged competition for assimilates between canopy and the dominant sinks (tubers). On the contrary, it was considered that the sweet varieties have not only a high ability of canopy development but also a high growth increment of source at the early establishment phase. Consequently, DM accumulation of tubers will be higher in the sweet varieties, showing a higher tuber yield potential. It has been known that among the many factors affecting growth of cassava, canopy architecture and leaf area for photosynthesis (*source potential*) become major characters (Grace, 1977; Matthews & Hunt, 1994, Ekanayake *et al.*, 1998). This result agreed with observation reported by Alves (2002) that TLA ranged from 1.24 to 3.38 m^2 per plant during 12 months. On the other hand, although Alves (2002) described that leaf senescence increased after 6 MAP, the reduction of TLA and DWL at 5 MAP in this study seemed to be due to both leaf abscission and the decrease of growth increment rate accelerated after long exposure to the temporary dry period. Ekanayake *et al.* (1998) also reported that when cassava is exposed to the dry season at the storage roots bulking phase, the leaf area reduces and crop growth slows down.

In all varieties, the initiation and formation of storage roots began after 2 MAP (Fig. 2), and this result supported reports by Ekanayake *et al.* (1998) and Alves (2002). During 8 MAP, even though the NL between varieties was not different, the NT, one of yield components, was significantly much more in the sweet varieties than in the bitter varieties at 8 MAP (Fig. 2). Also, although the changes of the NL and NT were similar in all varieties, the correlation between these parameters was negative (Table 3). This result may be due to competition for assimilates between leaves and tubers. According to Ekanayake *et al.* (1998), foliage and storage roots of cassava grow simultaneously, causing competition for assimilates.

The bulking and enlargement of storage roots began after 2 MAP in all varieties. In case of the sweet varieties, the accumulation of DM began to be much more in roots (tubers) than in shoot after 5 MAP but after 6 MAP in the bitter varieties. This result agreed with report by Alves (2002). Statistically, the TDW, DWR, and DWSP of the sweet varieties were significantly higher than those of the bitter varieties at 1 - 2 and 6 - 8 MAP, 1 - 2 and 8 MAP, and 1 - 2 MAP, respectively (Fig. 3). Therefore, these results showed that the sweet varieties established rapidly an enough source and canopy at the early growth phase, and then transported assimilates to storage roots with a higher partitioning rate. On the contrary, the bitter varieties still showed a relatively high partitioning to shoot until the later part of storage roots bulking phase (Table 2, Fig. 1 & 3). Grace (1977), Ekanayake *et al.* (1998), and Alves (2002) explained that storage root development depends on assimilate supply, which depends on photosynthetic efficiency and effective leaf area.

Patterns of matter production and accumulation

The LAI of the sweet varieties tended to be relatively higher than that of the bitter varieties during the whole growing period. In the sweet varieties the LAI decreased rapidly after 6 - 7 MAP, but, on the contrary, it still increased gradually in the bitter varieties (Fig. 4). Generally, LAI in cassava ranges from 1.0 to 7.0 and optimum LAI range in the tropics is from 3.0 to 4.0 (Ekanayake *et al.*, 1998) or 3.0 to 3.5 (Alves, 2002). In this study, mean LAI during 8 MAP was 3.0 in the sweet varieties (Gading 3.1, Adira1 2.9) and 2.3 in the bitter varieties (Pucuk Biru 2.3, Adira4 2.2). Moreover, the sweet varieties reached to an optimum LAI faster than the bitter varieties. For those reasons, it was shown that the sweet varieties kept an optimum LAI well by growth phases after 3 MAP and reached to a peak at 6 MAP.

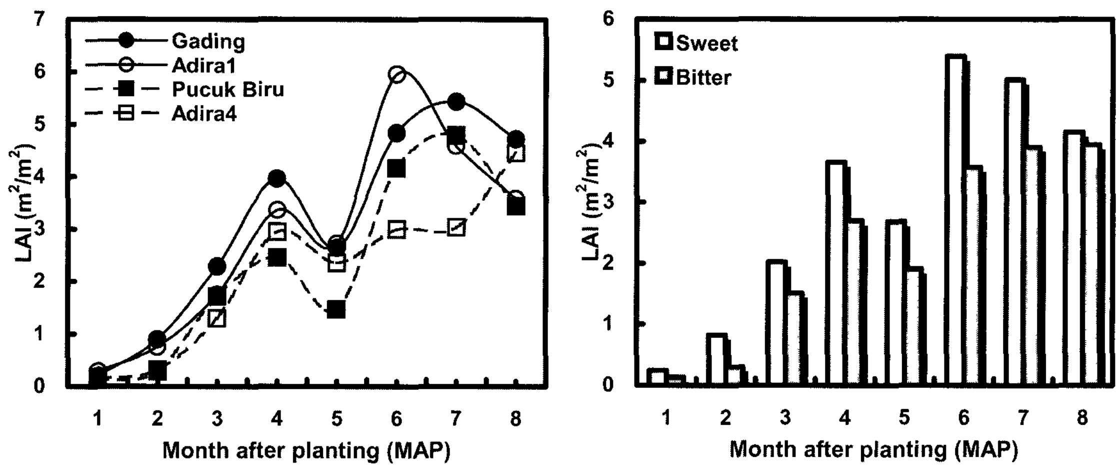

Fig. 4. Changes of leaf area index (LAI) by growth phases in cassava varieties

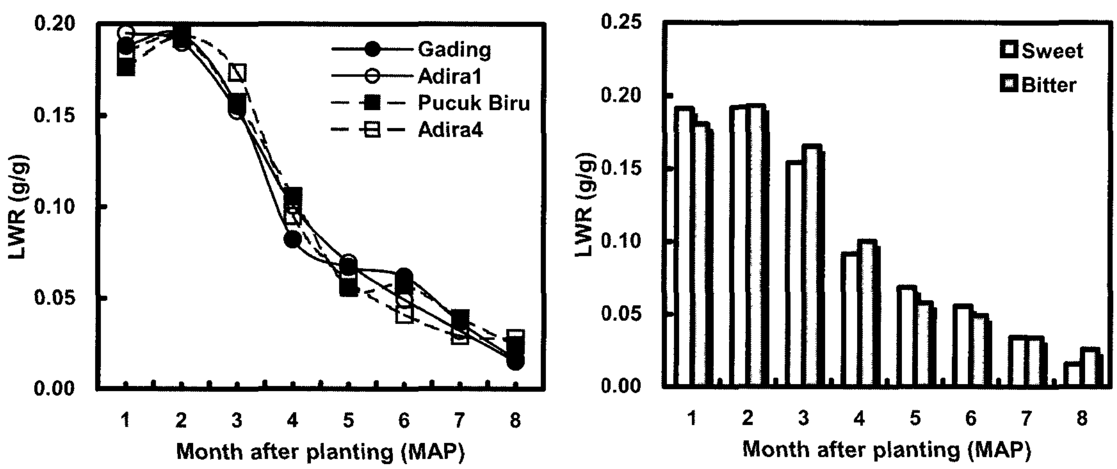

Fig. 5. Changes of leaf weight ratio (LWR) by growth phases in cassava varieties.

It has been generally known that LAI reaches to a peak at 4 - 6 MAP (Ekanayake *et al.*, 1998) or 4 - 5 MAP (Cock *et al.*, 1979) in cassava.

After 2 MAP, the LWR in all varieties decreased keeping pace with the growth of the plants. The LWR of the bitter varieties, except 1 MAP, tended to be higher than that of the

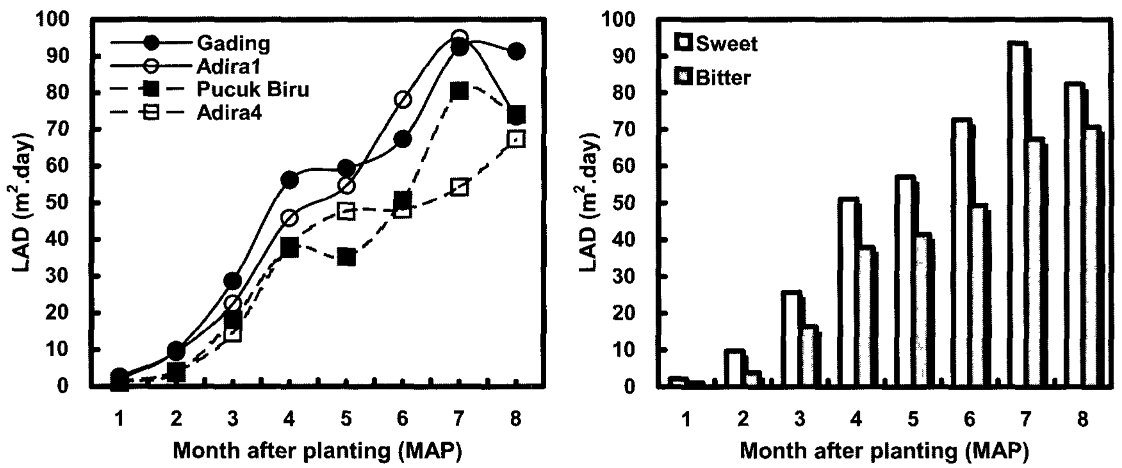

Fig. 6. Changes of leaf area duration (LAD) by growth phases in cassava varieties.

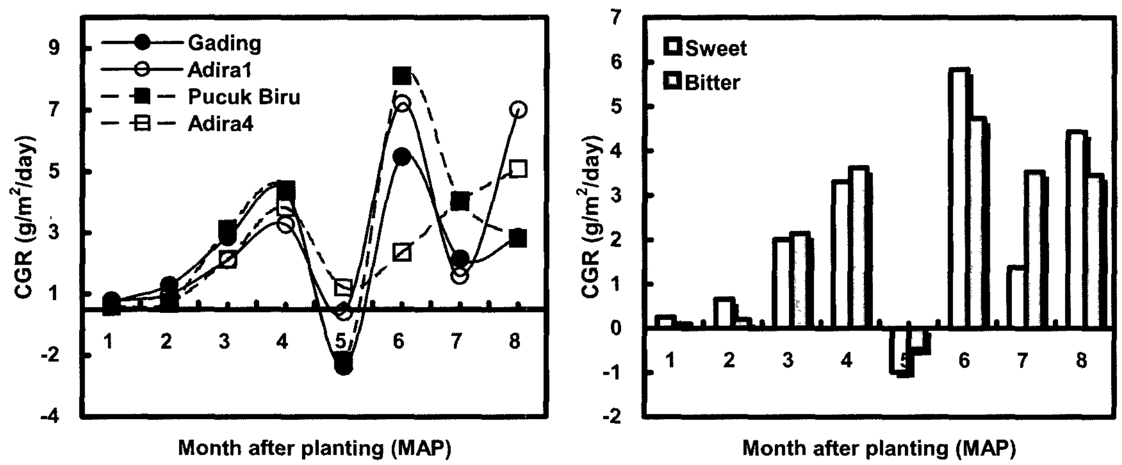

Fig. 7. Changes of crop growth rate (CGR) by growth phases in cassava varieties.

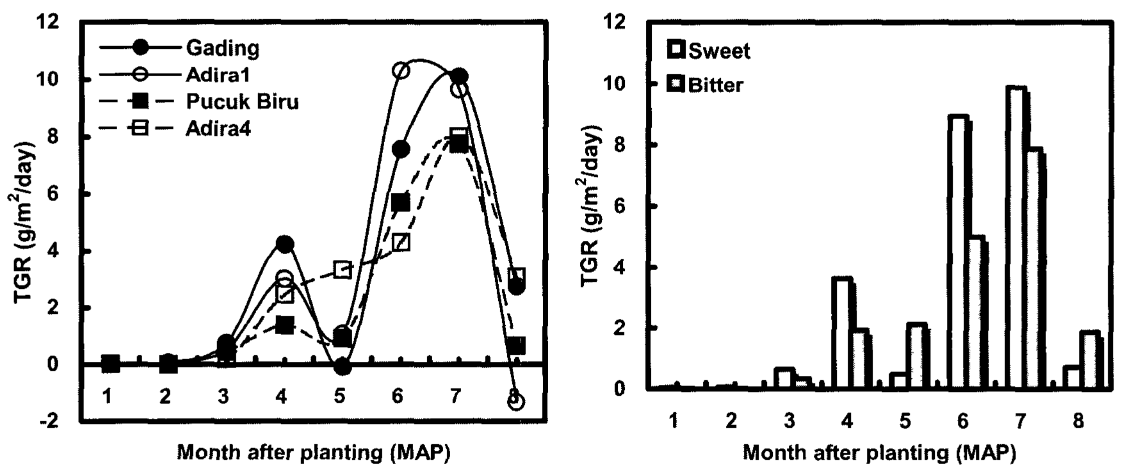

Fig. 8. Changes of tuber growth rate (TGR) by growth phases in cassava varieties.

sweet varieties until 4 MAP. Also, it was significantly higher in the bitter varieties at 8 MAP (Fig. 5). These results show that leaf formation and tuber enlargement were inducted earlier in the sweet varieties, resulting in the higher accumulation of assimilates into storage roots at the latter storage roots bulking phase.

The LAD also tended to be higher in the sweet varieties during the whole growing period, showing significant differences at 6 and 7 MAP (Fig. 6). Particularly, Gading showed a greater LAD during the early storage roots bulking phase. Therefore, because the time for the leaf area to produce assimilates was longer in the sweet varieties, especially at the early storage roots bulking phase, much more DM would be accumulated in the roots of the sweet varieties at the storage roots bulking phase. Ekanayake *et al.* (1998) and Alves (2002) observed that genotypes with relatively long LAD had high root yields, while continuous leaf harvest could reduce the root yields.

In all varieties, the TGR began to be higher than the CGR after 4 - 5 MAP and reached to a peak at 7 MAP. The CGR at 1 MAP and the TGR at 1 and 2 MAP were significantly higher in Gading and Adira1. Particularly, Adira1 showed a vigorous TGR at 6 - 7 MAP followed by Gading and, subsequently, these sweet varieties showed a significant difference compared with the bitter varieties at 6 - 7 MAP. It was considered that these sweet varieties accumulated more DM in source at the early developmental phase, and then translocated more assimilates to the dominant sinks (tubers). Also,

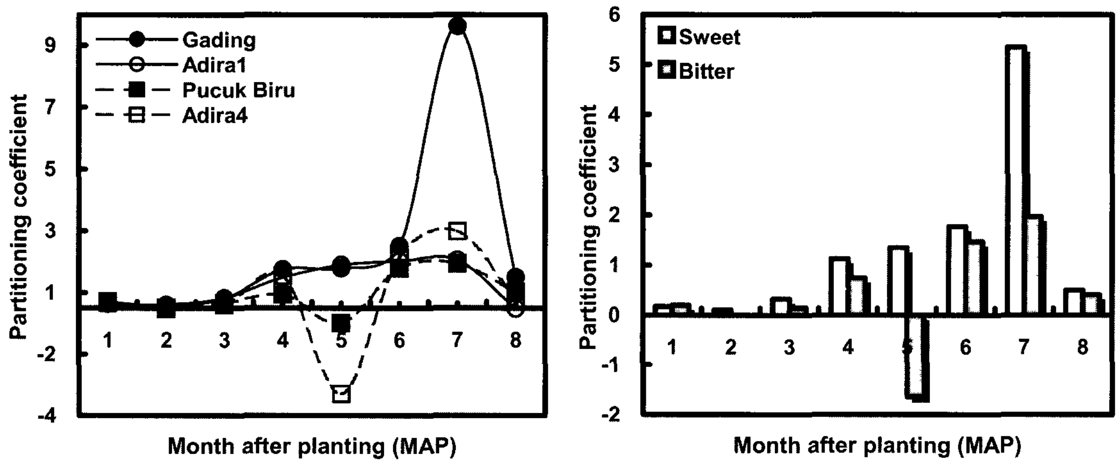

Fig. 9. Changes of partitioning coefficient (PC) by growth phases in cassava varieties.

Table 3. Phenotypic correlation between major growth characters and dry weight of roots (tubers) during growing period in cassava[†]

Characters	NL	TLA	DWL	TDW	NT	R/SR	LAI	LGR	LAD	CGR	TGR	PC
TLA	0.502**	-										
DWL	0.361*	0.727**	-									
TDW	0.558**	0.694**	0.435*	-								
NT	-0.071	0.636**	0.294	0.545**	-							
R/SR	-0.128	0.395*	-0.148	0.443*	0.618**	-						
LAI	0.502**	1.000**	0.727**	0.694**	0.636**	0.395*	-					
LGR	0.347	0.527**	0.508**	0.121	0.292	-0.129	0.527**	-				
LAD	0.378*	0.861**	0.544**	0.757**	0.576**	0.560**	0.861**	0.056	-			
CGR	0.421*	0.187	0.405*	0.344	0.032	-0.339	0.187	0.513**	-0.022	-		
TGR	0.339	0.724**	0.414*	0.490**	0.563**	0.407*	0.724**	0.519**	-0.140	0.092	-	
PC	-0.218	0.338	0.181	0.004	0.295	0.448*	0.338	0.133	0.533**	-0.257	0.083	-
DWR	0.238	0.580**	0.069	0.796**	0.649**	0.841**	0.580**	0.016	0.689**	-0.046	0.571**	0.202

[†]The correlation coefficient was estimated using the mean value of 4 varieties. NL: number of leaves, TLA: total leaf area, DWL: dry weight of leaves, TDW: total dry weight, NT: number of tubers, R/SR: root/shoot ratio, LAI: leaf area index, LGR: leaf growth rate, LAD: leaf area duration, CGR: crop growth rate, TGR: tuber growth rate, PC: partitioning coefficient, DWR: dry weight of roots (tubers).
*Significant at P=0.05 (t-test), ** Significant at P=0.01 (t-test).

the increase of the CGR and the reduction of the TGR after 7 MAP in all varieties indicates that cassava plant began to set in the recovery phase to produce a new canopy (Fig. 7 & 8). The reduction of the TGR at 5 MAP may be due to the decrease of source potential, which resulted in the CGR reduction at the same time. Duke (1983) has reported that averaged over the 365-day growing season, cassava in Java, Indonesia, had a mean growth rate of 11.0 g m^{-2} day^{-1}. Showing the maximum CGR at 6 MAP in this study agreed with observation reported by Hozyo *et al.* (1984) that the maximum CGR occurs at about 5 - 6 MAP.

The above results were confirmed with Fig. 9. The PC of the sweet varieties was significantly higher than that of the bitter varieties at 2 MAP but, as a whole, it tended to be much higher in the sweet varieties during the whole growing period. Particularly, Gading showed a very higher value at 7 MAP. In contrast, the PC of Pucuk Biru and Adira4 showed negative results at 5 MAP. It seemed that these results were induced because the CGR of these varieties at 5 MAP was negative compared with former month but the TGR was not, on average, and also the CGR increment was much lower than that of the TGR at that time. This result shows that the growth of these sweet varieties at the early developmental phase was accelerated to make an optimum canopy in short period, which resulted in higher ability to produce assimilates and partition them to storage roots. In all varieties, on the other hand, the PC decreased sharply after 7 MAP because the partitioning of assimilates occurred to support the shoot in order to produce a new canopy.

Table 4. Direct effect (path coefficient) of major characters on dry weight of roots (tubers) in cassava†.

Characters	Direct effect	Characters	Direct effect
NL	-0.090	LAI	0.114
TLA	-0.028	LGR	0.183
DWL	-0.163	LAD	-0 068
TDW	0.753	CGR	-0.139
NT	-0.093	TGR	-0.018
R/SR	0.543	PC	-0.058

†The abbreviations are same with those in Table 3

Relationship among leading characters

The DWR showed significant positive phenotypic correlations with the TLA, TDW, NT, R/SR, LAI, LAD, and TGR. Among these major characters, the R/SR, TDW, LAD, and NT showed higher correlations with the DWR (Table 3). Table 4 shows the direct effects of the major characters on the DWR. The direct effect of TDW on the DWR was highest, and it was followed by the R/SR, LGR, DWL, and LAI. However, the DWL showed a negative direct effect on the DWR.

The LAI of the sweet varieties showed an almost linear relationship with the DWR and the roots began to bulk after the LAI value reached to more than 1 0. However, the DWR of the bitter varieties began to increase when the LAI reached to about 2.0. These results showed that the initial leaf area establishment was faster in the sweet varieties (Fig. 10). These results were consistent with report by Ekanayake *et al.* (1998) that cassava genotypes with relatively high LAI have high root yields. Alves (2002) also reported that mean LAI is closely related to the rate of root bulking.

On the other hand, the relationship between the TDW and DWR was almost linear, showing very high correlation

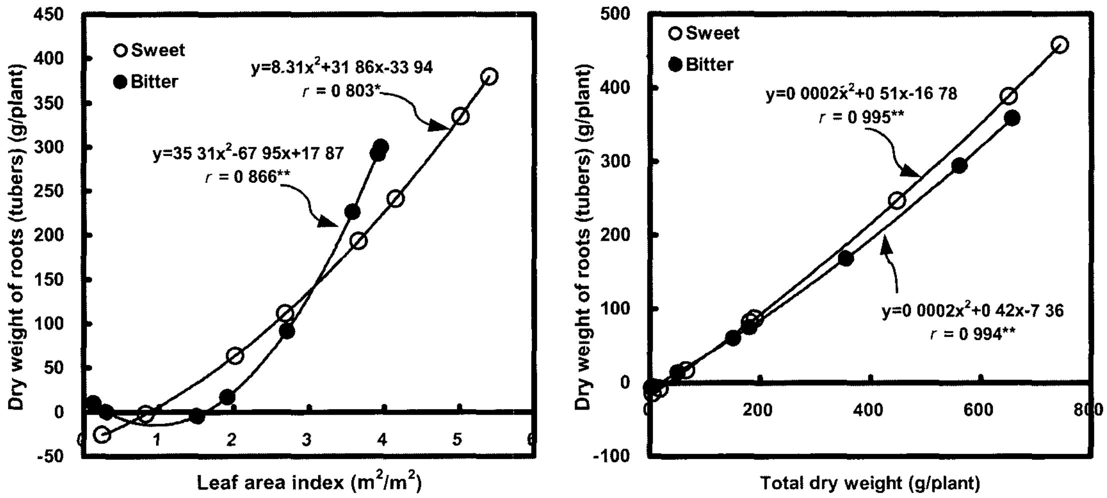

Fig. 10. Relationship between leaf area index (left) or total dry weight (right) and dry weight of roots (tubers) during growing period in sweet (Gading & Adira1) and bitter (Pucuk Biru & Adira4) varieties of cassava

coefficients in both varieties (Fig. 10). These results agreed with reports by Ekanayake *et al.* (1998) and Alves (2002) that the relationship between total dry weight of cassava and dry weight of storage roots is linear, suggesting that the rate of root growth keeps pace with the rate of crop growth in cassava.

In summary, the results in this study indicated that source characters had higher effects on DM accumulation in storage roots than sink characters in cassava, and the direct effects of TDW, R/SR, and LAI on the DWR were higher among major growth characters. Subsequently, these characters will be useful target characters to screen cassava varieties with high yield potential and high DM in aspect of tuber production. Gading and Adira1 showed early-bulking characteristics, and the source and sink potentials of these varieties were superior enough to be introduced into further improvement programs of cassava from the standpoint of increasing the yields and DM content of tubers.

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