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Full Length Research Paper

Accumulation and distribution of dry matter in relation to root yield of cassava under a fluctuating water table in inland valley ecology

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Cassava an important staple food is grown both in upland and inland valley in the tropics. A trial to assess dry matter production and partitioning in relation to root yield was conducted in 3 positions along inland valley toposequence using 4 x 4 Latin square design. Dry matter partitioning differed among cultivars, toposequence positions, sites and years due to differences in water table depth and weather conditions. High dry matter partitioning to leaves, stems, fibrous roots and rootstocks reduced yield, while high biomass allocation to storage roots increased yield. High dry matter partitioning to leaves reduced yield more in the landrace likely due to low sink capacity. Partitioning high dry matter to leaves reduced yield more at deep than shallow water table depth. Excess moisture stress increased dry matter accumulation in rootstock, fibrous and storage roots, but decreased partitioning to stems and leaves. Drought stress reduced dry matter allocation to storage roots, but increased partitioning to rootstocks, fibrous roots and stems. TMS 91/02324 and TMS 91/02327 with lowest dry matter accumulation in stems and fibrous roots and highest in storage roots had the highest yields and therefore better adapted to inland valley conditions.

Key words: Dry matter partitioning, root yield, groundwater table depth, inland valley ecology, weather condition, cassava.

INTRODUCTION

Cassava is an important staple food in the tropics used mainly as a source of carbohydrates (El-Sharkawy and Cadavid, 2002) for an estimated 800 million people (Akparobi et al., 1998). Cassava is normally an upland crop, but in west and central Africa, it is widely grown in inland valleys during the dry season utilizing residual soil moisture (Ekanayake et al., 1994a). Inland valleys are the upper reaches of river systems comprising valley bottoms, hydromorphic fringes and continuous upland slopes (Andriesse et al., 1994). They show substantial potential for intensified and sustainable land use, due to better water retention and availability throughout the growing season (Ekanayake et al., 1994a) and high soil fertility as a result of high level of organic matter formation and deposition of sediments of top soil lost from the uplands (Agboola, 1987). Inland valleys occupy about 130 million ha of land in tropical Africa (Andriesse, 1986) and 25 million ha in West Africa, but only about 10 to 25% of this land is used for crop production (Andriesse et al., 1994). The world arable land is limited, more so in Africa where as the population increases arable land is reducing at an alarming rate. This reduction in arable land coupled with drought conditions in some areas do lead to drastic declines in food production. Inland valleys hold the potential for addressing this situation as they cover a large land area high in fertility potential, which could be exploited with little harm to the environment and water resources.

Dry matter production and partitioning is an important determinant of storage root yield in cassava and could be an important selection criterion in breeding programmes

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for enhanced yield. Total dry matter production is a good estimator of the degree of adaptation of a genotype to the environment in which it is grown (Kamara et al., 2003). Differences in total dry matter accumulation in genotypes reflect differences in photosynthetic production (Kamprath et al., 1982). Cassava genotypes that produce high dry matter also produce high leaf area index and root yield (Akparobi et al., 1999). Partitioning of dry matter is particularly important in cassava because the crop has simultaneous development of leaves, stems and storage roots and supply of assimilate is partitioned between these parts (Cock, 1984; Ekanayake et al., 1998). This results in a delicate balance between shoot and storage root growth for maximum yield (Ramanujam, 1985). Generally, genotypes that allocate higher proportion of dry matter to storage roots than the stems and leaves give higher yields (Osiru and Hahn, 1998). However, Manrique (1990) reported that dry matter partitioning to storage roots had little seasonal variation and increased with plant age, but allocation to branches was more sensitive to the environment, indicating that differences in root yield between seasons were largely due to differences in dry matter partitioning to branches. Thus, relationship between storage root and shoot weight is very important in cassava production, a high root:shoot ratio being desirable for storage root production (Enyi, 1973; Lahai et al., 1999).

Dry matter production and partitioning studies in cassava have been conducted mainly under upland conditions where storage roots are harvested after 12 to 18 months of growth, hence information obtained may not be applicable to the short cultivation period (5 - 6 months) in the dry season in inland valley where dry spell and high light intensity in mid-season and excess moisture in late season are often constraints to cassava production. The paper reports on dry matter production and partitioning in cassava, particularly genotypic variation in partitioning dry matter to various plant parts and their effects on storage root yield under inland valley conditions.

MATERIALS AND METHODS

Trial sites, design, plant establishment and groundwater table depth measurement

The trials were carried out at 2 inland valley sites, one at the international institute of tropical agriculture (IITA) research farm at Ibadan (7° 30' N and 3° 54' E, 243 m above sea level) and the other on a farmer's field at Alabata (4 46' N and 2°34' E, 210 m above sea level) in the forest-savanna transition zone in southwestern Nigeria. Meteorological data for the sites were monitored at the IITA weather station at Ibadan, since the 2 sites are about 5 km apart. During the trial period mean minimum temperature in 2001 (19.8°C) was higher than in 2002 (19.1°C), but mean maximum temperature was lower in 2001 (27.5 °C) than in 2002 (28.4 °C). Rainfall (mm) and mean relative humidity (%) were higher in 2001 (955.9 mm; 68%) than in 2002 (642.6 mm; 63%), but evaporation (mm) and solar radiation (MJ/m/day) were higher in 2002 (962.8 mm; 13.49 MJ/m/day) than in 2001 (891.1 mm; 13.09 MJ/m/day). The valley bottom soils classified as tropaquents (Moormann et al., 1975) were loamy sand at both sites. At Alabata, soil pH (H_2O) was 3.91, organic C (%) 0.99, N (%) 0.11, P (mg/kg) 7.43 and K (cmol/kg) 0.18 in 2001. In 2002, pH was 4.60, organic C; 0.46, N; 0.13, P; 6.80 and K; 0.20. The corresponding values at Ibadan were 4.87, 1.66, 0.15, 3.75 and 0.08 in 2001 and 5.40, 0.53, 0.13, 2.78 and 0.10 in 2002.

At each site, 3 positions were marked out along the toposequence and designated as valley fringe, valley intermediate and valley bottom. Each toposequence position had 16 flat-top mounds arranged in 4 x 4 Latin square design. Each mound (2 m x 2 m and 0.6 m high, spaced 1 m apart) was a plot. Three 2.1 m-long PVC pipes with diameter of 0.05 m, which served as modified piezometers were buried to a depth of 1.5 m in furrows between mounds in each toposequence position to monitor water table depth on weekly basis. This was done by placing a graduated meter ruler inside the PVC pipe so that the base of the ruler just touched the ground water surface and the reading from the surface to the top of the exposed pipe noted. The height of the exposed pipe which was the same as the mound height (0.6 m) was deducted from the reading obtained to give the water table depth below the mound surface.

Six stem cuttings (0.25 m long) from healthy mature plants were planted on each mound at a spacing of 1 m between rows and 0.75 m between plants. TMS 4(2)1425, TMS 91/02324 and TMS 91/02327 (improved cultivars) and Isunikankiyan (landrace) were used. Planting was done at Ibadan and Alabata on 12 February and 12 March 2001 in the first season and on 18 and 24 December 2001 in the second season, respectively. Hand weeding was done as required but no fertilizer was applied. The first and second season trials were terminated on 15 August 2001 and 23 July 2002 at Ibadan and 13 September 2001 and 28 July 2002 at Alabata, respectively.

Dry matter and storage root yield measurement

Dry matter was measured at the time of harvesting. Weight of fallen leaf biomass was included in the measurement by collecting it on a fortnightly basis in each plot from 2 months after planting until the final harvest. On each occasion the fallen leaves were oven dried and weights recorded. At harvest the 6 plants in each plot (a total of 24 plants per cultivar per toposequence position) were separated into leaves (petioles and laminae), stems, rootstocks, fibrous and storage roots and the fresh weights recorded. Sub-samples of the fresh materials (500 g) were dried in a ventilated oven at 70°C for 48 h. The total fallen leaf weight in each plot was added to the respective weight obtained at harvest. Dry-matter content (%) was calculated as the ratio of dry weight/ fresh weight x 100. Dry matter allocation to various plant parts (%) was determined as ratio of dry weight of each part/ total plant dry weight x 100.

Statistical analyses

Statistical analyses were performed using statistical analysis system (SAS) for microsoft windows, Release 6.12. Mixed model procedure (PROC MIXED) using the restricted maximum likelihood method (REML) for the estimation of the random variance components was used for the analyses of variances. Rows and columns were the random effects and cultivars, toposequence position, site and year the fixed effects. Standard errors were used to detect differences between treatment means. Relationships between dry matter accumulation in various plant parts and dry root yield, groundwater table depth and weather variables were examined by correlation analysis using PROC CORR procedure in SAS (SAS Institute, 1997).

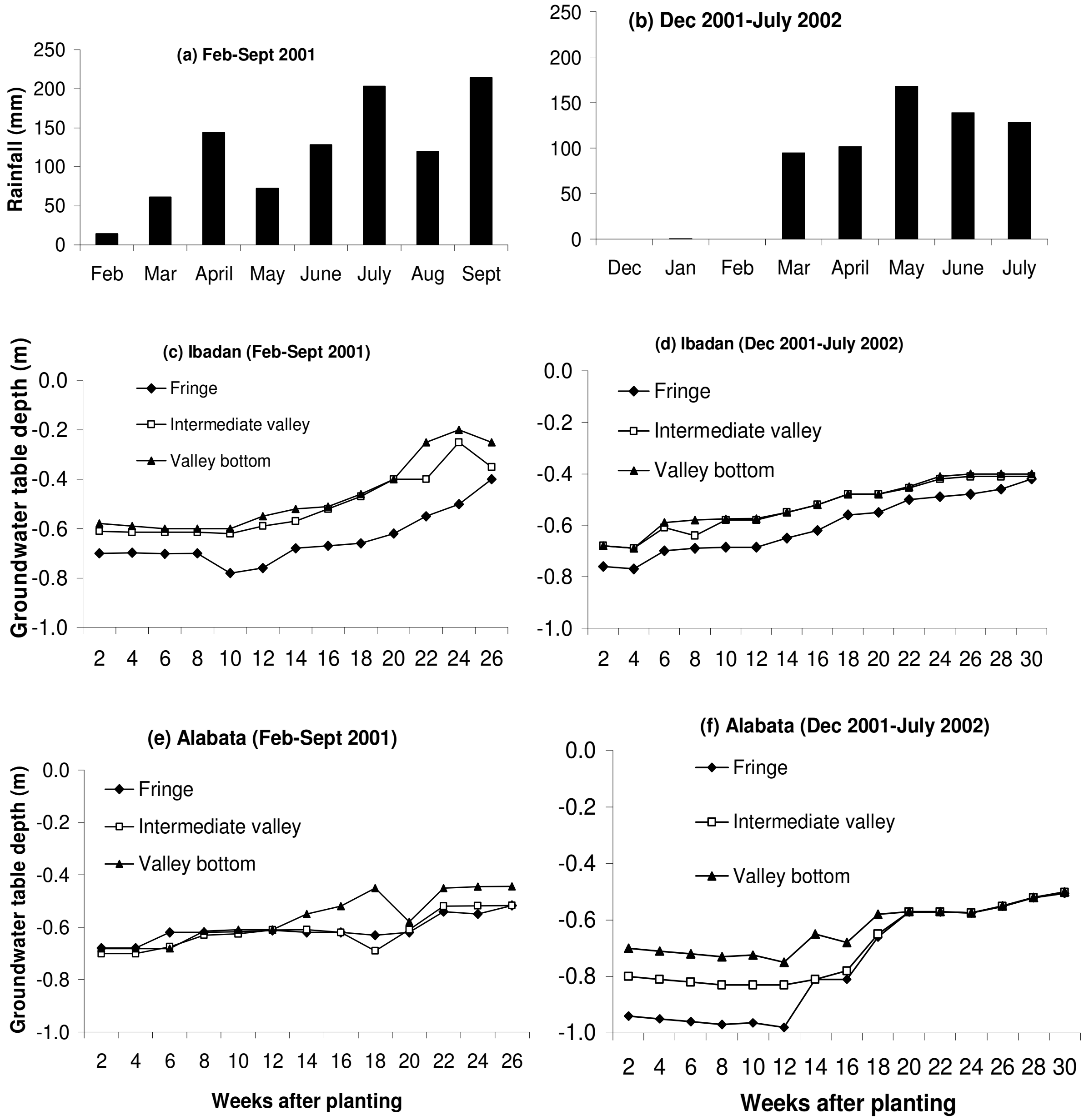

Figure 1. Variations in rainfall (at Ibadan) and groundwater table depth during 2001 and 2002 cropping seasons in inland valley at Ibadan and Alabata, Nigeria.

RESULTS

Groundwater table depth

As rainfall increased groundwater table depth decreased at both sites and in both years. Both sites had deeper water table in 2002 with lower rainfall than in 2001. Water table was deeper in the fringe and shallower in valley bottom than in the other positions at both sites in both years. The shallowest water table depth obtained ranged from 0.15 to 0.40 m in 2001 and from 0.35 to 0.45 m in 2002 at Ibadan, while at Alabata it ranged from 0.45 to 0.50 m in 2001 and from 0.51 to 0.58 m in 2002 below the 0.6 m high mound surface (Figure 1).

Dry tuberous root yield

The improved cultivars had significantly higher root yields than Isunikankiyan (landrace). TMS 91/02324 and TMS 91/02327 recorded similar and significantly the highest yields. Root yield was about 65 and 39% higher in 2001 than in 2002 at Alabata and Ibadan, respectively. It was also about 40% higher at Alabata than Ibadan (Table 1).

Table 1. Dry tuberous root yield (t ha^{-1}) and proportion of dry matter (DM) accumulated the leaves of four cassava cultivars in various toposequence positions at two inland valley locations in 2001-2002 in Nigeria.

Location (Loc)	Cultivar	2001				2002			
		Toposequence (Topo)				Toposequence (Topo)			
		Fringe	Inter-mediate	Bottom	Cultivar Mean	Fringe	Inter-mediate	Bottom	Cultivar mean
Dry tuberous root yield (t ha^{-1})									
Alabata	TMS4(2)1425	5.04	6.16	16.94	9.38	3.28	2.24	3.01	2.84
	TMS91/02324	4.68	4.71	17.24	8.88	4.12	4.01	4.66	4.26
	TMS91/02327	5.31	5.50	17.21	9.34	5.15	3.60	3.12	3.96
	Isunikankiyan	4.17	4.98	15.23	8.13	1.86	1.97	0.95	1.59
	s. e ±	0.64	0.64	0.64	0.32	0.64	0.64	0.64	0.32
	Topo mean (s. e ± 0.32)	4.80	5.34	16.66		3.60	2.96	2.94	
	Year mean (s. e ± 0.17)	8.93				3.17			
	Loc mean (s. e ± 0.13)	6.05							
Ibadan	TMS4(2)1425	4.56	4.22	3.23	4.00	3.18	2.30	1.67	2.38
	TMS91/02324	7.77	4.13	5.04	5.65	5.48	2.52	2.62	3.54
	TMS91/02327	6.12	4.51	4.41	5.01	5.14	2.38	2.04	3.19
	Isunikankiyan	3.83	2.99	3.15	3.32	2.58	1.35	1.56	1.83
	s. e ±	0.64	0.64	0.64	0.32	0.64	0.64	0.64	0.32
	Topo mean (s. e ± 0.32)	5.50	3.96	3.96		4.10	2.14	1.97	
	Year mean (s. e ± 0.17)	4.47				2.74			
	Loc mean (s. e ± 0.13)	3.61							
Proportion (%) of DM accumulated in leaves									
Alabata	**TMS4(2)1425**	**7.32**	**3.72**	**1.90**	**4.31**	**2.28**	**3.61**	**3.27**	**3.05**
	TMS91/02324	6.40	5.27	2.20	4.62	4.89	4.65	3.70	4.41
	TMS91/02327	6.45	3.93	1.73	4.04	3.32	4.82	3.02	3.72
	Isunikankiyan	4.00	4.26	1.73	3.33	4.03	3.86	5.66	4.52
	s. e ±	0.95	0.95	0.95	0.50	0.95	0.95	0.95	0.50
	Topo mean (s. e ± 0.48)	6.04	4.30	1.89		3.63	4.24	3.91	
	Year mean (s. e ± 0.27)	4.08				3.93			
	Loc mean (s. e ± 0.21)	4.01							
Ibadan	TMS4(2)1425	12.14	6.16	7.89	8.73	13.55	6.50	7.16	9.07
	TMS91/02324	5.75	2.32	2.89	3.65	9.60	4.89	4.69	6.39
	TMS91/02327	6.78	2.17	2.80	3.92	9.90	3.74	4.11	5.92
	Isunikankiyan	6.29	3.31	3.10	4.23	7.08	6.31	3.04	5.48
	s. e ±	0.95	0.95	0.95	0.50	0.95	0.95	0.95	0.50
	Topo mean (s. e ± 0.48)	7.74	3.49	4.17		10.03	5.36	4.75	
	Year mean (s. e ±)0.27	5.13				6.71			
	Loc mean (s. e ± 0.21)	5.92							

There were significant toposequence position x site, toposequence position x year, site x year and toposequence position x site x year interactions. In 2001 at Alabata, the highest root yield was produced in valley bottom and the lowest in the fringe. On the contrary, in 2002 at Alabata and in both years at Ibadan, the highest yield was obtained in the fringe, while valley bottom and valley intermediate had similar and lowest root yield (Table 1).

Dry matter accumulation in the leaves

TMS 4(2)1425 partitioned significantly more dry matter to the leaves than the other cultivars. The accumulation of biomass in the leaves did not differ significantly among the other cultivars. Plants in the fringe accumulated more biomass in the leaves than those in the other positions, with the lowest recorded in valley bottom. Dry matter partitioned to the leaves was about 9% higher in 2002 than in 2001 and about 32% higher at Ibadan than Alabata (Table 1). There were significant toposequence position x site and toposequence position x site x year interactions. At Alabata in 2001, plants in the fringe partitioned the highest proportion of biomass to the leaves and those in valley bottom had the lowest in the leaves. On the other hand, in 2002, plants in the fringe accumulated the lowest proportion of dry matter in the leaves, while those in intermediate valley had the highest proportion. At Ibadan, the fringe recorded higher proportion of dry matter in the leaves in both years than the other positions. Also cultivar x site, site x year, cultivar x year and cultivar x site x year interactions were significant.

In 2001 at Alabata, TMS 91/02324 had the highest proportion of dry matter in the leaves, with the lowest recorded for the landrace. However, in 2002 the landrace had the highest dry matter biomass in the leaves. At Ibadan, TMS 4(2)1425 accumulated the highest proportion of dry matter in the leaves in both years, but while the landrace had higher biomass in the leaves than the other improved cultivars in 2001, the reverse was noted in 2002.

Dry matter accumulation in the stems

The proportion of dry matter partitioned to the stems was significantly higher for the landrace than the improved cultivars. TMS 4(2)1425 also accumulated more dry matter in the stems than TMS 91/02324 and TMS 91/02327. Plants in valley fringe partitioned the highest proportion of dry matter to the stem, while those in valley bottom had the lowest proportion of dry matter. There was a significant site x year interaction. Dry matter partitioned to the stems was about 30% higher in 2002 than in 2001 at Alabata, but was about the same in both years at Ibadan. Plants also had about 27% more biomass in the stem at Alabata than Ibadan (Table 2).

Dry matter accumulation in the rootstocks

All the cultivars accumulated similar proportion of dry matter in the rootstocks, but plants in valley bottom partitioned significantly the highest proportion of dry matter to the rootstocks, with the lowest proportion recorded in valley fringe. Also the proportion of biomass in the rootstocks was about 29% higher in 2002 than in 2001 and 11% higher at Ibadan than at Alabata (Table 2).

Dry matter accumulation in the fibrous roots

The proportion of dry matter partitioned to the fibrous roots was significantly higher for the landrace than the improved cultivars. TMS 4(2)1425 also had more dry matter in the fibrous roots than TMS 91/02324 and TMS 91/02327. Plants in valley bottom accumulated higher proportion of dry matter in fibrous roots than those in the other positions. The proportion of dry matter in the fibrous roots was about 28% higher in 2002 than in 2001 (Table 3). Interactions between toposequence position x site, toposequence position x year and toposequence position x site x year were significant. At Alabata, plants in the fringe partitioned the highest proportion of dry matter to the fibrous roots and those in the valley bottom had the lowest dry matter in 2001. In 2002, plants in valley bottom had the highest, while those in valley intermediate accumulated the lowest amount of dry matter in fibrous roots. At Ibadan, plants in valley bottom in both years had the highest, while those in valley intermediate recorded the lowest proportion of dry matter in fibrous roots.

Dry matter accumulation in the storage roots

Dry matter accumulation in the storage roots was significantly higher for the improved cultivars than the landrace, with TMS 91/02324 and TMS 91/02327 partitioning similar and highest proportions of dry biomass to storage roots. Plants in valley bottom had the highest proportion of dry matter in the storage roots, while than those in the fringe had the lowest. The proportion of dry matter in storage roots was about 21% higher in 2001 than in 2002. Also plants had about 9% higher dry matter in storage roots at Ibadan than Alabata (Table 3). There was a significant toposequence position x year interaction. In 2001 plants in valley bottom had higher proportion of dry matter in the storage roots than those in valley fringe and valley intermediate, but in 2002 the reverse was observed.

Relationships between dry matter accumulation in various plant parts with root yield, ground water table depth and selected weather variables

The proportions of dry matter accumulated in leaves, stems and fibrous root correlated negatively with root yield, while the proportion of dry matter in storage roots had positive correlation with yield at Alabata. Similar results were obtained at Ibadan for dry matter in fibrous and storage roots, but the proportion of dry matter in the leaves and stems showed no significant correlation with yield. Proportion of dry matter in rootstocks correlated negatively with yield at Ibadan. At Alabata, dry matter biomass in leaves and stems related positively, while that of rootstock had negative correlation with water table depth. At Ibadan dry matter biomass in the leaves correlated negatively, while that in rootstock correlated positively with water table depth. Proportion of dry matter in storage root related positively with rainfall, minimum temperature and relative humidity, but negatively with evaporation rate, solar radiation and maximum temperature. Dry matter partitioned to leaves, stems, rootstocks and fibrous roots related negatively with rainfall, minimum temperature and relative humidity, but positively with evaporation rate, solar radiation and maximum temperature (Table 4).

DISCUSSION

Accumulation of dry matter in leaves

The proportion of dry matter in the leaves was significantly higher in the fringe with deeper water table than the other positions. At the deep water table site, dry

Table 2. Proportion of dry matter (DM) partitioned into the stems and root stocks of four cassava cultivars in various toposequence positions at two inland valley locations in 2001-2002 in Nigeria.

Location (Loc)	Cultivar	2001				2002			
		Toposequence (Topo)				Toposequence (Topo)			
		Fringe	Inter-mediate	Bottom	Cultivar Mean	Fringe	Inter-mediate	Bottom	Cultivar Mean
Proportion (%) of DM accumulated in stem									
Alabata	TMS4(2)1425	38.06	28.71	13.64	26.80	43.89	38.68	32.53	38.37
	TMS91/02324	35.03	25.33	13.27	24.54	37.72	34.41	37.92	36.68
	TMS91/02327	30.92	22.45	9.12	20.83	39.08	32.02	28.31	33.14
	Isunikankiyan	51.97	36.61	14.90	34.49	50.41	43.35	36.01	43.26
	s. e ±	3.67	3.67	3.67	1.90	3.67	3.67	3.67	1.90
	Topo mean (s. e ± 1.85)	39.00	28.28	12.73		42.78	37.12	33.69	
	Year mean (s. e ± 1.05)	26.67				37.86			
	Loc mean (s. e ± 0.84)	32.27							
Ibadan	TMS4(2)1425	34.92	27.12	9.50	23.85	25.80	23.51	21.90	23.74
	TMS91/02324	37.68	18.12	8.85	21.55	22.15	12.20	17.77	17.37
	TMS91/02327	35.58	16.40	9.18	20.39	28.61	13.91	17.07	19.86
	Isunikankiyan	40.25	35.14	10.88	28.76	42.37	25.01	29.68	32.35
	s. e ±	3.67	3.67	3.67	1.90	3.67	3.67	3.67	1.90
	Topo mean (s. e ± 1.85)	37.11	24.20	9.60		29.73	18.66	21.61	
	Year mean (s. e ± 1.05)	23.64				23.33			
	Loc mean (s. e ± 0.84)	23.49							
Proportion (%) of DM accumulated in root stock									
Alabata	TMS4(2)1425	12.51	8.33	18.30	13.05	14.98	15.22	21.86	17.35
	TMS91/02324	12.02	13.99	17.18	14.40	17.56	16.24	15.01	16.27
	TMS91/02327	11.22	12.41	17.04	13.56	14.43	15.37	24.42	18.07
	Isunikankiyan	8.41	9.72	18.59	12.24	17.33	14.17	26.90	19.45
	s. e ±	2.31	2.31	2.31	1.18	2.31	2.31	2.31	1.18
	Topo mean (s. e ± 1.15)	11.04	11.11	17.78		16.08	15.25	22.00	
	Year mean (s. e ± 0.84)	13.31				17.78			
	Loc mean (s. e ± 0.61)	15.55							
Ibadan	TMS4(2)1425	11.11	10.39	17.89	13.13	13.34	19.77	29.21	20.77
	TMS91/02324	11.22	15.31	16.15	14.23	10.38	23.42	27.25	20.35
	TMS91/02327	11.77	10.68	18.28	13.58	9.18	23.46	32.94	21.86
	Isunikankiyan	15.06	11.26	20.08	15.47	12.25	22.05	27.39	20.56
	s. e ±	2.31	2.31	2.31	1.18	2.31	2.31	2.31	1.18
	Topo mean (s. e ± 1.15)	12.29	11.91	18.10		11.26	22.18	29.20	
	Year mean (s. e ± 0.84)	14.10				20.88			
	Loc mean (s. e ± 0.61)	17.49							

matter partitioned to the leaves correlated positively with water table depth, but negatively with root yield. At the shallow water table site, proportion of dry matter in the leaves related negatively with water table depth, but correlation with yield was not significant. This suggests that shallow water table decreased dry matter accumulation in the leaves. The data also indicated that at deep water table, partitioning high amount dry matter to leaves reduced root yield, whereas at shallow water table, accumulation of high dry matter in leaves did not adversely affect yield. In fact under shallow water table, valley fringe with the highest dry matter accumulation in the leaves also had the highest yield, indicating a tendency for root yield to increase with increase in dry matter allocation to leaves. Thus dry matter accumulation in the leaf may be a good indicator of the degree of adaptation of cassava genotypes to shallow water table depth. Higher dry matter accumulation in the leaves occurred in 2001

Table 3. Proportion of dry matter (DM) accumulated the fibrous and tuberous roots of four cassava cultivars in various toposequence positions at two inland valley locations in 2001-2002 in Nigeria.

Location (Loc)	Cultivar	2001				2002			
		Toposequence (Topo)				Toposequence (Topo)			
		Fringe	Inter-mediate	Bottom	Cultivar Mean	Fringe	Inter-mediate	Bottom	Cultivar Mean
Proportion (%) of DM accumulated in fibrous root									
Alabata	TMS4(2)1425	0.73	0.66	0.34	0.58	0.52	0.65	0.69	0.62
	TMS91/02324	0.71	0.73	0.31	0.58	0.37	0.30	0.37	0.35
	TMS91/02327	0.51	0.44	0.27	0.41	0.24	0.28	0.64	0.39
	Isunikankiyan	0.47	0.74	0.58	0.76	1.43	0.80	2.44	1.56
	s. e ±	0.18	0.18	0.18	0.09	0.18	0.18	0.18	0.09
	Topo mean (s. e ± 0.09)	0.73	0.64	0.38		0.64	0.51	1.04	
	Year mean (s. e ± 0.05)	0.58				0.73			
	Loc mean (s. e ± 0.04)	0.66							
Ibadan	TMS4(2)1425	0.46	0.34	0.57	0.46	0.78	0.61	0.84	0.74
	TMS91/02324	0.25	0.20	0.50	0.32	0.50	0.38	0.73	0.54
	TMS91/02327	0.26	0.18	0.35	0.26	0.36	0.28	0.52	0.39
	Isunikankiyan	0.93	0.53	1.62	1.03	1.36	1.10	2.03	1.50
	s. e ±	0.18	0.18	0.18	0.09	0.18	0.18	0.18	0.09
	Topo mean (s. e ± 0.09)	0.48	0.31	0.76		0.75	0.59	1.03	
	Year mean (s. e ± 0.05)	0.52				0.79			
	Loc mean (s. e ± 0.04)	0.66							
Proportion (%) of DM accumulated in tuberous root									
Alabata	TMS4(2)1425	41.30	58.90	65.87	55.36	38.30	42.17	41.89	40.79
	TMS91/02324	45.98	54.80	67.37	56.05	39.61	44.51	43.33	42.48
	TMS91/02327	50.92	60.89	71.79	61.03	42.94	47.11	43.54	44.53
	Isunikankiyan	34.56	48.63	63.88	49.02	26.71	37.77	28.67	31.05
	s. e ±	3.77	3.77	3.77	1.92	3.77	3.77	3.77	1.92
	Topo mean (s. e ± 1.89)	42.19	55.68	67.23		36.89	42.89	39.36	
	Year mean (s. e ± 1.01)	55.37				39.71			
	Loc mean (s. e ± 0.77)	47.54							
Ibadan	TMS4(2)1425	41.30	56.33	64.13	53.92	46.60	49.93	40.98	45.84
	TMS91/02324	45.25	64.16	71.96	60.46	57.51	59.22	49.91	55.55
	TMS91/02327	45.63	70.16	69.44	61.74	51.98	58.21	44.92	51.70
	Isunikankiyan	37.39	49.73	63.97	50.36	36.84	45.51	37.51	39.95
	s. e ±	3.77	3.77	3.77	1.92	3.77	3.77	3.77	1.92
	Topo mean (s. e ± 1.89)	42.39	60.10	67.38		48.23	53.22	43.33	
	Year mean (s. e ± 1.01)	56.62				48.26			
	Loc mean (s. e ± 0.77)	52.44							

with higher rainfall than in 2002 at Alabata, while at Ibadan more dry matter was partitioned to the leaves in 2002 than in 2001. Carsky et al. (1993) and Lahai et al. (1999) reported that water table depth between 0.20 - 0.40 m below soil surface was most stressful to cassava. Mohamoud (1994) noted reduced top yield at the site where waterlogging conditions resulted in chlorosis on the leaves. At Ibadan, the shallowest water table depths in 2001 (0.15 - 0.40 m below mound surface) was shallower and that in 2002 (0.35 - 0.45 m) was about the same as the most stressful water table depth. This shows that the water table depth in both years was stressful to cassava, but the depth in 2001 was more stressful, and hence the lower leaf dry matter accumulation during this period than in 2002. At Alabata, the shallowest water table depths were deeper in both years (0.45 - 0.50 m in 2001 and 0.51 - 0.58 m in 2002) than the most stressful water table depth, but water table in 2002 was much

Table 4. Correlations between selected dry matter (DM) components of cassava and tuberous root yield (n = 32), groundwater table depth (n = 32) and weather variables (n= 64) in inland valley.

Dry matter components	Tuberous root yield (t ha^{-1})				Groundwater table depth (m)				Weather variable											
	Alabata		Ibadan		Alabata		Ibadan		Rainfall (mm)		Evaporation rate (mm)		Solar radiation (MJ/m/day)		Minimum temperature (^{0}C)		Maximum temperature (^{0}C)		Mean relative humidity (%)	
	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p	r	p
DM (%) in leaf	-0.53	0.0020	0.08	0.6627	0.46	0.0075	-0.38	0.0316	-0.11	0.3681	0.11	0.3681	0.11	0.3681	-0.11	0.3681	0.11	0.3681	-0.11	0.3681
DM (%) in stem	-0.87	0.0001	0.10	0.5779	0.56	0.0009	-0.18	0.3189	-0.35	0.0047	0.35	0.0047	0.35	0.0047	-0.35	0.0047	0.35	0.0047	-0.35	0.0047
DM (%) in rootstock	-0.02	0.9029	-0.73	0.0001	-0.64	0.0001	0.87	0.0001	-0.49	0.0001	0.49	0.0001	0.49	0.0001	-0.49	0.0001	0.49	0.0001	-0.49	0.0001
DM (%) in fibrous root	-0.46	0.0076	-0.54	0.0015	-0.13	0.4919	0.28	0.1189	-0.27	0.0339	0.27	0.0339	0.27	0.0339	-0.27	0.0339	0.27	0.0339	-0.27	0.0339
DM (%) in tuberous root	0.90	0.0001	0.38	0.0339	-0.33	0.0678	-0.31	0.0815	0.63	0.0001	-0.63	0.0001	-0.63	0.0001	0.63	0.0001	-0.63	0.0001	0.63	0.0001

deeper. This indicated that plants at Alabata in 2002 likely encountered drought stress, particularly during the peak of the dry season, resulting in lower dry matter accumulation in the leaves than in 2001. El-Sharkawy and Cadavid (2002) also showed that drought imposed at 2 - 4 months after planting reduced leaf area index and shoot biomass, suggesting that both drought and excess moisture stress reduce leaf dry matter biomass in cassava in inland valley.

In the study, TMS 4(2)1425 partitioned the highest proportion of dry matter to the leaves. This is excepted as this cultivar produced more branches and leaves than the other cultivars. The results are in line with Irikura et al. (1979) who reported that leaf production depends partly on apex or branch number and with Ramanujam and Biradar (1987) who recorded higher dry matter accumulation in the shoots of profusely branching cultivars than non-branching ones. Root growth rate is the difference between the dry matter required for leaf and stem growth and total crop growth (Cock et al., 1979), indicating that the higher the dry matter partitioned to the leaves the lower the root yield. Results of this study are consistent with these findings in that the location and year with the lowest yield had the highest amount of dry matter in the leaves, while those with the highest yield had the least proportion of dry matter in the leaves.

Similarly, TMS 4(2)1425 which partitioned higher dry matter to the leaves yielded lower than the other improved cultivars, with lower accumulation of dry matter in the leaves. However, the proportion of dry matter partitioned to the leaves in the improved cultivars was either higher than or similar to that of the landrace, but the improved cultivars had higher root yields. These results indicated that the negative correlation between root yield and leaf dry matter accumulation was largely due to the landrace in which high dry matter partitioning to leaves reduced yield more than in the improved cultivars likely due to low sink capacity (Pellet and El-Sharkawy, 1993) of the landrace. Also, differences in leaf dry matter accumulation between sites and years were lowest for TMS 91/02324 and highest for TMS 4(2)1425. Thus leaf dry matter accumulation in TMS 91/02324 was less affected by the environment, suggesting a tendency to increase yield under both favourable and less favourable conditions since dry matter allocation in the leaves, which competes with that of storage roots varied relatively little with changes in the environment, hence the high yield of this cultivar at both sites and in both years.

Dry matter accumulation the in stems

As with the case of dry matter partitioning to leaves, a strong positive correlation existed between dry matter allocation to stems and water table depth at Alabata with deep water table, but at Ibadan with shallow water table, the correlation was negative, suggesting that shallow water table reduced stem dry matter accumulation. The landrace with the highest proportion of dry matter in the stems at deep water table was likely influenced by water table depth more than the other cultivars. Results also showed that the negative correlation between root yield and stem dry matter accumulation at Alabata was largely due to the landrace as it partitioned the highest proportion of dry matter to the stems at this site. According to

Connor et al. (1981) cassava, on encountering drought stress, reduces its water uptake but conserves the carbon and nitrogen invested in leaves and stems so that when water is again available, it can resume growth. This was confirmed in this study, with the leaves and stems accumulating about 9 and 30%, respectively more dry matter in 2002 with 33% lower rainfall than in 2001. Also, stem and leaf dry matter accumulation related negatively with rainfall, minimum temperature and relative humidity, but positively with evaporation, solar radiation and maximum temperature. This indicated an increase in stem and leaf dry matter accumulation to the detriment of allocation to storage roots due to drought stress, which likely reduced root yield in 2002.

The landrace partitioned significantly higher proportion of dry matter to the stems than the improved cultivars. TMS 4(2)1425 also had more dry matter in the stems than TMS 91/02324 and TMS 91/02327. At Alabata with 27% higher dry matter in the stems than Ibadan, root yield correlated negatively with dry matter partitioned to the stem, but at Ibadan correlation was not significant. Ekanayake et al. (1998) noted that since cassava has simultaneous development and supply of assimilate is partitioned between top and root growth, high dry matter allocated to the top reduces dry matter accumulation in the roots. Thus the low root yield of the landrace was partly due to partitioning of higher dry matter to the stems at the expense of storage root dry matter accumulation. Also, TMS 91/02324 and TMS 91/02327 with the lowest stem dry matter content had the highest root yields. The results agree with Manrique (1990) who noted that differences in yield among cultivars were mainly due to differences in dry matter allocation to branches.

Dry matter accumulation in rootstock

The cassava cultivars partitioned similar proportions of dry matter to rootstock, but the effects of toposequence position, site and year were significant. Plants in valley bottom had the highest accumulation of dry matter in rootstock, while those in the fringe had the lowest accumulation. Dry matter partitioned to rootstock was about 11% higher at Ibadan than Alabata. There was a strong positive correlation between water table depth and dry matter accumulation in rootstock at the shallow water table site, but at the deep water table site, the correlation was negative. The results indicated that shallow water table depth increased dry matter accumulation in rootstock, while deep water table reduced it. This was partly due to sink-limitation as shallow water table reduced root number (Pellet and El-Sharkawy, 1993). Thus as water table depth decreased, the proportion of dry matter partitioned to rootstock increased because part of the dry matter destined for storage roots was likely allocated to the rootstocks close to the storage roots due to sink limitation. The negative correlation between root yield and rootstock dry matter accumulation at Ibadan, suggests that high dry matter partitioned to rootstock at shallow water table depth contributed to the low yield at this site. Rootstock dry matter biomass was about 29% higher in 2002 with 3 months of drought than in 2001 with relatively well distributed rainfall. Also, rainfall, minimum temperature and relative humidity related negatively with rootstock dry matter biomass, while evaporation, solar radiation and maximum temperature correlated positively with this biomass. This suggests an increase in dry matter allocation to rootstocks as a result of drought stress, which partly contributed to the low root yield in 2002. The results revealed that both excess moisture and drought stress increase dry matter accumulation in rootstocks.

Dry matter accumulation in fibrous roots

There was a strong negative correlation between fibrous root dry matter biomass and root yield at both sites. The landrace had the highest accumulation of dry matter in fibrous roots, with the lowest recorded for TMS 91/02324 and TMS 91/02327 across toposequence positions at both sites in both years. The low accumulation of dry matter in the fibrous roots in the latter cultivars was accompanied by high root yields, while the high dry matter partitioned to fibrous roots of the landrace was accounted for by low root yield. Similarly, TMS 4(2)1425 which produced the highest fibrous root dry matter biomass among the improved cultivars had the second lowest yield after the landrace across toposequence positions at both sites in both years.

Also, at Alabata, plants in the fringe that gave the lowest yield allocated the highest proportion of dry matter to the fibrous roots while those in valley bottom with the highest yield had the lowest amount of dry matter in fibrous roots in 2001. In 2002, plants in valley bottom with the lowest yield had the highest dry matter accumulation in the fibrous roots, while those in the fringe with the highest yield accumulated the lowest amount of dry matter in the fibrous roots. At Ibadan plants in valley bottom with the highest fibrous root biomass gave lower yield than those in valley fringe with the lowest fibrous root dry matter accumulation in both years. Also proportion of dry matter in fibrous root in 2002 was about 28% higher than in 2001 and root yield was about 56% higher in 2001 than in 2002. These results indicated that accumulation of high amount of dry matter in fibrous root reduced yield. The results confirmed the findings of Lahai et al. (1999) who reported lower dry matter accumulation in fibrous roots of high yielding cultivars in the upland.

Plants in valley bottom allocated higher dry matter to fibrous roots than those in other positions, suggesting high dry matter accumulation in fibrous roots at shallow water table depth. This agreed with Lahai et al. (1999) who observed higher dry matter partitioning to fibrous roots in inland valley than in the upland. Cassava plants likely compensated for low storage root number and inhibition of root extension by partitioning high amount of dry matter to fibrous roots at shallow water table depth. As with the case of dry matter partitioning to rootstocks, accumulation of dry matter in fibrous roots in 2002 with 33% lower rainfall was about 28% higher than 2001, indicating that drought stress increased dry matter allocation to fibrous roots, which partly reduced root yield in 2002. Results indicated that excess moisture and drought stress increased dry matter accumulation in rootstock and fibrous roots. Thus the low root yield obtained during drought or excess moisture stress could partly be attributed to high dry matter accumulation in rootstock and fibrous roots at the expense of allocation to storage roots.

Dry matter accumulation in storage root

Averaged across toposequence positions, TMS 91/02324 and TMS 91/02327 partitioned the highest proportion of dry matter to storage roots, while the landrace had the lowest storage root dry matter allocation in each year at both sites. This indicated higher root shoot ratio for improved cultivars than for the landrace with the highest accumulation of dry matter in stems and fibrous roots. Mean root shoot weight ratios were 0.40, 0.48, 0.49 and 0.53 at Alabata and 0.45, 0.50, 0.58 and 0.57 at Ibadan for the landrace, TMS 4(2)1425, TMS 91/02324 and TMS 91/02327, respectively. This means that more photosynthate was preferentially allocated to storage roots in the improved cultivars, particularly TMS 91/02324 and TMS 91/02327 than in the landrace, which contributed to their high root yields in all positions at both sites in both years. George et al. (1998), Osiru and Hahn (1998) and Lahai et al. (1999) reported higher root yields for cultivars that allocated higher proportion of dry matter to storage roots than those that accumulated higher dry matter in stems. This was confirmed in the present study, in that at both sites dry matter partitioned to storage roots correlated positively with yield, but the correlation was better at the deep at Alabata than shallow water table site at Ibadan. This was partly because the proportion of dry matter in storage roots was higher at Ibadan with lower yield than at Alabata with higher yield, likely due to lower dry matter allocation to stems at Ibadan, which might have increased storage root dry matter accumulation at Ibadan.

As is the case with dry matter allocation to fibrous roots, accumulation of dry matter in storage roots did not significantly correlate with water table depth. However, the proportion of dry matter in the storage roots was higher in valley bottom with shallow water table than in valley fringe with deep water table. Consistent with these results, Wouamane (1994) reported higher dry matter accumulation in storage roots for some cassava cultivars in inland valley with shallower water table than the upland. The results indicated that excess moisture stress tended to increase dry matter accumulation in the below ground plant parts (rootstock, fibrous and storage roots) partly by decreasing dry matter partitioning to the above ground plant parts (stems and leaves). However, unlike dry matter accumulation in rootstock and fibrous roots, the proportion of dry matter allocated to storage roots in 2001 with well distributed rainfall, low temperature and high relative humidity, was 21% higher than in 2002 during which drought spell for the first 3 months, high temperature and low relative humidity were experienced. Also, positive correlations of storage root dry matter accumulation with rainfall, minimum temperature and relative humidity and negative correlations with evaporation rate, solar radiation and maximum temperature were noted. These results corroborate those of Mahon et al. (1976) who showed that as cassava plants increased in size, storage root dry matter increased at low temperatures because in plants grown at high temperatures root respiration might exceed root growth. The adverse effects of early water stress (2 - 4 months after planting) on storage root growth (El-Sharkawy and Cadavid, 2002; Oliveira et al., 1982) and increase in root yield with increasing humidity have been reported elsewhere (El-Sharkawy, 1993; Ekanayake et al., 1994b).

Thus, dry matter allocation to various plant parts differed among cultivars, toposequence positions, sites and years. High dry matter accumulation in storage roots increased yield, while high partitioning to leaves, stems, fibrous roots and rootstocks reduced yield. High dry matter partitioning to leaves reduced yield more in the landrace than improved cultivars and also decreased yield more at deep than shallow water table depth. Excess moisture stress increased dry matter allocation to rootstock, fibrous and storage roots, but decreased accumulation in stems and leaves. Drought stress reduced dry matter allocation to storage roots, but increased partitioning to rootstocks, fibrous roots and stems. TMS 91/02324 and TMS 91/02327 with the lowest proportion of dry matter in stems and fibrous roots and highest in storage roots had the highest yield and therefore better adapted to inland valley conditions than the other cultivars.

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