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Leaf gas exchange and photosynthetic light-response curves of cassava genotypes under drought stress during the early growth stage and after recovery

K. VONGCHAROEN[*], S. SANTANOO[**], P. ITTIPONG[***], P. BANTERNG[***], N. VORASOOT[***],
S. JOGLOY[***], and P. THEERAKULPISUT[**,+]

Faculty of Science and Health Technology, Kalasin University, 46000 Kalasin, Thailand[*]
Department of Biology, Faculty of Science, Khon Kaen University, 40002 Khon Kaen, Thailand[**]
Department of Agronomy, Faculty of Agriculture, Khon Kaen University, 40002 Khon Kaen, Thailand[***]

Abstract

This study aimed to gain insights into the photosynthesis capacity and genotypic differences in response to drought imposed at an early growth stage of cassava. Leaf water potential (LWP), leaf gas exchange, and photosynthetic light-response curves were investigated in six field-grown cassava genotypes under full irrigation and drought imposed for 60 d during 3–5 months after planting. During the drought period, mean LWP at predawn (LWP_{pre}) was significantly lower than that in the control plants, while the mean midday LWP (LWP_{mid}) was similar. During the drought period, the mean stomatal conductance was reduced from 0.36 to 0.09 mol(H_2O) m^{-2} s^{-1}, mean transpiration rate from 5.30 to 1.86 mmol(H_2O) m^{-2} s^{-1} with the concomitant reduction in net photosynthetic rate (P_{N}) from 27.45 to 16.34 μmol(CO_2) m^{-2} s^{-1}. Analysis of the light-response curves revealed a reduction in the light-saturation point (I_{sat}), the light-saturated net photosynthetic rate (P_{Nmax}), and the apparent quantum yield (AQY). After rewatering for 30 d, the drought plants could fully recover. In conclusion, P_{N} at high light intensity, P_{Nmax}, I_{sat}, and AQY were useful parameters to differentiate genotypes for variability in drought tolerance.

Keywords: apparent quantum yield; cassava; drought; leaf water potential; photosynthesis.

Introduction

Drought is one of the most important abiotic stresses that adversely affect plant growth and development, and ultimately constrains yields of economic crops, including cassava (Yang and Guo 2018). One of the essential factors in determining cassava physiological expression and the yield of each genotype is water availability (Ruangyos *et al.* 2024). The favorable growing conditions for cassava were reported for precipitations between 1,000 to 1,500 mm annually with well-distributed rainfall, and temperature range from 25 to 35°C (El-Sharkawy 2004,

Highlights

- Cassava was highly efficient in maintaining leaf water status during prolonged drought
- Cassava was also efficient in recovering photosynthetic capacity after rewatering
- Drought tolerant genotypes showed higher P_{N}, P_{Nmax}, I_{sat}, and AQY during drought

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[+]Corresponding author
e-mail: piythe@kku.ac.th

Abbreviations: AQY – apparent quantum yield; DAR – day after recovery; DAS – day after stress; *E* – transpiration rate; g_s – stomatal conductance; *I* – photosynthetic photon flux density; I_{comp} – light-compensation point; I_{sat} – light-saturation point; LP – light penetration through canopy; LWP_{pre} – leaf water potential at predawn; LWP_{mid} – leaf water potential at midday; MAP – month after planting; P_{N} – net photosynthetic rate; P_{Nmax} – light-saturated net photosynthetic rate; P_{N}/I – photosynthetic light-response curves; R_{D} – dark respiration rate; RH – relative humidity; T_{air} – air temperature; T_{leaf} – leaf temperature; VPD_{leaf} – leaf vapor pressure deficit.

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Hauser *et al.* 2014). Under near optimum edaphic–climatic conditions, the highest recorded experimental yield potential of cassava was 80–90 t ha^{-1} (Cock *et al.* 1979, El-Sharkawy 1990). However, the national average yield of Thai cassava was recorded at approximately 14.15 t ha^{-1} (MOAC 2025). This huge yield gap might be due to a lack of sufficient agro-advisory information about cassava genotypes suitable for planting and appropriate management practices during the dry period.

Most cassava-producing areas in Thailand are in the northeast, accounting for approximately 60%, while those in the Central Plain and the north take 27 and 13%, respectively (MOAC 2025). Approximately 90% of the production area of cassava in the northeast is rain-fed, and climate variability often affects cassava yields due to weather conditions and soil water content (Sawatraksa *et al.* 2018). Due to limited water and low water-holding capacity of soils in this region, cassava is planted both before the start of the rainy season (April–June) and at the end of the rainy season (September–November) (Polthanee and Promkhambut 2014). Cassava planted near or at the end of the rainy season is generally affected by drought stress during the early growth phase. Wasonga *et al.* (2020) reported that the whole-plant dry mass of the 3-month-old plants can decrease by 48.4% under water-deficit conditions. If water deficit occurs during canopy establishment and tuberous root development (2–5 months after planting), dry root yield of 15 cassava genotypes planted in September displayed significant yield reduction at the final harvest (12 and 15 months after planting) (Bakayoko *et al.* 2009).

Generally, cassava is drought-tolerant, but water deficit could inhibit cassava physiological responses, growth, development, and yield (Vongcharoen *et al.* 2018, Santanoo *et al.* 2024). Drought stress causes various undesirable effects on physiological processes, such as disturbance of water relations, osmotic balance, and photosynthesis (Sanders and Arndt 2012). Leaf water potential (LWP) is the most important metric of plant water status, which is associated with dehydration avoidance mechanisms (Rodriguez-Dominguez *et al.* 2022). LWP of the crop plants was recorded from –1.00 to –1.2 MPa under non-stress and –1.2 to –1.58 MPa under water stress conditions, depending on plant cultivars (Chowdhury *et al.* 2018). For cassava, the predawn and midday LWP were above –0.8 and –2.0 MPa, respectively, indicating the striking stomatal control in cassava regardless of soil water status (El-Sharkawy *et al.* 2012b). The relationship between LWP and stomatal opening has been well documented. Under drought, stomatal regulation maintained plant water status by reducing stomatal conductance (g_s) and transpiration rate (E) and adapted leaf anatomy (Yavas *et al.* 2024). Low g_s can also cause a decrease in net photosynthetic rate (P_N) due to limiting CO_2 uptake for the Calvin cycle, leading to growth and yield reduction (Faralli *et al.* 2020). Photosynthetic activity is highly dependent on the stable and suitable water status of leaves (Xiong and Nadal 2020). Positive relationships between P_N and productivity in cassava have been demonstrated in a series of experiments (El-Sharkawy 2016). Importantly, Rosenthal *et al.* (2012) found a strong stimulation of root yield when cassava photosynthesis was stimulated by elevated CO_2 under open-air concentration enrichment. Furthermore, higher yield and shoot biomass of cassava under drought stress conditions were associated with higher P_N and carbon-fixing enzymes activity (El-Sharkawy *et al.* 2012a). The ability of cassava to survive and grow in marginal soils under the conditions of prolonged water shortage was primarily dependent on the stomatal sensitivity to low air humidity and soil water deficit (El-Sharkawy 2004). From experiments both in the pots (El-Sharkawy and Cock 1984) and the field (Cock *et al.* 1985), at low levels of VPD (0.8 to 1.8 kPa), transpiration increases with increasing VPD. When air humidity was reduced and VPD became greater than 1.8 to 2.0 kPa, transpiration declined sharply, leading to an increase in water-use efficiency (WUE). Reduced transpiration together with the deep rooting system allows cassava plants to save water and survive during prolonged drought, slowly depleting deeper storage soil water, resulting in higher seasonal crop WUE, although with reduced P_N (El-Sharkawy *et al.* 2012b). Therefore, high P_N and WUE under drought can be used as criteria for selection in the cassava improvement program. In addition to P_N, De Souza *et al.* (2017) proposed that the yield potential of cassava could be greatly improved by increasing light interception efficiency and radiation conversion efficiency, which were determined by canopy structure and leaf photosynthesis performance, respectively.

The objective of this study was to investigate the effects of drought stress during the early growth stage of six (three commercial and three breeding lines) genotypes of cassava on LWP, canopy light penetration, leaf gas exchange, and photosynthetic parameters evaluated from P_N/I curves including P_{Nmax}, I_{sat}, I_{comp}, R_D, and AQY to obtain some insights into photosynthesis capacity and genotypic differences in response to drought imposed at an early growth stage. Studies on the photosynthesis of cassava are limited relative to those in other important crops. The potential of cassava genotypes to maintain water balance and their photosynthetic performance under water stress is essential. Growth and development during water deficit is crucial for ensuring stable yields, especially during the limited rainfall period in Thailand.

Materials and methods

Study site: The experiment was conducted at the Field Crop Research Station, Division of Agronomy, Faculty of Agriculture, Khon Kaen University (KKU) (altitude 16°47'N, 102°81'E, 195 m above sea level) from 25 August 2021 to 25 February 2022. The soil texture at the experimental site is sandy loam (Oxic Paleustult), which is distributed widely in the northeast of Thailand. The soil physical compositions, including sand, silt, and clay contents at the soil depth of 0–60 cm were 70.97–74.99%, 16.97–17.99%, and 7.02–12.06%, respectively. Chemical properties including total nitrogen (0.02–0.03%), available phosphorus (277–364 mg kg^{-1}), exchangeable potassium (21–54 mg kg^{-1}), organic matter (0.29–0.43%), cation exchange capacity (3.33–3.59 cmol kg^{-1}), electrical conductivity (0.02–0.03 dS m^{-1}) at pre-planting were determined.

Land preparation before cassava planting followed the standard procedures for cassava, which included plowing with a 3-disk plow, followed by a 7-disk harrow, and ridging (Watananonta *et al*. 2006). A minioverhead sprinkling system regularly applied water to maintain soil water status for the control plot throughout the growing period. For the drought plot, cassava plants received no irrigation water at the plant age of 3MAP until 5MAP (2 months without watering during December to January), after which the plants were rewatered until 6MAP. The plants in the control plots, on the other hand, received regular watering throughout the 6-month investigation period. The fertilizer was applied at 1MAP and 2MAP based on soil analysis and the nutrient requirements for cassava, following recommendations by Howeler (2002).

Environmental conditions in the cassava field: Weather conditions, including the daily mean and maximum PAR, air temperature (T_{air}), relative humidity (RH), total rainfalls, and number of rainy days at the cassava field during August 2021 to February 2022, were recorded from the date of planting until the plants were six months old. The mean maximum daily PAR, T_{air}, RH, rainfalls, and number of rainy days of each month were displayed in the text table below. The monthly mean daily PAR of the wet (August–October) and dry seasons (November–February) were 1,046 and 1,176 μmol(photon) m^{-2} s^{-1}, while maximum daily PAR were 2,018 and 1,894 μmol(photon) m^{-2} s^{-1}, respectively. Monthly T_{air} means were 27.3 and 24.7°C, with the mean minimum of 23.9°C and 18.7°C, and mean maximum of 32.7°C and 31.7°C in the wet and dry seasons, respectively. The monthly RH means (89.8%), total rainfall (162.4 mm) and number of rainy days (16 d) of the wet season were much higher than those of the dry season, which displayed RH, total rainfall and number of rainy days at 62.6%, 9.0 mm, and 3 d, respectively. There was absolutely no rainfall during November and December 2021.

For both control and drought plots, soil water status at the depth of 0–60 cm were recorded at the 0 day after stress (0DAS) when the plants were three months old old (3MAP), 30 d after stress (30DAS), 60 d after stress (60DAS), and 30 d after water recovery (30DAR), which corresponded with the plant age at 3MAP, 4MAP, 5MAP, and 6MAP, respectively. At 0DAS, the soil moistures were not significantly different between the control (9.96%) and the drought plot (9.95%). At 30DAS and 60DAS, soil moisture content in the drought plot exhibited significant ($p<0.05$) reduction compared with that in the control plot, which was 7.46 and 5.07% for 30DAS and 60DAS, respectively. At 30DAR, the soil moisture of the drought plot (10.72%) increased to a similar level as that of the control (12.24%).

Plant materials: Six cassava genotypes were selected for plant water status, canopy growth, and physiological studies. All were improved cultivars or lines with high yield, suitable for industrial uses. Rayong 9 (RY9, non-forking plant type), Kasetsart50 (KU50, forking plant type), and CMR38-125-77 (forking plant type) were reported as high yielding, while Rayong 72 (RY72, forking plant type), CMR35-91-63 (forking plant type), and CM523-7 (forking plant type) produced moderate yield (Ruangyos *et al*. 2024). The planting materials used were 20-cm-long stem cuttings from 10-month-old plants grown in the same experimental field at the field crop station, KKU. Stem cuttings of six cassava genotypes were planted vertically on the soil ridges at a 1 × 1 m distance with 2/3 of the stem length buried. The experimental design was split-plot in a randomized complete block design (RCBD) with four replications. Each sub-plot contained 35 plants (5 plants × 7 rows) in each replication. The main plot of this experiment was the different water conditions (control and drought), while the sub-plot was the six cassava genotypes. Cassava was planted in the mid-rainy season on 25 August 2021. The control plants received regular watering from planting (0MAP) until 6MAP (August–February). The drought plants received regular watering from 0MAP to 3MAP

Weather conditions including daily mean and maximum photosynthetically active radiation (PAR), daily mean temperature (T_{air}), relative humidity (RH), total rainfalls, and number of rainy day in the cassava field were measured during August 2021 to February 2022 at the Field Crop Station, Division of Agronomy, Faculty of Agriculture, Khon Kaen University (KKU). Soil moisture of full watering plot (control) and early drought plot (drought) were determined at 0 d after stress (0DAS), 30 d after stress (30DAS), 60 d after stress (60DAS), and 30 d after water recovery (30DAR) at the plant age of 3MAP, 4MAP, 5MAP, and 6MAP, respectively. Significant differences ($p<0.05$) in soil moisture content between the control and drought conditions are denoted by *.

Month	Plant age (MAP)	PAR [μmol(photon) m^{-2} s^{-1}]		T_{air} [°C]			RH [%]	Total rainfall [mm]	Number of rainy days	Soil moisture at 0–60 cm [%]	
		max	mean	max	min	mean				Control	Drought
Aug. 2021	0MAP	2,253	1,180	34.0	24.7	28.3	75.6	112.9	11	-	-
Sep. 2021	1MAP	1,968	827	32.1	23.9	26.9	85.2	246.7	23	-	-
Oct. 2021	2MAP	1,834	1,132	32.0	23.1	26.8	78.6	127.5	13	-	-
Nov. 2021	3MAP	1,934	1,108	32.4	20.7	26.0	66.1	0.0	0	9.96	9.95
Dec. 2021	4MAP	1,865	1,164	30.6	16.6	23.3	58.8	0.0	0	10.63^{*}	7.46
Jan. 2022	5MAP	1,728	1,145	32.7	18.1	24.8	59.6	1.5	3	10.55^{*}	5.07
Feb. 2022	6MAP	2,049	1,286	30.9	19.3	24.6	65.9	34.3	7	12.24	10.79

(25 August to 25 October 2021). Then, watering was withheld for 60 d from 3MAP to 5MAP (26 October to 26 December 2021), followed by rewatering for 30 d until 6MAP. More details of the cultural practices and treatment procedures were given in the previous paper (Ruangyos *et al*. 2024, Santanoo *et al*. 2024).

Plant water status: For comparison of leaf water potential (LWP) between control and droughted plants, leaves of six cassava genotypes were measured in the field using the pressure chamber technique (Scholander *et al.* 1965). Briefly, measurements were taken at predawn (05:00 h) and midday (12:00 h) on the 5th healthy, fully expanded leaves from the top of the canopy. The sampled leaves of each genotype and water management were covered with a small plastic bag immediately after excision to avoid water loss during the transfer of each leaf to the chamber. The time between chamber pressurization and leaf excision was as brief as possible, generally less than 2 min. The leaf petiole was cut with a sharp razor and placed in a chamber. The chamber was sealed and gradually and slowly pressurized with nitrogen gas. The amount of pressure that it takes to cause water to appear at the cut surface determines how much tension the leaf was experiencing at this point; the balance pressure was recorded as leaf water potential (MPa). The measurements were made on one plant per replication ($n = 4$). LWP of cassava plants were measured at the 0 d after stress (0DAS), 30 d after stress (30DAS), 60 d after stress (60DAS), and 30 d after water recovery (30DAR), which corresponded to the plant age of 3MAP, 4MAP, 5MAP, and 6MAP, respectively.

Determination of light penetration: Light penetration was recorded for the control and drought plants at 0DAS, 30DAS, 60DAS, and 30DAR to reflect the amount of light reception within the plant canopy. Light intensity (PAR) data were measured above and below the canopy from 10:00 to 11:30 h on sunny days using a line quantum sensor (*LI-191R*, *Li-Cor Inc*., Lincoln, NE, USA). Light penetration was transformed into a percentage of light that penetrated through the canopy.

Determination of photosynthetic performance: Leaf gas exchange was performed on the fully expanded leaves of six cassava genotypes, one plant/replication, at plant ages of 3, 4, 5, and 6MAP in the control and drought plots. Leaf gas exchange was performed on sunny days from 8:30 to 11:30 h using an infrared gas analyzer (IRGA) model *Li-Cor 6400xt* with a LED light source using a standard 2 × 3 cm leaf chamber (*Li-Cor Inc*., Lincoln, NE, USA). The measurement conditions were controlled as follows: light intensity at 1,500 μmol(photon) m^{-2} s^{-1}, CO_2 concentration at 400 μmol mol^{-1}, temperature at 30°C, and RH at 60–65%. Light-response (P_N/I) curves were determined on one plant/replication ($n = 4$). Net photosynthetic rates were measured at different PAR levels of 1,800; 1,500; 1,000; 800, 500, 200, 100, 50, 30, 10, and 0 μmol(photon) m^{-2} s^{-1} with a constant concentration of CO_2 (400 μmol mol^{-1}) and temperature (30 ± 2°C). The photosynthetic performance of six cassava genotypes in drought and control plants was measured at 0DAS, 30DAS, 60DAS, and 30DAR on sunny days. Photosynthesis measurement was performed on the leaves which were close in position to the leaves collected for measurement of LWP.

The predictions of light-saturated net photosynthetic rate (P_{Nmax}), respiration in the dark (R_D), light-compensation point (I_{comp}), light-saturation point (I_{sat}), and apparent quantum yield (AQY) were estimated from the modeled light-response curve using the *Solver* function of *Microsoft Excel* in routines provided by Lobo *et al.* (2013): $P_N = (\varphi_{Io} \times I \times P_{gmax})/(\varphi_{Io} \times I + P_{gmax}) - R_D$, where P_N = net photosynthetic rate [μmol(CO_2) m^{-2} s^{-1}], φ_{Io} = quantum yield at $I = 0$ [μmol(CO_2) μmol^{-1}(photon)], I = photosynthetically active radiation [μmol(photon) m^{-2} s^{-1}], P_{gmax} = maximum gross photosynthetic rate [mmol(CO_2) m^{-2} s^{-1}], and R_D = dark respiration rate [μmol(CO_2) m^{-2} s^{-1}].

Data and statistical analysis: Analysis of variance (*ANOVA*) according to a split plot in RCBD was done for assessing the significance of quantitative changes in various parameters, including LWP at predawn (LWP_{pre}), LWP at midday (LWP_{mid}), light penetration through canopy (LP), leaf gas-exchange parameters at 1,500 μmol(photon) m^{-2} s^{-1} (P_N, g_s, E, and T_{leaf}), and photosynthetic parameters evaluated from the P_N/I curves ($P_{Nmax,}$ I_{sat}, R_D, I_{comp}, and AQY) among cassava genotypes and between water managements. The interaction between water treatments (W) × cassava genotypes (G) was analysed, in which the main plot was water treatments, while the sub-plot was cassava genotypes (Table 5S, *supplement*). *Tukey*'s honest significant difference test (HSD) was used for multiple comparisons of means at an alpha level of 0.05. All statistical analyses were conducted using *Statistix version 10* software following the procedure described by Gomez and Gomez (1984). All the graphs were taken using the *Sigmaplot version 15.0* software (San Jose, CA, USA). The correlation of LWP_{pre}, LWP_{mid}, LP, leaf gas-exchange parameters at 1,500 μmol(photon) m^{-2} s^{-1}, and photosynthetic parameters evaluated from P_N/I curves of six cassava genotypes at the four plant ages was conducted for each water condition. *Pearson*'s correlation, principal component analysis (PCA), and hierarchical clustering analysis (HCA) with a heatmap was used to cluster cassava genotypes based on LWP at predawn and midday, canopy light penetration, and predicted values of photosynthetic parameters using *R version 3.4.3* (*R Core Team* 2024) and *Rstudio version 2023.12.1.402* (*Posit Team* 2024).

Results

Plant water status of the well-watered and droughted cassava: The effect of drought stress on the leaf water potential (LWP) of six cassava genotypes including RY9, KU50, CMR38-125-77, RY72, CMR35-91-63, and CM523-7 growing under regular watering (control) and drought (early drought) conditions were estimated at predawn and midday in the plant age 3MAP (before drought stress), 4MAP (30DAS), 5MAP (60DAS), and 6MAP (30DAR) (Fig. 1; Table 1S, *supplement*). At predawn, the mean LWP_{pre} across genotypes varied with plant age. The LWP_{pre} of the control plants at 4MAP (–0.66 MPa) were significantly reduced from that of the 3MAP plants (–0.50 MPa), while LWP_{pre} of the 5MAP (–0.54 MPa) and 6MAP (–0.38 MPa) plants significantly increased from that of the 4MAP plants (Fig. 1*A*). The drought plants showed a similar pattern of changes in LWP_{pre} with plant age but displayed significant reductions compared with the controls at 4MAP and 5MAP after experiencing 30 and 60 d of drought, respectively (Fig. 1*B*). However, after rewatering for 30 d, at 6MAP, the LWP_{pre} of the drought plants fully recovered to the same level as that of the controls. The significant differences between cassava genotypes in each water condition were not observed in the LWP_{pre} values; however, RY9 showed slightly higher mean LWP_{pre} than the others. RY72 and CM523-7 were noted to have the lowest LWP_{pre} after experiencing drought for 30 and 60 d, respectively (Fig. 1*B*). The LWP of cassava plants at midday (LWP_{mid}) showed much decreased values compared to those at predawn due to high transpiration rates. The LWP_{mid} of the well-watered plants also varied significantly with age, with the lowest mean value at 3MAP (–1.54 MPa), slightly increased to –1.28 MPa at 4MAP, significantly decreased to –1.69 MPa at 5MAP, and then hugely increased to –0.94 MPa at 6MAP after rewatering (Fig. 1*C*). The pattern of changes in LWP_{mid} of the drought plants was different from that of the predawn values. Despite the lack of irrigation water and rainfall, the LWP_{mid} of the plants at 4MAP (–1.43 MPa) and 5MAP (–1.56 MPa) did not reduce; in contrast, it slightly increased compared to the value of –1.61 MPa at 3MAP (Fig. 1*D*). Moreover, at the same plant age, no significant differences in LWP_{mid} were observed between the drought and well-watered plants. For genotypic comparisons, the significantly different LWP_{mid} were only observed in the 6MAP control plants, *i.e.*, LWP_{mid} of RY9 (–0.69 MPa) and RY72 (–0.74 MPa) were significantly higher than CMR38-125-77 (–1.23 MPa), while other genotypes showed intermediate values (Table 1S).

Light penetration of six cassava genotypes: The appearance of the fully irrigated 5MAP cassava plants compared with the plants experiencing drought for 60 d was photographed from two representative experimental sub-plots and displayed in Fig. 2*A*,*B*, which demonstrated the inhibitory effects of drought on plant growth. Canopy structure and density of the control and drought plants at the ages of 3MAP, 4MAP, 5MAP, and 6MAP were indicated by the percentage of light penetration through the canopy in Fig. 2*C* and 2*D*, respectively. The genotypic mean light penetration decreased with plant age, indicating an increase in the number and size of cassava leaves. The 3MAP control plants showed the highest mean light penetration of 73.1%, which was dramatically and significantly reduced to 46.1 and 12.2% at 4MAP and 5MAP, respectively, indicating highly active canopy development (Fig. 2*C*; Table 2S, *supplement*). The light penetration at 6MAP (9.9%) was not significantly different from that at 5MAP, indicating a reduced rate of canopy growth. For drought plants, the mean light penetration at the plant age of 3MAP, 4MAP, 5MAP, and 6MAP were 70.6, 55.9, 22.2, and 18.3%, respectively (Fig. 2*D*). The significantly higher light penetration of the drought compared with the well-watered plants was observed after 30 (4MAP) and 60 DAS (5MAP) indicating the drought-induced retardation of canopy growth and higher leaf shedding. The significant differences in light penetration between cassava genotypes were not observed at any plant age, although widely different values for droughted plants at 6MAP were noted, indicating different levels of response to rewatering.

Leaf gas-exchange parameters: The monthly mean daily PAR and mean daily maximum PAR in the experimental

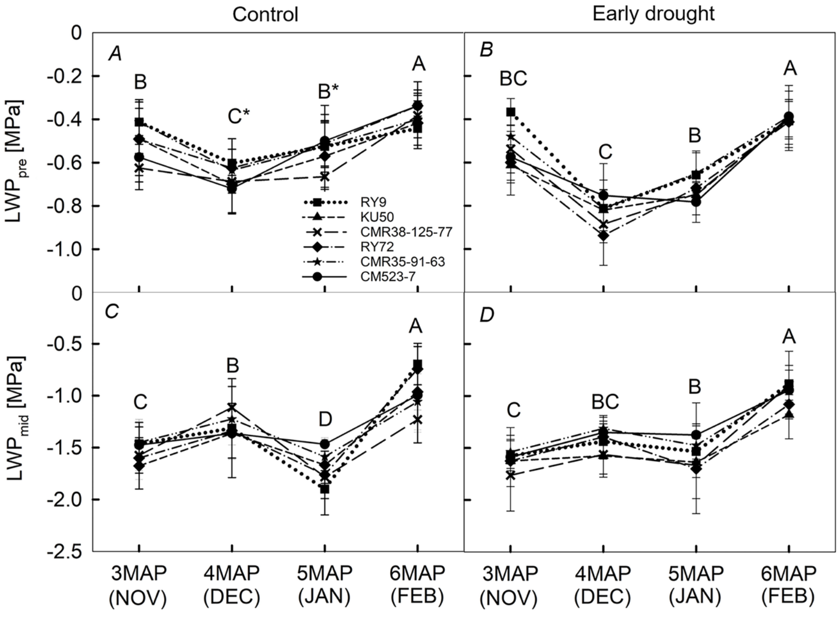

Fig. 1. Leaf water potential (LWP) of six cassava genotypes at the plant age of 3, 4, 5, and 6 months after planting (MAP). LWP at predawn and midday was measured in control plants (*A* and *C*; continuous irrigation from 0MAP to 6MAP) and drought plants (*B* and *D*; irrigation was withheld for 60 d in the dry season from 3MAP to 5MAP, then rewatered until 6MAP). *Different capital letters* indicated significant ($p<0.05$ and $p<0.01$) differences in genotypic means among the ages of plants. The significant differences ($p<0.05$) between water regimes at each plant age are denoted by *.

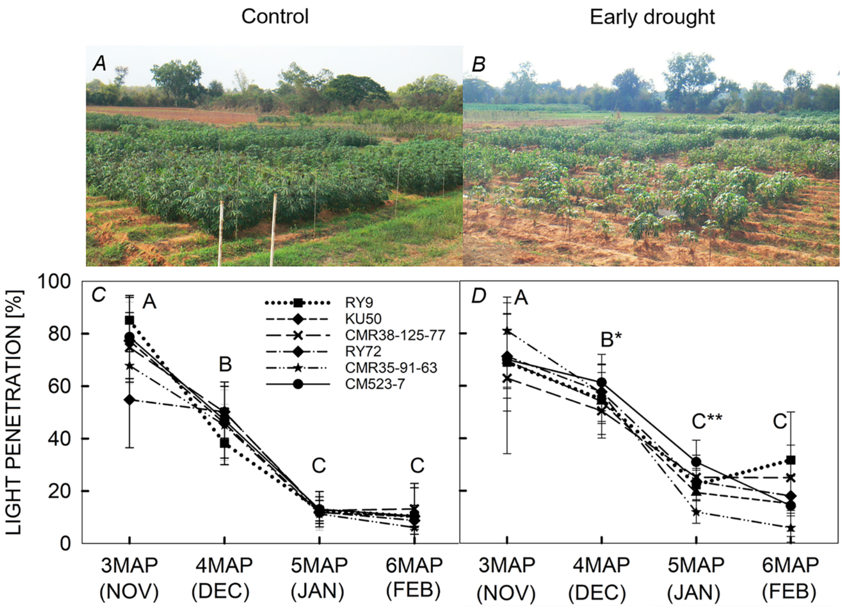

Fig. 2. The control irrigated (*A*) and drought (*B*) plot of cassava at the plant age of 5 months. Light penetration [%] of six cassava genotypes at the plant age of 3, 4, 5, and 6 months after planting (MAP). Light penetration was estimated for control plants (*C*; continuous irrigation from 0MAP to 6MAP) and drought plants (*D*; irrigation was withheld for 60 d in the dry season during 4MAP and 5MAP, then rewatered until 6MAP). *Different capital letters* indicated significant ($p<0.05$ and $p<0.01$) differences between the ages of plants. The significant differences ($p<0.05$ and $p<0.01$) between water regimes are denoted by * and **, respectively.

field during the observation period varied between 827–1,286 and 1,728–2,253 μmol(photon) m^{-2} s^{-1}, respectively, therefore leaf gas exchange at 1,500 μmol(photon) m^{-2} s^{-1} was recorded to represent photosynthetic performance at high light intensity (Table 1). The 3MAP plants before stress induction had similar mean P_N across genotypes in the control [21.68 μmol(CO_2) m^{-2} s^{-1}] and drought [21.56 μmol(CO_2) m^{-2} s^{-1}] plots. After irrigation was withheld for 30 and 60 d, all cassava genotypes were under increasing water stress, resulting in the mean P_N of 21.13 and 16.34 μmol(CO_2) m^{-2} s^{-1} (20 and 40% reduction), compared with the controls. After 30 d of water withholding, photosynthesis of CMR38-125-77 and KU50 was the most negatively affected, showing the low P_N of 20.43 and 17.08 μmol(CO_2) m^{-2} s^{-1}, respectively, which were significantly lower than those of the controls. The P_N of the remaining four genotypes was also reduced but not significantly different from the controls, with RY9 showing the highest P_N of 24.05 μmol(CO_2) m^{-2} s^{-1}, followed by CM523-7 [22.41 μmol(CO_2) m^{-2} s^{-1}]. In contrast, prolonged water shortage for 60 d resulted in significant reduction in P_N of all genotypes ranging from 29% [from 28.84 to 20.44 μmol(CO_2) m^{-2} s^{-1}] in RY9 to 50% [from 27.11 to 13.52 μmol(CO_2) m^{-2} s^{-1}] in KU50 with RY9 still attained the highest while KU50 had the lowest P_N. After 30 d of rewatering, the stressed plants of all genotypes were able to effectively recover from stress, leading to an increase in P_N to match that of the non-stressed plants. Similar trends in changes in response to drought stress and recovery were observed for g_s and transpiration rate (E). The mean g_s across genotypes was significantly reduced from 0.16 to 0.09 mol m^{-2} s^{-1} (47% reduction), and from 0.36 to 0.12 mol m^{-2} s^{-1} (68% reduction), after 30 and 60 d of water stress, respectively. Similarly, E was reduced by 38% [from 3.05 to 1.86 mmol(H_2O) m^{-2} s^{-1}] and 55% [from 5.30 to 2.41 mmol(H_2O) m^{-2} s^{-1}] after 30 and 60 d of water stress, respectively. Stomatal activity and transpiration were fully recovered when the stressed plants were rewatered for 30 d. Before stress treatment, the water-use efficiency (WUE; P_N/E) was similar for both plant groups, but after 30 d of water stress, WUE of the drought plants [18.29 μmol(CO_2) mmol(H_2O)$^{-1}$] was almost double that of the well-watered ones [9.73 μmol(CO_2) mmol(H_2O)$^{-1}$]. However, after 60 d of stress, there were no significant differences between the plant groups [8.37 and 8.50 μmol(CO_2) mmol(H_2O)$^{-1}$]. In addition, no significant differences in WUE between genotypes were recorded. Reduced E after prolonged stress was associated with a significant increase in leaf temperature (T_{leaf}) of the 5MAP plants from 31.47 to 32.47°C. The genotypes which showed a significant increase in leaf temperature under stress included KU50 (33.15°C), CMR38-125-77 (32.46°C), CM523-7 (32.42°C), and RY9 (32.35°C).

Photosynthetic light-response (P_N/I) curves: At each plant age, cassava growing under different water managements showed differential responses to varying light intensity (Fig. 3). The parameters evaluated from P_N/I curves, including light-saturated net photosynthetic rate (P_{Nmax}), light-saturation intensity (I_{sat}), light-compensation point (I_{comp}), dark respiration (R_D), and apparent quantum yield (AQY), are displayed in Fig. 4. The influences of drought stress on P_{Nmax} are shown in Fig. 4*A*,*B* and Table 4S (*supplement*). The highest mean P_{Nmax} across genotypes of control plants was found at 4MAP [28.60 μmol(CO_2) m^{-2} s^{-1}] and 5MAP [29.16 μmol(CO_2) m^{-2} s^{-1}], which were significantly higher than that at 3MAP plants [23.14 μmol(CO_2) m^{-2} s^{-1}]. At 6MAP, mean P_{Nmax} across genotypes [23.31 μmol(CO_2) m^{-2} s^{-1}] was significantly reduced from the 5MAP (Fig. 4*A*). For the drought plants, the mean P_{Nmax} across genotypes of the 4MAP plants [22.69 μmol(CO_2) m^{-2} s^{-1}] was similar to that of the 3MAP plants [23.48 μmol(CO_2) m^{-2} s^{-1}]. However, at 5MAP (60DAS), the mean P_{Nmax} across genotypes was significantly reduced to 17.01 μmol(CO_2) m^{-2} s^{-1} (Fig. 4*B*). During 30 and 60 d after drought stress,

Table 1. Leaf gas-exchange parameters of six cassava genotypes at the plant age of 3, 4, 5, and 6 months after planting (MAP). Net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E), water-use efficiency (WUE), and leaf temperature (T_{leaf}) under PAR of 1,500 µmol(photon) m^{-2} s^{-1} were measured in cassava growing under the control (continuous irrigation from 0MAP to 6MAP) and drought (irrigation withheld for 60 d in the dry season during 3MAP and 5MAP then rewatered until 6MAP) treatment. *Different lowercase letters* in each plant age indicated significant ($p<0.05$ and $p<0.01$) differences between the genotypes. *Different capital letters* indicated significant *(*$p<0.05$ and $p<0.01$) differences between the ages of plants. The significant differences ($p<0.05$ and $p<0.01$) between water regimes are denoted by * and **, respectively.

Plant age	Genotype	P_N [µmol(CO$_2$) m^{-2} s^{-1}]		g_s [mol(H$_2$O) m^{-2} s^{-1}]		E [mmol(H$_2$O) m^{-2} s^{-1}]		WUE [µmol(CO$_2$) mmol(H$_2$O)$^{-1}$]		T_{leaf} [°C]	
		Control	Drought	Control	Drought	Control	Drought	Control	Drought	Control	Drought
3MAP	RY9	22.29^{a-c}	24.07^{a}	0.25^{a-c}	0.30^{a}	5.05^{a-c}	5.43^{a}	4.51^{a}	4.59^{a}	29.61^{a}	28.96^{a}
	KU50	22.35^{a-c}	20.52^{bc}	0.27^{a-c}	0.22^{a-c}	5.55^{a}	4.87^{a-c}	4.28^{a}	4.32^{a}	28.85^{a}	29.96^{a}
	CMR38-125-77	23.10^{a-c}	23.60^{ab}	0.28^{ab}	0.28^{a}	5.29^{ab}	5.21^{ab}	4.38^{a}	4.56^{a}	29.66^{a}	29.71^{a}
	RY72	20.63^{a-c}	20.49^{bc}	0.18^{c}	0.21^{a-c}	3.64^{d}	4.50^{a-d}	5.67^{a}	4.71^{a}	29.17^{a}	29.99^{a}
	CMR35-91-63	21.41^{a-c}	20.90^{a-c}	0.19^{bc}	0.23^{a-c}	4.10^{b-d}	4.76^{a-d}	5.27^{a}	4.51^{a}	29.75^{a}	29.90^{a}
	CM523-7	20.25^{bc}	19.76^{c}	0.19^{c}	0.19^{c}	3.88^{cd}	4.43^{a-d}	5.24^{a}	4.60^{a}	30.26^{a}	30.19^{a}
	mean	21.68^{B}	21.56^{A}	0.23^{B}	0.24^{A}	4.59^{A}	4.87^{A}	4.89^{B}	4.55^{B}	29.55^{B}	29.79^{B}
4MAP	RY9	28.78^{ab}	24.05^{a-d}	0.19^{a}	0.09^{d-f}	3.51^{a}	1.94^{c-e}	8.61^{a}	13.46^{a}	31.31^{ab}	32.00^{ab}
	KU50	27.51^{a-c}	20.43^{de}	0.17^{a-c}	0.06^{ef}	3.35^{ab}	1.52^{de}	8.94^{a}	17.27^{a}	31.51^{ab}	32.44^{a}
	CMR38-125-77	29.15^{a}	17.08^{e}	0.18^{ab}	0.08^{d-f}	3.34^{ab}	1.83^{c-e}	9.28^{a}	21.54^{a}	31.22^{b}	32.23^{ab}
	RY72	24.71^{a-d}	21.07^{de}	0.13^{b-d}	0.05^{f}	2.57^{a-c}	1.32^{e}	11.80^{a}	24.61^{a}	31.37^{ab}	32.20^{ab}
	CMR35-91-63	25.99^{a-d}	21.70^{de}	0.15^{a-c}	0.09^{d-f}	2.84^{a-c}	2.06^{c-d}	10.43^{a}	15.80^{a}	31.43^{ab}	32.34^{ab}
	CM523-7	22.98^{b-d}	22.41^{c-e}	0.13^{b-d}	0.11^{c-e}	2.66^{a-c}	2.45^{b-d}	9.31^{a}	17.07^{a}	31.86^{ab}	31.96^{ab}
	Mean	26.52^{A**}	21.13^{A}	0.16^{C**}	0.09^{B}	3.05^{B**}	1.86^{C}	9.73^{A}	18.29^{A*}	31.46^{A}	32.20^{A}
5MAP	RY9	28.84^{a}	20.44^{bc}	0.43^{a}	0.17^{c-e}	5.74^{a-c}	3.37^{b-e}	6.07^{a}	6.80^{a}	31.15^{e}	32.35^{a-c}
	KU50	27.11^{a}	13.52^{e}	0.31^{a-d}	0.05^{e}	4.62^{a-d}	1.35^{e}	14.42^{a}	12.33^{a}	31.61^{b-e}	33.15^{a}
	CMR38-125-77	28.75^{a}	15.00^{de}	0.39^{ab}	0.10^{e}	6.02^{a}	2.22^{de}	5.31^{a}	9.24^{a}	31.42^{c-e}	32.46^{ab}
	RY72	24.78^{ab}	15.25^{de}	0.25^{b-e}	0.10^{e}	4.17^{a-d}	2.16^{de}	12.76^{a}	8.33^{a}	31.83^{b-e}	32.24^{b-d}
	CMR35-91-63	27.22^{a}	18.78^{cd}	0.37^{a-c}	0.14^{de}	5.84^{ab}	3.10^{c-e}	5.41^{a}	7.09^{a}	31.47^{b-e}	32.14^{b-e}
	CM523-7	27.94^{a}	15.02^{de}	0.38^{ab}	0.10^{e}	5.37^{a-c}	2.22^{de}	6.23^{a}	7.20^{a}	31.31^{de}	32.42^{a-c}
	Mean	27.45^{A**}	16.34^{B}	0.36^{A*}	0.12^{B}	5.30^{A*}	2.41^{C}	8.37^{A}	8.50^{B}	31.47^{A}	32.47^{A*}
6MAP	RY9	23.79^{a-c}	22.91^{a-d}	0.20^{a}	0.22^{a}	3.45^{a}	3.94^{a}	7.16^{a}	6.38^{a}	29.45^{a}	30.02^{a}
	KU50	20.82^{d}	22.31^{a-d}	0.14^{a}	0.23^{a}	2.79^{a}	4.23^{a}	7.79^{a}	5.61^{a}	29.68^{a}	30.23^{a}
	CMR38-125-77	24.52^{a}	23.94^{ab}	0.21^{a}	0.23^{a}	3.71^{a}	4.28^{a}	6.82^{a}	6.37^{a}	29.52^{a}	30.07^{a}
	RY72	21.59^{b-d}	23.45^{a-d}	0.18^{a}	0.22^{a}	3.39^{a}	4.12^{a}	6.88^{a}	6.32^{a}	29.58^{a}	30.11^{a}
	CMR35-91-63	21.44^{b-d}	21.05^{cd}	0.16^{a}	0.18^{a}	3.10^{a}	3.49^{a}	7.30^{a}	6.64^{a}	29.50^{a}	30.38^{a}
	CM523-7	21.69^{b-d}	21.72^{a-d}	0.15^{a}	0.21^{a}	2.96^{a}	4.04^{a}	7.35^{a}	5.72^{a}	29.93^{a}	30.22^{a}
	Mean	22.31^{B}	22.57^{A}	0.18^{BC}	0.22^{A}	3.24^{B}	4.02^{B}	7.22^{AB}	6.17^{B}	29.61^{B}	30.18^{B}

the 4MAP and 5MAP plants displayed significantly ($p<0.05$ and $p<0.01$, respectively) lower mean P_{Nmax} compared to the control plants with approximately 20.7% and 41.7% reduction, respectively. At 6MAP (30 d after rewatering), the mean P_{Nmax} across genotypes of stressed plants [24.17 µmol(CO$_2$) m^{-2} s^{-1}] was significantly recovered to a similar level as that of the 6MAP control plants. The mean P_{Nmax} values among genotypes showed nonsignificant differences at any plant ages and water treatments; however, RY9 tended to show slightly higher mean P_{Nmax} than the other genotypes in both water conditions.

The mean light-saturation point (I_{sat}) across genotypes was similar at 1,950 µmol(photon) m^{-2} s^{-1} for the well-watered plants at 3MAP to 5MAP, but it was slightly reduced at 6MAP (Fig. 4*C*). In contrast, after 30 d without irrigation and rainfall, the I_{sat} reduced to 1,893 µmol(photon) m^{-2} s^{-1} compared to 1,950 µmol(photon) m^{-2} s^{-1} at 3MAP. Significantly, the I_{sat} after 60 d of stress was reduced to 1,671 µmol(photon) m^{-2} s^{-1} but significantly increased to the normal level after rewatering (Fig. 4*D*). The mean I_{sat} of the drought plants after 30 and 60 d without watering tended to be reduced by 2.9% and 14.1%, respectively, from those of the well-watered plants. It was noted that I_{sat} values of the control plants of all genotypes were almost equal at any age. In contrast, during drought stress, genotypic differences were apparent. Particularly, the I_{sat} values of KU50 [1,458 µmol(photon) m^{-2} s^{-1}] and CMR38-125-77 [1,451 µmol(photon) m^{-2} s^{-1}] were significantly lower than other genotypes, with CMR35-91-63 and RY9 attaining the highest values of 1,894 and 1,793 µmol(photon) m^{-2} s^{-1}, respectively.

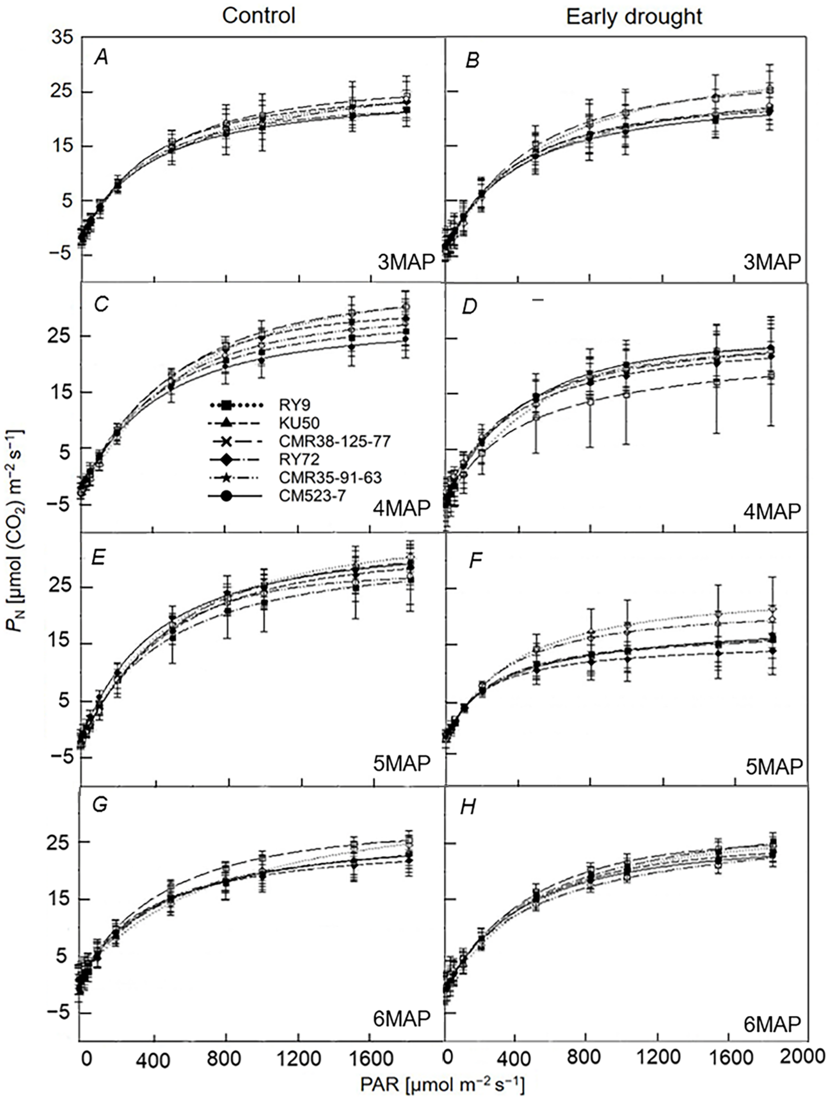

Fig. 3. Photosynthetic light-response curve (P_N/I curve) of six cassava genotypes at the plant age of 3, 4, 5, and 6 months after planting (MAP). The P_N/I curves were measured in cassava growing under the control (continuous irrigation from 0MAP to 6MAP and drought (irrigation was withheld for 60 days in the dry season during 4MAP and 5MAP then rewatered until 6MAP) treatment.

The light-compensation point (I_{comp}) varied with plant age under both control and drought stress, but the differences between water regimes were not significant. The mean I_{comp} of the 4MAP control plants [42.05 μmol(photon) m^{-2} s^{-1}] was significantly higher than that of the 3MAP and 5MAP plants, which were 27.78 and 29.60 μmol(photon) m^{-2} s^{-1}, respectively. At the 6MAP, the mean I_{comp} was significantly reduced to 10.90 μmol(photon) m^{-2} s^{-1} (Fig. 4*E*). In the drought condition, the mean I_{comp} of 4MAP plants [64 μmol(photon) m^{-2} s^{-1}] was not significantly reduced from that of the 3MAP plants even after 30 d of lack of water, while the mean I_{comp} of the 5MAP plants (60 d after stress) was significantly reduced to 22.74 μmol(photon) m^{-2} s^{-1} and remained stable at 6MAP after rewatering (Fig. 4*F*). The significant differences in the mean I_{comp} between genotypes were not observed at any plant age and water condition.

Changes in the mean dark respiration rate (R_D) with plant age across genotypes followed a similar pattern as that of the I_{comp}. For the well-watered plants, the highest R_D occurred at 4MAP [2.98 μmol(CO$_2$) m^{-2} s^{-1}] which was significantly higher than the other stages while the lowest was detected at 6MAP [0.68 μmol(CO$_2$) m^{-2} s^{-1}] (Fig. 4*G*). For stressed plants, the R_D of the 4MAP plants [30DAS, 3.63 μmol(CO$_2$) m^{-2} s^{-1}] was similar to that of the 3MAP plants [3.42 μmol(CO$_2$) m^{-2} s^{-1}] (Fig. 4*H*). After 60 d without watering and rainfall, R_D of the 5MAP plants [1.58 μmol(CO$_2$) m^{-2} s^{-1}] was hugely reduced which remained stable at 6MAP [1.37 μmol(CO$_2$) m^{-2} s^{-1}] despite 30 d of rewatering. Even though there were no significant differences between genotypes, it was noted that RY9 tended to have higher R_D at most ages.

The mean apparent quantum yield (AQY) across genotypes of the well-watered plants significantly increased with age from 0.046, 0.0512 to 0.0540 μmol(CO$_2$) μmol(photon)$^{-1}$ for 3, 4, and 5MAP plants, respectively, then was significantly reduced to 0.0475 μmol(CO$_2$) μmol(photon)$^{-1}$ at 6MAP (Fig. 4*I*). Drought induced by 30 and 60 d without irrigation and rainfall caused a significant reduction in AQY of the 4MAP and 5MAP plants to 0.0431 and 0.0398 μmol(CO$_2$) μmol(photon)$^{-1}$, respectively, compared to those of the well-watered plants. Notably, 30 d of rewatering resulted in a significant increase in AQY of the 6MAP plants to 0.0458 μmol(CO$_2$)

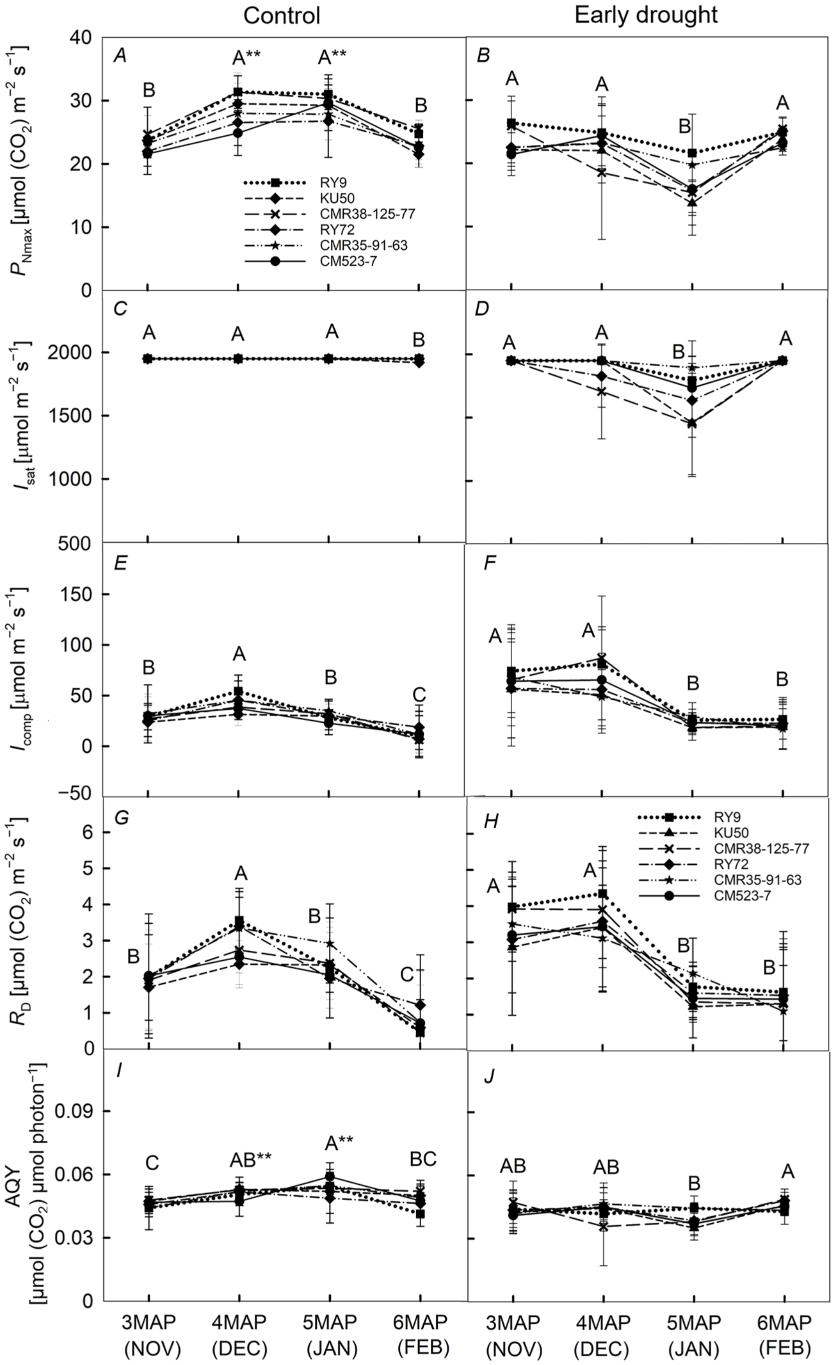

Fig. 4. Light-saturated net photosynthesis (P_{Nmax}) (*A* and *B*), light-saturation intensity (I_{sat}) (*C* and *D*), light-compensation point (I_{comp}) (*E* and *F*), dark respiration rate (R_{D}) (*G* and *H*), and apparent quantum yield (AQY) (*I* and *J*) of six cassava genotypes at the plant age 3, 4, 5, and 6 months after planting (MAP) calculated from P_{N}/I curves. The P_{N}/I curves were constructed in cassava growing under the control (*A*, *C*, *E*, *G*, and *I*; continuous irrigation from 0MAP to 6MAP) and drought (*B*, *D*, *F*, *H*, and *J*; irrigation was withheld for 60 d in the dry season during 4MAP and 5MAP then rewatered until 6MAP) treatment. *Different capital letters* indicated significant ($p<0.05$ and $p<0.01$) differences between the age of plants. The significant differences ($p<0.05$ and $p<0.01$) between water regimes are denoted by * and **, respectively.

μmol(photon)$^{-1}$ (Fig. 4*J*). A significant difference in AQY after 30 d of drought stress was noted in CMR35-91-63 and CMR38-125-77, which had AQY of 0.047 and 0.036 μmol(CO$_2$) μmol(photon)$^{-1}$, respectively. After 60 d of drought stress, CMR35-91-63 and RY9 showed the highest AQY of 0.045 μmol(CO$_2$) μmol(photon)$^{-1}$ while KU50 had the lowest AQY of 0.035 μmol(CO$_2$) μmol(photon)$^{-1}$.

Correlations among plant water status, light penetration, and physiological parameters of cassava: The relationship among plant water status (LWP at predawn and midday), light penetration (% PAR below the canopy compared to PAR above canopy), leaf gas-exchange parameters at high light intensity of 1,500 μmol(photon) m^{-2} s^{-1} [P_{N}, g_{s}, E, T_{leaf}, leaf vapor pressure deficit (VPD$_{\text{leaf}}$), and water-use efficiency (WUE)] and parameters evaluated from light-response curve (P_{Nmax}, R_{D}, I_{comp}, I_{sat}, and AQY) under the well-watered and drought condition are demonstrated by the matrix of correlation coefficient values (Table 2). The LWP at both predawn (LWP$_{\text{pre}}$) and midday (LWP$_{\text{mid}}$) showed a significant negative correlation with P_{N} for the well-watered control plants. However, for stressed plants, P_{N} showed a significant positive

Table 2. A correlation matrix of leaf water potential at predawn (LWP$_{pre}$) and midday (LWP$_{mid}$), % light penetration (LP), net photosynthetic rate (P_N), stomatal conductance (g_s), transpiration rate (E) at light intensity of 1,500 μmol(photon) m^{-2} s^{-1}, leaf temperature (T$_{leaf}$), and leaf vapor pressure deficit (VPD$_{leaf}$), light-saturated net photosynthetic rate (P_{Nmax}), dark respiration rate (R_D), light-compensation point (I_{comp}), light-saturation point (I_{sat}), apparent quantum yield (AQY), and water-use efficiency (WUE). The correlations that are significantly different ($p<0.05$ and $p<0.01$) are denoted with * and **.

		LWP$_{pre}$	LWP$_{mid}$	LP	P_N	g_s	E	T$_{leaf}$	VPD$_{leaf}$	P_{Nmax}	R_D	I_{comp}	I_{sat}	AQY
LWP$_{mid}$	Control	0.213*												
	Stress	0.355**												
LP	Control	–0.291**	–0.196											
	Stress	–0.215*	–0.360**											
P_N	Control	–0.287**	–0.272**	–0.229*										
	Stress	0.338**	0.189	0.108										
g_s	Control	0.042	–0.397**	–0.138	0.573**									
	Stress	0.578**	0.160	0.006	0.552**									
E	Control	0.059	–0.361**	0.023	0.393**	0.873**								
	Stress	0.471**	0.042	0.118	0.407**	0.881**								
T$_{leaf}$	Control	–0.290**	–0.175	–0.208*	0.198	–0.140	–0.094							
	Stress	–0.611**	–0.211*	–0.210^{g}	–0.425**	–0.632**	–0.682**							
VPD$_{leaf}$	Control	0.023	0.106	0.362**	–0.456**	–0.304**	0.134	0.082						
	Stress	–0.165	–0.197	0.207*	–0.333**	–0.173	0.282**	–0.158						
P_{Nmax}	Control	–0.313**	–0.289**	–0.186	0.948**	0.522**	0.363**	0.232*	–0.408**					
	Stress	0.323**	0.215*	0.170	0.899**	0.560**	0.448**	–0.425**	–0.276**					
R_D	Control	–0.302**	–0.365**	0.236*	0.318**	0.323**	0.267**	0.062	–0.179	0.362**				
	Stress	–0.251*	–0.280**	0.550**	0.096	0.092	0.193	–0.031	0.114	0.255*				
I_{comp}	Control	–0.331**	–0.319**	0.281**	0.208*	0.202*	0.154	0.077	–0.154	0.252*	0.958**			
	Stress	–0.227*	–0.254*	0.493**	–0.080	–0.019	0.157	–0.108	0.283**	0.070	0.885**			
I_{sat}	Control	–0.186	–0.145	0.162	0.160	0.151	0.150	0.084	–0.056	0.186	0.252*	0.250*		
	Stress	0.289**	0.120	0.204*	0.676**	0.427**	0.401**	–0.419**	–0.163	0.763**	0.331**	0.249*		
AQY	Control	–0.337**	–0.096	–0.021	0.572**	0.113	0.050	0.242*	–0.195	0.590**	0.381**	0.225*	0.044	
	Stress	–0.168	0.054	0.167	0.590**	0.080	–0.014	0.093	–0.238*	0.534**	0.052	–0.255*	0.354**	
WUE	Control	–0.223*	0.002	–0.170	–0.045	–0.413**	–0.511**	0.305**	–0.205*	–0.027	–0.067	0.015	–0.029	0.020
	Stress	–0.439**	–0.063	0.095	–0.058	–0.416**	–0.452**	0.434**	–0.147	0.038	0.199	0.095	0.007	0.376**

correlation with LWP_{pre} at predawn (r = 0.338) only and no significant correlation with LWP_{mid}. Similarly, LWP_{pre} also had significant positive correlations with g_s (r = 0.578) and E (r = 0.471) in the stressed plants but no correlations with those of the control plants. In contrast, LWP_{mid} had significant negative correlations with P_N (r = –0.272), g_s (r = –0.397), and E (r = –0.361) in the control plants but no correlations with those parameters of the stressed plants. The LWP_{pre} had a significant negative correlation with T_{leaf} of both control (r = –0.290, $p<0.01$) and stressed (r = –0.611, $p<0.01$) plants, while LWP_{mid} showed a negative correlation with T_{leaf} of the stressed plants (r = –0.211, $p<0.05$) only. For both control and stressed plants, P_N showed significant positive correlations with g_s and E but negative correlations with VPD_{leaf}. P_N was significantly negatively correlated with T_{leaf} (r = –0.425, $p<0.01$) only under drought conditions. Plants under drought stress also showed significant negative correlations between T_{leaf} and g_s (r = –0.632), and T_{leaf} and E (r = –0.682). The WUE was negatively correlated with LWP_{pre} (r = –0.223, $p<0.05$ for control; r = –0.439, $p<0.01$ for stressed plants) but did not correlate with LWP_{mid}. The WUE was significantly negatively correlated with g_s and E for both control and stressed plants, while positively correlated with T_{leaf}. The WUE was also positively correlated with AQY (r = 0.376, $p<0.01$).

Similar to P_N, P_{Nmax} of the well-watered plants showed significant negative correlations with both LWP_{pre} (r = –0.313) and LWP_{mid} (r = –0.289). In contrast, P_{Nmax} of the stressed plants had significant positive correlations with LWP_{pre} (r = 0.323, $p<0.01$) and LWP_{mid} (r = 0.215, $p<0.05$). The LWP_{pre} and LWP_{mid} had significant negative correlations with dark respiration rates (R_D) and light-compensation point (I_{comp}) of plants grown in both water regimes. The LWP_{pre} had a significant correlation with I_{sat} of stressed plants only (r = 0.289, $p<0.01$), while AQY of only the well-watered plants showed a significant correlation with LWP_{pre} (r = –0.337, $p<0.01$). We noted that LWP_{mid} showed no correlations with I_{sat} and AQY of both well-watered and stressed plants.

Principal component analysis (PCA) and hierarchical clustering analysis (HCA): For the clear visualization of relationships among the six cassava genotypes (RY9, RY72, KU50, CMR38-125-77, CMR35-91-63, and CM523-7) growing in different water regimes (well-watering and drought conditions), principal component analysis (PCA) and heatmap explaining an agglomerative hierarchical clustering analysis (HCA) was carried out; results are illustrated in Fig. 5. The PCA of 13 parameters at four plant ages including LWP at predawn (LWP_{pre}), LWP at midday (LWP_{mid}), % light penetration (LP), leaf gas-exchange parameters at PAR of 1,500 μmol(photon) m^{-2} s^{-1} (P_N, g_s, E, T_{leaf}, and VPD_{leaf}), parameters predicted from light-response curve (P_{Nmax}, R_D, I_{comp}, I_{sat}, and AQY) were generated to determine the parameters that were the major contributors of the variations. PC1 and PC2 explained 50.7% and 15.5% of the overall variations, respectively (Fig. 5*A*). The photosynthesis parameters occurring during the drought stress period (at 4MAP and 5MAP), including P_N, g_s, E, P_{Nmax}, AQY, and plant water status (LWP_{pre} at 4MAP and 5MAP and LWP_{mid} at 4MAP), were negatively related to PC1. On the other hand, T_{leaf}, VPD_{leaf}, and LP at 4MAP and 5MAP were positively related on PC1. We noted that most physiological parameters at 3MAP (before drought) and 6MAP (after rewatering) were associated with PC2. The PCA and HCA analysis of physiological responses separated cassava into two groups: the control and the drought stress (Fig. 5*B*). The intensity of physiological responses of RY9 and CMR38-125-77 were the most similar under both well-watered and drought conditions, being located together in the same subcluster separated from the other four genotypes.

Discussion

Although cassava requires fewer resources compared to other crops and is relatively tolerant to harsh environments, its productivity is diminished when subjected to drought stress, resulting in a significant reduction in photosynthesis performance. Significant correlations between net photosynthetic rates and yield have been reported in cassava germplasm grown under different climatic conditions, *i.e.*, subhumid, seasonally dry, and semi-arid (El-Sharkawy *et al.* 2012a). Therefore, breeding for cassava genotypes better adapted to drought, being able to maintain high photosynthetic activity with a greater ability to recover, is important for an ever-increasing drought-prone area.

After 30 and 60 d without irrigation, cassava cultivars under drought were able to maintain similar levels of midday LWP as those in the well-watered plots (Fig. 1*C*,*D*; Table 1S) despite the significant reduction in the predawn LWP (Fig. 1*A*,*B*; Table 1S), which is an indicator of a reduction in plant water status as affected by low soil water potential (Donovan *et al.* 2001). After 30 d without watering and irrigation, the mean midday LWP of the 4MAP plants was maintained by partially closing the stomata, hence reducing stomatal conductance [from 0.16 to 0.09 mol(H_2O) m^{-2} s^{-1}; 47% reduction] and transpiration rate [from 3.05 to 1.86 mmol(H_2O) m^{-2} s^{-1}; 38% reduction], while still maintained around 80% of net photosynthetic rate at high light intensity of 1,500 μmol(photon) m^{-2} s^{-1} (Table 1). This relatively large reduction in g_s and E and small reduction in P_N resulted in the much greater WUE of the stressed [18.29 μmol(CO_2) mmol(H_2O)$^{-1}$] than that of the well-watered plants [9.73 μmol(CO_2) mmol(H_2O)$^{-1}$]. Under drought, there were significant positive correlations between P_N, g_s, and E with predawn LWP, but these parameters did not correlate with midday LWP, as shown in Table 2. This indicated that cassava plants were negatively affected by low soil water availability in the drought plots and could not fully recover their water status during the night. However, drought-avoidance mechanisms during the day, through stomatal closure and reduced transpiration, effectively prevented the drought plants from leaf dehydration, hence displaying similar LWP_{mid} as the well-watered plants. Previous studies on cassava also reported nonsignificant

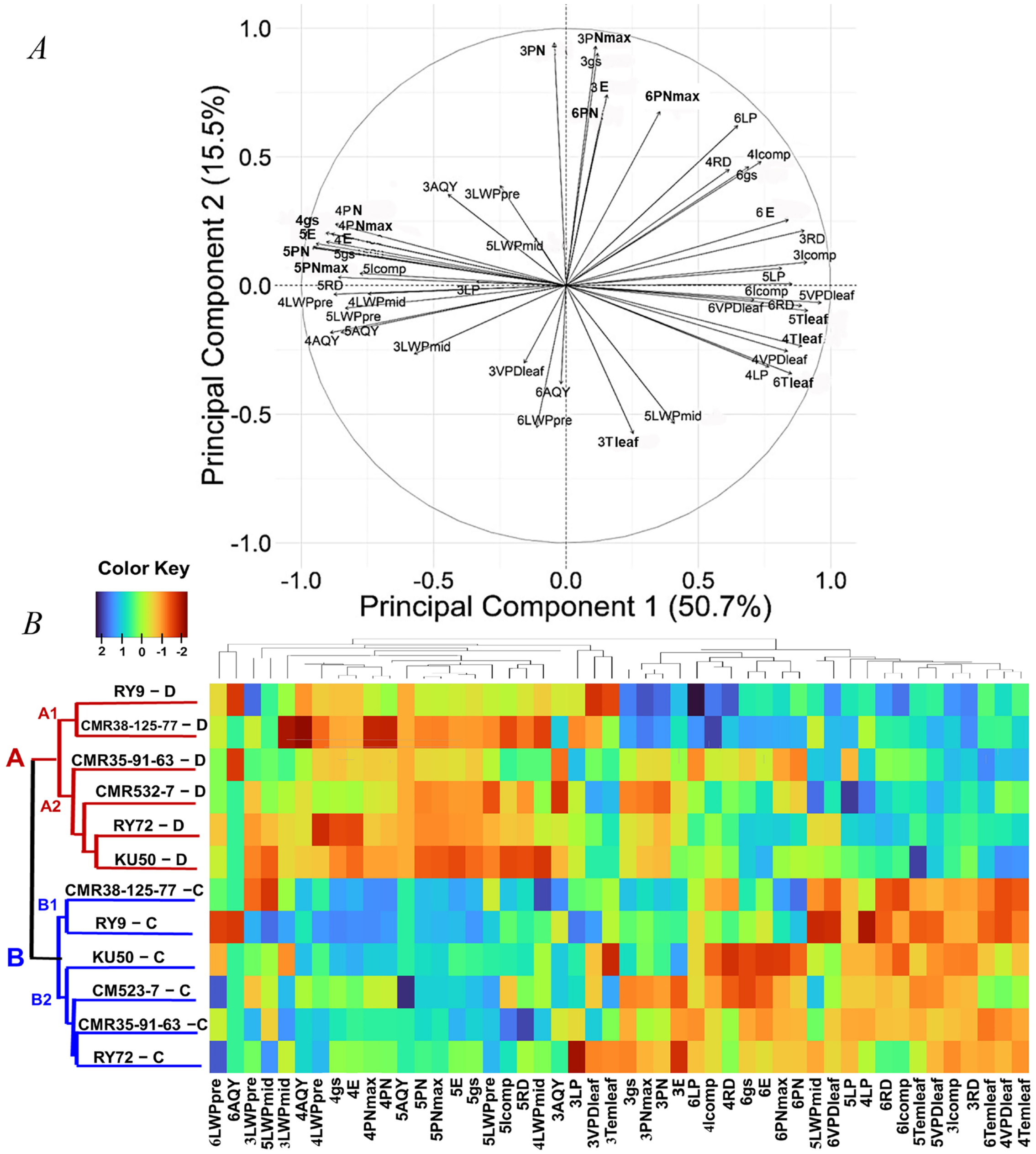

Fig. 5. Principal component analysis (PCA; *A*) and hierarchical clustering analysis (HCA; *B*) explaining the responses of six cassava genotypes, including RY9, RY72, KU50, CMR38-125-77, CMR35-91-63, and CM523-7, growing in different water regimes (well-watering and drought conditions). The PCA indicates variations based on leaf water potential (LWP), light penetration, and photosynthetic parameters recorded in well-watered and early drought-stress conditions at the plant ages of 3, 4, 5, and 6 MAP. For HCA, columns correspond to dependent variables, whereas rows correspond to different treatments (genotypes under different water conditions). Low numerical values are red, while high numerical values are blue (*see* the scale at the right corner of the heat map.

differences in midday LWP under prolonged drought compared with the well-watered conditions (Connor and Palta 1981, El-Sharkawy *et al*. 2012b, Pereira *et al*. 2018).

Cassava exhibits a striking sensitivity to changes in both atmospheric humidity and soil-water deficit (El-Sharkawy *et al*. 2012b). In this study, the significant reduction in g_s and E in the drought plants (Table 1) was due to responses to low humidity as indicated by higher VPD_{air} in the drought plot (Table 4S) associated with higher VPD_{leaf} of the drought plants (2.06 kPa compared with 1.87 kPa in the control plants; Table 2S) and also to limited soil water. Higher VPD_{leaf} in the drought plants was also associated with higher % light penetration (Fig. 2*C*,*D*; Table 2) as affected by reduced canopy size due to reduced leaf number, shortened petiole, and leaf falling (Mahakosee *et al*. 2019, Phosaengsri *et al*. 2019, Santanoo *et al*. 2020, 2024). It was reported in cassava that E increased with VPD_{leaf} in the range of 0.8–1.8 kPa but was sharply reduced when VPD_{leaf} was greater than

1.8–2.0 kPa and stressed plants had consistently lower E and higher WUE than water-stressed plants under the wide range of VPD, highlighting the efficient water-saving mechanism of cassava (El-Sharkawy and Cock 1984). In addition to high WUE, cassava leaves were found to have higher activity of PEP carboxylase (PEPC) compared to typical C_3 species, which enabled the leaf to refix respiratory CO_2, hence boosting the photosynthetic potential (El-Sharkawy *et al.* 2012b). Recently, the crucial role of PEPC in concentrating intercellular CO_2 was demonstrated by Punyasu *et al.* (2023) by using constraint-based metabolic modeling *via* flux balance analysis in cassava leaves (MeCBM). Their model predicted that when CO_2 from the atmosphere is limited by stomatal closure, the highly active PEPC assimilates intracellular CO_2 (from dark and photorespiration) into C_4 acids, which later release CO_2 through oxidative decarboxylation for fixing by Rubisco. Moreover, deep rooting characteristics of cassava under prolonged water stress enabled it to extract more water from deeper soil layers of 160–200 mm as water stress progressed over time (El-Sharkawy *et al.* 1992). Survival and maintenance of the plant water status of cassava during the dry season was also attributed to reduced whole plant transpiration due to leaf shedding and reduced leaf size (Alves and Setter 2004, Koundinya *et al.* 2024). According to De Souza *et al.* (2020), for cassava exposed to naturally fluctuating light intensity inside the canopy, it was also advised to consider photosynthesis performance not only at steady-state conditions but also during shade-to-sun transition. The cultivar that had the faster rate of stomatal opening during transition from low to high light, and also a faster rate of closing during high to low light transition, showed much greater cumulative carbon fixation while maintaining the WUE.

With prolonged water stress after 60 d of absence of irrigation and rainfall, the soil moisture level was reduced to 5.1% compared with 10.6% in the well-watered fields. The stressed 5MAP plants had significantly lower predawn LWP than that of the control, but still maintained similar midday LWP (Fig. 1, Table 1S). Although the mean g_s [0.12 mol(H_2O) m^{-2} s^{-1}] of the 5MAP plants was higher than that at 4MAP [0.09 mol(H_2O) m^{-2} s^{-1}], the leaves performed significantly lower P_N at 16.34 µmol(CO_2) m^{-2} s^{-1} compared with 21.13 µmol(CO_2) m^{-2} s^{-1} at 4MAP. This indicated that factors other than leaf water status and stomatal limitation of CO_2 uptake were affecting the photosynthesis process at this stage. We noted that at 5MAP, the mean leaf temperature of the stressed plants was significantly higher than that of the controls (Table 1), and leaf temperature was negatively correlated (–0.425, $p<0.01$) with P_N (Table 2). An increase in leaf temperature from 25 to 35°C led to an increasing trend in photorespiration and a declining trend in the activity of Calvin cycle enzymes, such as Rubisco and fructose 1,6-bisphosphatase (FBPase), resulting in a reduction in net CO_2 fixation (Kobza and Edwards 1987). At highly negative soil water tension of –70 kPa for a long period of 90 d, Pereira *et al.* (2018) also reported a nonsignificant reduction in midday LWP, indicating an efficient preservation of plant water status, but observed a significant reduction in the effective quantum efficiency of PSII and electron transport rate. Furthermore, prolonged water stress caused a significant increase in reactive oxygen species (ROS) such as H_2O_2 in cassava leaves, leading to the destruction of macromolecules as evidenced by a significant increase in malondialdehyde (Shan *et al.* 2018, Pereira *et al.* 2022). Therefore, under prolonged water stress, the photosynthesis efficiency of cassava was affected by both stomatal and nonstomatal limitations. Furthermore, the ability of cassava to resist drought not only depends on water-saving mechanisms during drought episodes, but also on its ability to quickly recover upon rewatering. As shown in Fig. 1 and Table 1, the 6MAP stressed plants (after receiving irrigation) recovered the leaf water status as well as all leaf gas-exchange parameters to the same levels as those of the well-watered plants. Moreover, photosynthesis performance of both new and old leaves increased to the same or even higher level than those of the well-watered plants (El-Sharkawy 2007, Santanoo *et al.* 2024).

The light-response curve (P_N/I) is an important tool for describing the response of the P_N to PAR, predicting several photosynthetic parameters (P_{Nmax}, I_{sat}, I_{comp}, R_D, and AQY), and evaluating the photosynthetic efficiency of plants (Ma *et al.* 2021). Constructing a P_N/I curve was helpful for the prediction of photosynthesis performance of cassava at different developmental stages subjected to different water conditions (Vongcharoen *et al.* 2018). Similar to the change in mean P_N at PAR of 1,500 µmol(photon) m^{-2} s^{-1} (Table 1), the mean light-saturated photosynthetic rate (P_{Nmax}) was significantly ($p<0.01$) reduced after the plants were subjected to 30 and 60 d without watering (Fig. 4*A*,*B*). The differences between cultivars followed the same pattern as those of the P_N at PAR of 1,500 µmol(photon) m^{-2} s^{-1} (Table 1) with RY9 achieving the highest P_{Nmax} (Table 2S) and P_N at PAR of 1,500 µmol(photon) m^{-2} s^{-1} (Table 1), while CMR38-125-77 and KU50 displayed the lowest values of both parameters at 30 and 60 d, respectively. The ability to harvest light energy was stable showing light-saturation point (I_{sat}) at 1,950 µmol(photon) m^{-2} s^{-1} in the well-watered cassava at the age of 3 to 5 months, with no differences between cultivars (Fig. 4*C*). However, in the drought conditions, I_{sat} tended to reduce with increasing intensity of stress (Fig. 4*D*) and clear differences between cultivars were apparent in the stressed 5MAP plants with CMR35-91-63, RY9, and CM523-7 showing significantly higher I_{sat} [1,894; 1,793, and 1,735 µmol(photon) m^{-2} s^{-1}, respectively] than that of KU50 and CMR38-125-77 [1,450 µmol(photon) m^{-2} s^{-1}] (Table 3S, *supplement*).

The light-compensation point (I_{comp}), the light intensity at which CO_2 uptake for photosynthesis balances with CO_2 release from dark respiration (R_D), is highly positively correlated with R_D (Table 2). Although R_D and I_{comp} under stress at any plant age were not significantly different from those in the control conditions (Fig. 4*G*,*H*), they were significantly negatively correlated with LWP but positively correlated with light penetration (% LP) (Table 2). This indicated that drought could lead to lower LWP which consequently resulted in the inhibition of leaf growth and accelerated leaf falling, hence higher % LP and less dense canopy (Fig. 1). Greater light penetration in the drought-stressed plants led the cassava leaves to acclimate to higher light intensity, hence stressed plants tended to have higher mean I_{comp} and R_D than the control (Fig. 4; Tables 2S, 3S). Under water stress, dark respiration has been reported to decrease, to be almost unaffected, or to increase depending on several factors, including leaf temperature, substrate availability, efficiency of respiratory pathways, and use of respiratory products (Wright *et al.* 2006, Tombesi *et al.* 2022). Concerning the relationship between dark respiration and photosynthesis, we noted in this study that these parameters were significantly ($p<0.01$) positively correlated under well-watered conditions (Table 2). It was proposed that the optimal activity of Rubisco and other Calvin cycle enzymes depended on the ATP energy supply by daytime respiration of mature leaves to support protein turnover (Wang *et al.* 2020). Furthermore, high net photosynthetic rates resulted in greater starch accumulation and greater rates of starch degradation and sucrose export at night, which required higher respiratory ATP demand at night (Turnbull *et al.* 2002, Ren *et al.* 2024).

The apparent quantum yield (AQY) represents the maximum light-use efficiency, which is indicated by the initial slope of the light-response curve. Higher AQY is related to increased photosynthesis capacity, growth, and biomass accumulation (Sekhar *et al.* 2015). In this study, the mean AQY of six cassava genotypes after 30 and 60 d of drought stress was 0.043 and 0.040 µmol(CO_2) µmol(photon)$^{-1}$, respectively, which were significantly ($p<0.05$) lower than the efficiency in the well-watered condition [0.051 and 0.054 µmol(CO_2) µmol(photon)$^{-1}$ for 30 and 60 d after stress, respectively] (Table 3S). The AQY of cassava under non-stress conditions in this study conformed with the average value of 0.05 µmol(CO_2) µmol(photon)$^{-1}$ for C_3 plants measured in various ecophysiological studies (Singsaas *et al.* 2001). Vongcharoen *et al.* (2018) found that cassava cv. RY9 at the age of 3 and 6 months growing in rainfed and irrigated fields had AQY ranging from 0.056 to 0.042 µmol(CO_2) µmol(photon)$^{-1}$, which were not significantly different among water conditions, age, and seasons. The meta-analysis of AQY estimated from light-response curves of plants growing in 90 sites in various terrestrial ecosystems over 10-year observations concluded that water availability (soil water content and atmospheric VPD) was the main driver for the variations in AQY (Yu *et al.* 2025). The significant reduction in AQY under stress was caused mainly by a huge difference in soil moisture content between the well-watered and drought plots, but not by the atmospheric VPD, which was similar among the two plots (Table 4S). Compared with other parameters estimated from P_N/I curves, the AQY is the most informative parameter expressing the significant differences between genotypes (Table 3S). After 30 d of drought stress, CMR35-91-63 displayed the highest AQY of 0.047 µmol(CO_2) µmol(photon)$^{-1}$, which was significantly higher than that of CMR38-125-77 [0.036 µmol(CO_2) µmol(photon)$^{-1}$]. When drought was extended to 60 d, RY9 and CMR35-91-63 showed the highest AQY of 0.045 µmol(CO_2) µmol(photon)$^{-1}$, which was significantly higher than that of KU50 [0.035 µmol(CO_2) µmol(photon)$^{-1}$]. The variation in AQY or light-conversion efficiency is one of the major factors determining the gross primary production of plants in the ecosystems (Garbulsky *et al.* 2010) and the yield potential of crop plants (De Souza *et al.* 2017). Therefore, AQY estimated from the P_N/I curve could be employed as one of the criteria for selecting cassava for use as parents for breeding high photosynthetic potential under drought stress.

PCA and HCA analysis revealed that important parameters which differentiated the well-watered from the drought group included those that were reduced in response to drought at 4MAP and 5MAP including LWP_{pre}, LWP_{mid} (at 4MAP), photosynthetic parameters (P_N, g_s, E, P_{Nmax}, and AQY), I_{comp} and R_D (at 5MAP), and those that increased during drought including T_{leaf}, VPD_{leaf}, and LP (Fig. 5). According to Fig. 5*B*, under drought (D), RY9 was the most distinguishable from the others by showing high (less negative, represented by pale green) numerical values in $4P_N$ (P_N at 4MAP), $5LWP_{pre}$ (predawn LWP at 5MAP), $5LWP_{mid}$ (midday LWP at 5MAP), $5P_N$ (P_N at 5MAP), $5P_{Nmax}$ (P_{Nmax} at 5MAP), and $5E$ (E at 5MAP). In addition, compared to the others, RY9 had high numerical values (pale blue to dark blue) of photosynthetic parameters at 3MAP, including $3P_{Nmax}$, $3P_N$, $3g_s$, and $3E$, indicating that RY9 had intrinsically high photosynthetic potential. CMR38-125-77 was distinguishable from the others by showing high recovery ability as indicated by its high numerical values (blue color) in photosynthetic parameters at 6MAP, *i.e.*, $6P_N$, $6P_{Nmax}$, $6g_s$, and $6E$. Therefore, RY9 possesses high photosynthetic potential during drought stress, while CMR38-125-77 has a greater ability to recover upon rewatering.

Conclusion: Although plant water status of cassava was negatively affected by drought as indicated by the significantly reduced predawn LWP after 30–60 d of water shortage, the plants avoided drought stress during daytime by the highly efficient stomatal regulation to protect the stressed plants from dehydration, thereby maintaining similar LWP as the irrigated plants at midday. The P_N, g_s, and E were dramatically reduced during the stress periods. Upon 30 d of rewatering, plant water status and all photosynthetic parameters efficiently recovered. In addition to P_N, the parameters calculated from the P_N/I curves, including I_{sat} and AQY, could be useful criteria for identifying genotypes with better drought tolerance. The PCA analysis based on LWP, LP, leaf gas exchange, and photosynthetic parameters predicted from P_N/I curves separated the cultivars RY9 and CMR-38-125-77 from the other genotypes because their physiological parameters were less affected during drought and better recovered after rewatering.

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