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Growth, Gas Exchange, Chlorophyll a Fluorescence, Biomass Accumulation and Partitioning in Droughted and Irrigated Plants of Two Enset (*Ensete ventricosum* Welw. Cheesman) Clones

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Abstract: Enset (*Ensete ventricosum*) plants grown in the middle and low altitudes are experiencing different degrees and length of summer drought every year. Information is lacking on plant responses to drought stress, underlying mechanisms of response and effect of drought on the growth and yield of enset. The effect of induced drought/irrigation on growth parameters, gas exchange and biomass accumulation and partitioning of enset clones was studied in the field at Guebre, Southern Ethiopia. One year old plants of two enset clones were either irrigated or droughted by with holding water for 90 days. Prolonged drought markedly and significantly reduced growth parameters of both enset clones. Drought stress significantly reduced specific leaf area and net assimilation rate and these reductions showed significant positive correlations with relative growth rate. Stomatal conductance, net photosynthesis rate and transpiration declined considerably after 60 and 90 days of drought. Despite the reduction in stomatal conductance, leaf water status showed little change. Quantum yield of PSII photochemistry showed a reversible diurnal depression which was accompanied by a marked increase in non-photochemical fluorescence quenching. Proportionally, droughted plants accumulated significantly more dry matter to belowground parts and drought appeared to increase harvest index of the corm. The enset clone *Ameratye* produced a significantly higher total dry matter than *Yesherakinkye* both under drought and/or irrigation. Both stomatal and non-stomatal factors might have contributed for the observed decline in carbon dioxide uptake rates of droughted plants. Present findings indicated that seasonal dry periods could considerably alter enset physiology and reduce growth and yield. Moreover, harvest index of the corm can be used as a selection criterion in screening enset clones suitable for drought prone areas.

Key words: Enset, clones, drought, growth, gas exchange, quantum yield of PSII photochemistry

INTRODUCTION

Plant responses to drought is influenced by different factors including the duration and magnitude of stress (Munne-Bosch and Algere, 2004), previous exposure to drought and developmental phase of the plant (Kozlowski and Pallardy, 2001). Under field conditions, water stress develops progressively and gradually, eliciting morphological, physiological and biochemical responses. These responses can be synergistically or antagonistically modified by the superimposition of other stresses (Chaves *et al*., 2002). Stomatal closure is among the earliest responses to soil drying and it is generally assumed to be the main causes of drought-induced decreases in photosynthesis (Cornic and Massacci, 1996). When leaves have to withstand drought, dissipation of excess excitation energy at the chloroplast level is often accompanied by down regulation of photochemistry and in the longer-term, of photosynthetic capacity and growth (Chaves *et al*., 2002). Responses to drought involve morphological and/or growth modifications such as leaf area reduction (Blum, 1996), altered biomass partitioning often involving a change in root-shoot dry mass ratio (Turner, 1997) and reduced growth rate and yield (Kumar and Singh, 1998).

Ensete ventricosum Welw. Cheesman, is a monocarpic, perennial herb domesticated only in Ethiopia mainly for its starchy food processed from the pseudostem and the underground corm and serves as a staple/co-staple food source for an estimated 7-10 million

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people (Tsegaye, 2007). Enset agriculture is a rain-fed agriculture and involves transplanting (every year or two) of different developmental stages in different plots. Enset cultivation is common in the middle and high altitudes that receive an annual rainfall ranging from 1100 to 1500 mm (Tsegaye, 2002). Owing to increasing population pressure and land shortage, however, enset farming is now expanding to moisture stressed lowlands (Kena, 1996). Consequently, enset plants in the middle and low altitudes are experiencing differing degrees and length of summer drought every year. The effect of drought would be detrimental particularly for young plants at early transplanting stage. Observational reports claim that enset withstands an extended dry period (> 3 months) (Belihu, 1996) and that some clones perform relatively better under drought than others.

Despite its role in providing food for a sizable population and its acclaimed potential in alleviating food security in Ethiopia, research information on enset is generally scarce. Notable works are limited to farming system description (Kippie, 2001) and/or enset clonal diversity assessment (Tsegaye, 2002) and optimization of production (Tsegaye, 2007). Information on crop ecology and stress physiology is virtually absent and remained a crucial gap and nothing is known about enset plant water relations. Investigation into the effect of prolonged water stress in the field and the performance of enset clones provide insights into the morphological, growth and physiological responses of the plant and the mechanisms underlying these responses. Knowledge of drought resistance mechanisms is crucial in identification of plant traits and the use of such traits for selection. Therefore, the objectives of this study were to investigate the effect of prolonged drought on the growth, gas exchange characteristics, biomass accumulation and partitioning of field grown plants of two enset clones.

MATERIALS AND METHODS

Site description: The field experiment was conducted at Guebre, Gurage Zone, in the Southern Nations Nationalities Regional State, Ethiopia ca. 169 km south-west of Addis Ababa. The study site is located 08°11.4N N and 37°48.2N E and has an elevation range of 1750-1880 m a.s.l. It has a mean monthly temperature of 19.9°C and a mean annual rainfall of ca. 1150 mm. Rainfall distribution has a bimodal character with a long rainy season extending between June and September and a short rainy season between January and March. The soil is reddish brown in color, has clay-loamy texture and pH (H_2O) of 6.8 (0-30 cm depth).

Clone selection and sucker propagation: Two enset clones locally known as *Ameratye* (Am) and *Yesherakinkye* (Yk) were selected based on farmers, preference and farmers, response to a questionnaire on the ranking of supposed drought tolerance of the available enset clones. In January 2004, suckers of each enset clone were produced through vegetative propagation (Kippie, 2001) from immature enset corms which were pre-treated and buried for 1 year.

Plot establishment and growth conditions: Equal sized suckers were separated from the corm in January 2005 and were transplanted on a pre-prepared plot (384 m^2) with a spacing of 1.5×1.5 m. Suckers were watered twice a week during the dry period while dried manure (1 kg $plant^{-1}$) was applied every 2 months and plants were allowed to grow for about a year. On February 2006, plants were watered adequately to keep the soil moisture at field capacity and watering was interrupted a day before drought induction/irrigation. A stationary rain-out plastic shelter was constructed bordering the edges of the plot and covering the sides and the top with transparent plastic shutters.

Plant selection and experimental design: Before drought induction/irrigation, plant girth and height was recorded for all plants. Above ground parameters were measured directly and corm weight was estimated from pseudostem girth (R^2 = 0.90-0.96). Accordingly, 56-58 standing plants/clone of comparable size were selected and labeled. Following a randomized block design, the selected plants from each clone were then systematically divided between upper (droughted groups) and lower (irrigated groups) compartments separated with a corridor (3 m). Since the plot was slightly sloppy, all plants in the irrigated treatments were pre-assigned to the lower compartment so that seepage of water between treatment groups could be prevented. There were four treatment groups (2 clones×2 watering regimes) labeled as AmDR (droughted *Ameratye*), YkDR (droughted *Yesherakinkye*), AmIR (irrigated *Ameratye*) and YkIR (irrigated *Yesherakinkye*). Upon drought induction, plants in the irrigated treatment received 20 L water every 3rd day keeping the soil water content at field capacity through out the experiment. Plants in the droughted treatment received no water.

Morphological and growth measurements: Plant height, green leaf number, pseudostem girth and leaf area development were monitored on 10 plants at the beginning (a day before drought induction) and on 30, 60 and 90 days after drought induction/irrigation. Leaf Area (LA) was calculated by multiplying the leaf length, l (from the base of the petiole to the tip of the lamina) by the width, w (the widest point) and a form factor, 0.83 and dividing the product by the number of leaves per individual plant (P_n) as used for banana (Turner, 1972). Thus,

$$L_A = \sum (0.83 \times l \times w) / P_n \quad (1)$$

Physiological measurements: The daily course of gas exchange and chlorophyll a fluorescence measurements were recorded between the 60th and 63rd day and between the 90th and 93rd day after drought induction/irrigation. Measurements were made every 2 h (7:00 am to 5:00 pm) on fully expanded 2nd and 3rd order pair of leaves of five plants in each treatment. Net photosynthesis (P_n), stomatal conductance (g), transpiration (E), internal carbon dioxide (CO_2) concentration (C_i) and leaf-to-air vapor pressure deficit (Vpd) were determined using an open system Li-Cor 6400 portable photosynthetic system (L_i-COR, Lincoln, USA) under ambient irradiance and CO_2 levels. A portable pulse-amplitude-modulated fluorimeter (Mini-PAM, Heinz Waltz, Effeltrich, Germany) described in Fetene *et al.* (1997) was used to measure minimum fluorescence (F_o) and maximum fluorescence (Fm) on dark adapted leaves at predawn (5:00-5:30 am) and steady state (F) and maximum fluorescence (FNm) on light adapted leaves. Using the measured parameters, the daily course of the quantum yield of photosystem II (PSII) photochemistry (Φ_{PSII}) in the light was calculated according to Genty *et al.* (1989) where:

$$\Phi_{PSII} = (F'm \ F)/F'm = F'v/F'm \quad (2)$$

and non-photochemical fluorescence quenching (NPQ) according to Bilger and BjÖrkman (1990) where:

$$(NPQ) = F'm / Fm - 1 \quad (3)$$

Biomass estimation: At the beginning of the experiment and 60 and 90 days after drought induction/irrigation, six sample plants per treatment group were labeled. These plants were uprooted and belowground biomass was excavated. For determination of Specific Leaf Area (SLA), leaves were destructively sampled and leaf area was measured with a portable leaf area meter (Delta-T Devices, UK). Leaf pieces were then oven dried and dry weight was recorded. Sample plants were then assorted into leaves (including the petiole), pseudostem, corm and roots (coarse and fine roots). Fresh weight of plant parts was recorded and samples of plant parts were dried at 80°C for 48 h to constant weight. The data obtained from the above destructive sampling were used to compute biomass accumulation and partitioning, Leaf Mass Ratio (LMR), Leaf Area Ratio (LAR), Net Assimilation Rate (NAR) and Relative Growth Rate (RGR) as follows:

$$SLA\ (m^2\ kg^{-1}) = \frac{\text{Leaf area}}{\text{Total leaf dry mass}} \quad (4)$$

$$LMR\ (g\ g^{-1}) = \frac{\text{Leaf dry weight}}{\text{Total plant dry weight}} \quad (5)$$

$$LAR\ (m^2\ kg^{-1}) = \frac{\text{Leaf area}}{\text{Total plant dry weight}} \quad (6)$$

$$NAR\ (g\ m^{-2}\ day^{-1}) = \frac{(W_2 - W_1)\times(\ln L.A._2 - \ln L.A._1)}{(t_2 - t_1)\times(L.A._2 - L.A._1)} \quad (7)$$

s

$$RGR\ (mg\ g^{-1}\ day^{-1}) = \frac{\ln W_2 - \ln W_1}{t_2 - t_1} \quad (8)$$

where, W_2 and W_1 are plant dry weights and $L.A_1$ and $L.A_2$ are plant leaf areas of two consecutive harvests (t_2) and (t_1) of the time interval t_1-t_2.

Statistical analysis: Data were subjected to analysis of variance (ANOVA) and regression analysis using SPSS version 12.1 for Windows statistical software to test significant differences between treatment means and correlations. Through out the text (graphs and tables), differences between treatment means is considered significant, when $p \leq 0.05$.

RESULTS

Morphological and growth parameters: Sampling made prior to drought induction showed a statistically significant difference in plant height and leaf area (Table 1) between plants assigned to droughted and

Table 1: Changes in green leaf number, leaf area, pseudostem girth and plant height with time in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am)

	Days after drought induction/irrigation			
Treatments	0	30	60	90
Green leaf No.				
YkDR	4.50±0.30^{a}	7.40±0.60^{ac}	8.60±0.30^{a}	7.20±0.80^{a}
YkIR	4.50±0.50^{a}	8.00±0.50^{c}	11.30±0.30^{b}	13.20±0.70^{b}
AmDR	4.40±0.50^{a}	7.30±0.50^{a}	8.00±0.30^{a}	6.90±0.50^{a}
AmIR	4.60±0.50^{a}	8.80±0.60^{b}	11.80±0.20^{b}	13.40±0.30^{b}
Leaf area (m^2)				
YkDR	0.18±0.01^{a}	0.19±0.02^{c}	0.24±0.02^{a}	0.22±0.02^{a}
YkIR	0.25±0.02^{b}	0.25±0.02^{ac}	0.42±0.03^{b}	0.66±0.05^{b}
AmDR	0.23±0.01^{b}	0.31±0.03^{ab}	0.30±0.03^{a}	0.30±0.03^{a}
AmIR	0.26±0.01^{b}	0.34±0.03^{a}	0.49±0.03^{b}	0.58±0.03^{b}
Pseudostem girth (m)				
YkDR	0.47±0.03^{a}	0.61±0.02^{a}	0.52±0.02^{a}	0.52±0.02^{a}
YkIR	0.60±0.02^{a}	0.66±0.02^{a}	0.67±0.03^{b}	0.84±0.04^{b}
AmDR	0.49±0.02^{a}	0.60±0.02^{a}	0.47±0.03^{a}	0.51±0.03^{a}
AmIR	0.58±0.02^{a}	0.66±0.02^{a}	0.67±0.02^{b}	0.71±0.03^{b}
Plant height (m)				
YkDR	1.00±0.04^{a}	1.12±0.09^{c}	1.43±0.07^{a}	1.56±0.09^{a}
YkIR	1.17±0.05^{b}	1.31±0.09^{b}	1.89±0.08^{b}	2.78±0.15^{b}
AmDR	1.19±0.04^{b}	1.32±0.09^{b}	1.37±0.08^{a}	2.14±0.09^{a}
AmIR	1.27±0.03^{b}	1.51±0.10^{a}	2.14±0.08^{c}	2.65±0.08^{b}

Values are mean±SE n = 5. Under each growth parameter, values in the same column followed by same letter do not differ significantly

irrigated groups of the ensete clone *Yesherakinkye*. Irrigated plants of both clones had higher mean values than droughted counterparts for all the parameters after 30 days of treatment. However, except for green leaf number in the enset clone *Ameratye* and plant height in the clone *Yesherakinkye*, none of these differences were significant. On the other hand, there was a significant treatment effect for all the parameters after 60 days where irrigated plants of both clones had mean values which were 24-36% (plant height), 24-32% (green leaf number), 22-29% (pseudostem girth) and 39-43% (leaf area) higher and above that of droughted counterparts. At the end of the experiment, plants from the irrigated treatment of both clones had significantly higher green leaf number (45-49%), plant height (30-44%), pseudostem girth (28-38%) and leaf area (48-67%) higher and above that of droughted plants.

Biomass accumulation and partitioning: Treatment effects were significant for all the parameters except corm dry matter (Table 2) after 60 days. Irrespective of clone type, irrigated plants accumulated 29-45% significantly higher total dry matter than plants in the droughted treatment (data not shown). At the end of the experiment, the amount of total dry matter in irrigated plants was 63-69% higher and above that of droughted plants. With respect to dry matter partitioning, droughted plants of both clones allocated a significantly higher proportion of the total dry matter to belowground parts, which amounts to 27-29% (60 days) and 33-41% (90 days) more than plants in the irrigated treatment. Moreover, this allocation pattern increased the harvest index (HI) with respect to the corm where droughted plants had HI which was 36-45% higher and above irrigated counterparts. On the other hand, the enset clone *Ameratye* produced a significantly higher total biomass both under drought and irrigated conditions. However, despite the differences in mean performance, biomass partitioning did not differ significantly between the two clones.

Growth rate: After 60 days of irrigation, irrigated plants of the clone *Ameratye* had a significantly higher Specific Leaf Area (SLA) and Leaf Area Ratio (LAR) than droughted plants but there was only a non-significant increase in Leaf Mass Ratio (LMR) (Fig. 1). For the enset clone *Yesherakinkye*, LMR and LAR differ significantly between droughted and irrigated plants. At the end of the experiment, SLA, LAR and LMR were generally significantly higher in the irrigated treatment than in droughted treatment (Fig. 1). Moreover, the variation in RGR between irrigated and droughted groups was significant on both sampling occasions. There was a significant positive correlation between NAR and RGR (R^2 = 0.62 -0.93) and also between SLA and RGR (R^2 = 0.5-0.52) for all treatment groups (Table 3).

Physiological parameters: Leaf water status (estimated from % RWC) (Table 4) was little affected by imposed drought. After 90 days of drought/irrigation, there was a significant difference in predawn RWC among treatments but there was no significant difference among treatments in the midday RWC. Moreover, the difference between predawn and midday RWC was smaller for droughted than irrigated plants. Despite this little change in leaf water status, there were significant treatment effects on net photosynthesis and stomatal conductance (Fig. 2).

Table 2: Changes in dry matter accumulated in different plant parts; leaf, pseudostem, corm, root and dry matter partitioned to aboveground and belowground parts of droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am)

	Days after drought induction/irrigation					
	Leaf dry weight (kg)			Pseudostem dry weight (kg)		
Treatments	0	60	90	0	60	90
YkDR	0.04±0.005^a	0.19±0.010^a	0.24±0.01^a	0.19±0.01^a	0.20±0.010^a	0.24±0.02^b
YkIR	0.04±0.003^a	0.39±0.020^b	1.15±0.09^b	0.20±0.03^a	0.26±0.020^b	0.82±0.13^c
AmDR	0.04±0.005^a	0.18±0.005^a	0.29±0.03^a	0.18±0.02^a	0.19±0.003^a	0.33±0.03^a
AmIR	0.06±0.008^a	0.43±0.020^b	1.16±0.05^b	0.21±0.01^a	0.42±0.040^c	0.87±0.02^c
	Corm dry weight (kg)			Root dry weight (kg)		
YkDR	0.09±0.003^b	0.20±0.020^a	0.25±0.009^a	0.03±0.003^a	0.04±0.004^a	0.04±0.001^a
YkIR	0.07±0.004^b	0.20±0.020^a	0.47±0.040^{bc}	0.04±0.002^a	0.05±0.004^c	0.10±0.005^b
AmDR	0.07±0.004^b	0.19±0.004^a	0.37±0.040^b	0.03±0.002^a	0.03±0.002^a	0.05±0.004^a
AmIR	0.11±0.010^a	0.25±0.030^a	0.63±0.030^d	0.03±0.001^a	0.07±0.005^b	0.11±0.009^b
	Above-ground dry matter (%)			Below-ground dry matter (%)		
YkDR	67.2±1.9^a	61.8±1.0^a	61.2±2.0^a	31.8±1.9^a	38.2±1.0^b	38.7±2.0^b
YkIR	66.8±4.6^a	72.6±1.9^b	77.3±1.7^b	33.2±4.6^a	27.4±1.9^a	22.7±1.7^a
AmDR	68.6±2.1^a	62.7±0.4^a	59.7±1.9^a	31.4±2.1^a	37.2±0.4^b	40.3±1.9^b
AmIR	65.5±1.6^a	73.2±1.9^b	73.6±0.9^b	34.5±1.6^a	26.7±1.9^a	26.9±0.9^a

Values are mean±SE n = 5. Under each growth parameter, values in the same column followed by same letter do not differ significantly

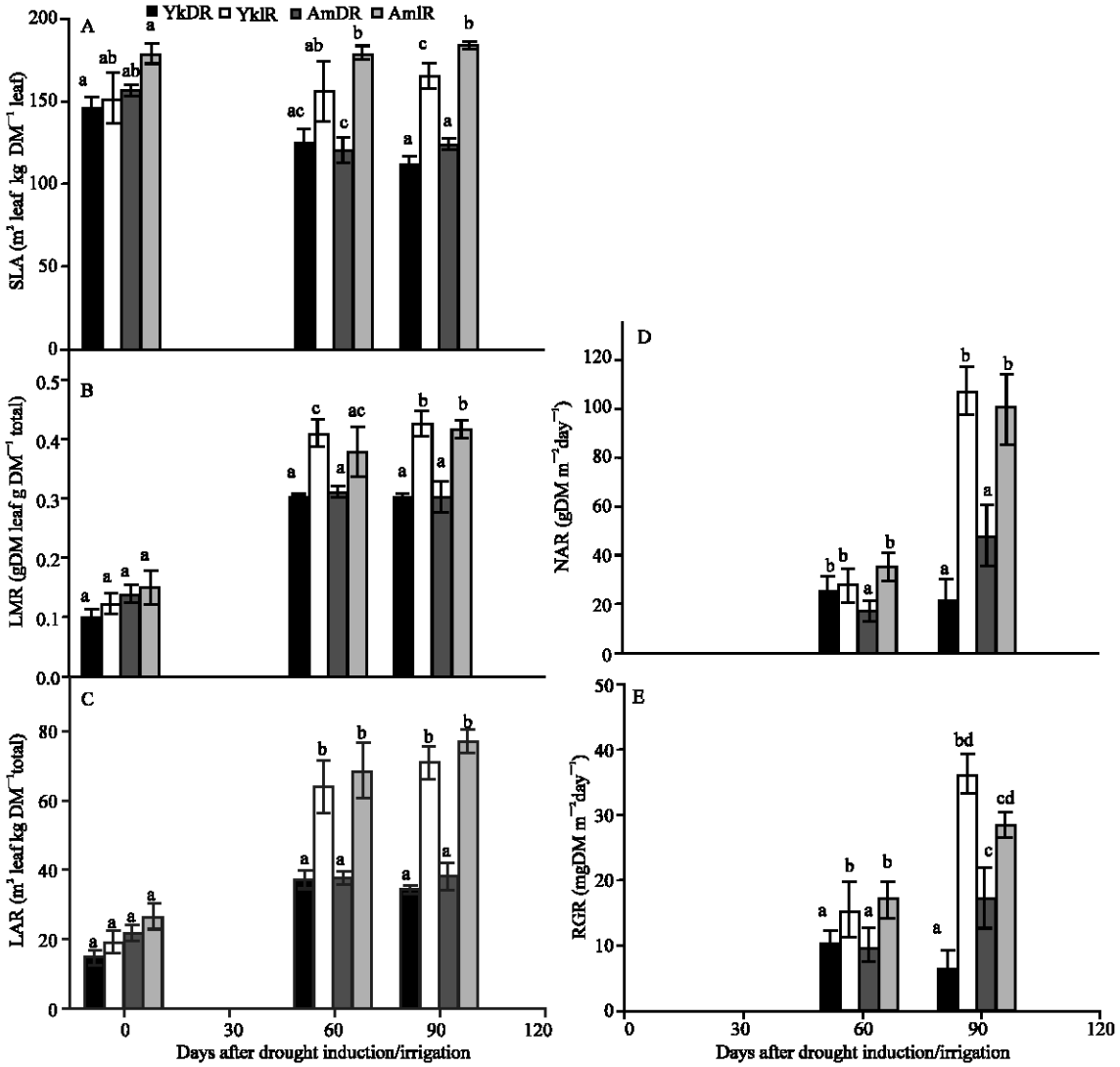

Fig. 1: Changes in SLA (A), LMR (B), LAR (C), NAR (D) and RGR (E) over time in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am). Bars represent mean and SE n = 4. Statistical comparisons consider differences among treatments within each sampling period. Bars followed by same letter(s) do not differ significantly

Table 3: Diurnal course of non-photochemical quenching (NPQ) in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am) after 60 and 90 days of drought induction/irrigation. Values are means, n = 5

	Day time (h)					
Treatments	7:00 am	9:00 am	11:00 am	13:00 am	15:00 am	17:00 am
A						
YkDR	0.37	1.81	3.42	7.80	1.70	0.88
YkIR	0.37	1.12	2.62	2.44	1.24	0.95
AmDR	0.38	2.50	6.14	6.70	1.80	1.07
AmIR	0.30	1.39	2.17	3.44	1.59	0.96
B						
YkDR	0.28	1.67	3.10	3.70	1.02	0.72
YkIR	0.22	1.29	1.75	2.42	1.19	0.91
AmDR	0.44	3.08	5.54	5.50	3.95	1.80
AmIR	0.17	0.74	1.86	2.23	0.69	0.73

A: 60 days after drought induction/irrigation; B: 90 days after drought induction/irrigation

Table 4: Pre-dawn and mid-day leaf relative water content (%RWC) in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am) after 60 and 90 days of drought/irrigation

	RWC after 60 days (%)		RWC after 90 days (%)	
Treatments	Predawn	Midday	Predawn	Midday
YkDR	89.08±1.28^{a}	85.70±0.94^{a}	93.06±1.11^{a}	92.80±0.62^{a}
YkIR	93.12±1.39^{b}	90.36±1.08^{bc}	95.20±0.55^{b}	93.13±0.55^{a}
AmDR	93.93±0.76^{b}	91.90±1.15^{ac}	94.33±0.63^{a}	94.13±0.50^{a}
AmIR	96.32±0.86^{b}	90.73±2.87^{bc}	96.00±0.63^{b}	92.70±0.88^{a}

Values are mean and SE n = 5. Values in the same column followed by same letter do not differ significantly

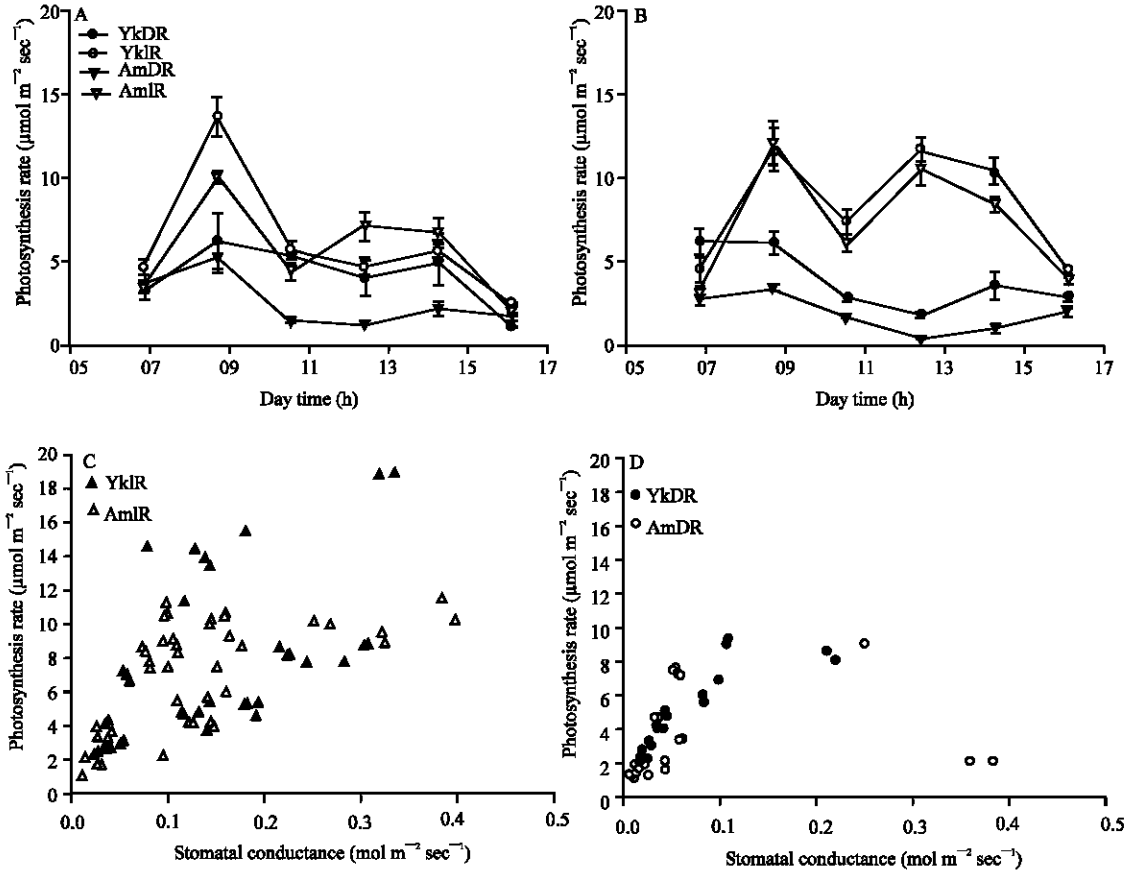

Fig. 2: Diurnal course of net photosynthesis rate in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am) after 60 (A) and 90 (B) days of drought/irrigation and the relationship between net photosynthesis and stomatal conductance (C and D)

For both sampling occasions, net photosynthesis in droughted plants peaked at the early hours of the day and showed a midday depression. Droughted plants generally had a lower stomatal conductance and the correlation between stomatal conductance and photosynthesis was weak though significant (R^2 = 0.25) for the enset clone *Ameratye* but strong for the enset clone *Yesherakinkye* (R^2 = 0.89). Internal CO_2 concentration (C_i) in droughted plants remained lower than irrigated plants for most of the drought course until late in the drought course (90 days) where droughted *Ameratye* plants had a higher C_i than the irrigated counterparts for most of the daily course (data not shown).

The net photosynthesis rate in irrigated plants was 2-3 folds higher than that of droughted plants. The mean differences in net photosynthesis rate recorded around mid-morning and mid-day hours were significant and these periods are characterized by high air temperature and leaf-to-air vapor pressure deficit (Vpd). For a range of Photosynthetically Active Radiation (PAR)

Table 5: The daily course of quantum yield of PSII (F'v/Fm') of light adapted leaves of droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am) after 60 and 90 days of drought/irrigation

	Day time (h)					
Treatments	7:00 am	9:00 am	11:00 am	13:00 am	15:00 am	17:00 am
A						
YkDR	0.70±0.05^{a}	0.61±0.06^{a}	0.35±0.05^{a}	0.38±0.06^{a}	0.68±0.05^{a}	0.80±0.01^{a}
YkIR	0.79±0.01^{a}	0.62±0.02^{a}	0.41±0.05^{a}	0.61±0.03^{b}	0.70±0.02^{a}	0.80±0.01^{a}
AmDR	0.74±0.02^{a}	0.46±0.02^{a}	0.31±0.05^{a}	0.41±0.06^{a}	0.66±0.02^{a}	0.78±0.01^{a}
AmIR	0.79±0.01^{a}	0.59±0.06^{a}	0.46±0.08^{a}	0.56±0.03^{b}	0.69±0.03^{a}	0.78±0.01^{a}
B						
YkDR	0.78±0.01^{a}	0.56±0.09^{a}	0.46±0.09^{a}	0.29±0.09^{a}	0.62±0.05^{a}	0.73±0.02^{a}
YkIR	0.78±0.01^{a}	0.63±0.09^{a}	0.53±0.05^{a}	0.48±0.04^{b}	0.64±0.03^{a}	0.74±0.01^{a}
AmDR	0.77±0.01^{a}	0.40±0.05^{a}	0.25±0.05^{b}	0.27±0.07^{a}	0.43±0.01^{a}	0.62±0.06^{a}
AmIR	0.78±0.01^{a}	0.59±0.06^{b}	0.52±0.06^{a}	0.51±0.08^{b}	0.62±0.03^{b}	0.72±0.02^{b}

Values are mean±SE n = 5. Values in the same column followed by same letter do not differ significantly; A: 60 days after drought induction/irrigation; B: 90 days after drought induction/irrigation

Table 6: Net photosynthetic rate for a range of photosynthetically active radiation (PAR) levels (A) and the light response curve (B) of photosynthesis (measured at ambient CO_2) in droughted (DR) and irrigated (IR) plants of two enset clones, *Yesherakinkye* (Yk) and *Ameratye* (Am). Values represent means (in B) and mean and SE (in A) n = 5. Values in the same column followed by same letter do not differ significantly

	Photosynthetic rates (μmol CO_2 m^{-2} sec^{-1})			
PAR ranges (μmol m^{-2} s^{-1})	YkDR	YkIR	AmDR	AmIR
A				
700-800	6.00±0.7^{a}	11.60±1.2^{b}	3.30±0.2^{a}	11.90±1.3^{b}
1000-1100	1.70±0.2^{a}	11.60±0.7^{b}	0.30±0.09^{a}	10.50±0.9^{b}
B				
50	0.42	0.52	0.11	1.48
200	2.50	6.25	0.53	5.16
400	4.76	9.28	0.42	6.97
600	5.18	11.50	0.75	4.93
800	4.68	12.00	0.76	7.20
1000	4.14	15.90	0.64	8.64
1500	4.40	19.20	0.75	11.40

Values in the same column followed by same letter do not differ significantly

levels, droughted plants had a significantly lower net photosynthesis rates than irrigated groups and the mean difference between the two groups became more pronounced at higher PAR levels (Table 6A). The light response curve of photosynthesis (Table 6B), measured at ambient CO_2 levels, showed that net photosynthesis rate of droughted plants saturated at low PAR levels.

On the other hand, the quantum yield of PS II showed a similar diurnal fluctuation (Table 5A and B) as in gas exchange. The diurnal F′v/F′m ratio varied between 0.8 and 0.46 for irrigated groups and between 0.8 and 0.25 for droughted enset plants during the course of the drought period. Net photosynthesis rate of irrigated plants is largely independent of changes in chlorophyll fluorescence. Whereas, that of stressed plants was (R^2 = 0.4-0.5) correlated with diurnal changes in F′v/F′m. Plants in the droughted treatments exhibited a significantly higher Non-Photochemical Quenching (NPQ) than irrigated treatments in general and particularly during the warmest periods of the day (Table 3). Moreover, the decline in F′v/F′m in the course of the day was accompanied by an increase in (NPQ) for all treatment groups.

DISCUSSION

Growth and biomass partitioning: Several studies indicated that leaf expansion is sensitive to water deficit (Randall and Sinclair, 1988; Lecoeur *et al*., 1999) and that this sensitivity is expressed in terms of smaller cells and reductions in the numbers of cells produced by leaf meristems (Tardieu *et al*., 2000; Alfredo *et al*., 2004). The reduction in leaf area of droughted enset plants in this study could be attributed to leaf senescence, reduced rate of leaf emergence and thus fewer leaves per plant. A reduction in leaf number and leaf size while minimizes water loss it does simultaneously reduce the gas exchange surface and in effect biomass accumulation and growth rate of droughted plants. By the end of the experiment, the total dry matter in droughted groups was 25-50% of that in irrigated groups and the former allocated proportionally more to belowground (corm + root) parts than the latter. Altered biomass partitioning under drought have been considered as long-term plant strategy in coping up with the stress condition (Arndt *et al*., 2001; Liu and Stutzel, 2004; Lei *et al*., 2006), improve plant water balance and enhance the likelihood of

survival (Tschaplinski *et al*., 1994). Present findings are in general agreement with previous observations in different plant species (e.g., Steinberg *et al*., 1990; Chartzoulakis *et al*., 1993; Liu and Stutzel, 2004).

On the other hand, one outstanding observation with important practical implications is the increased biomass allocation to belowground parts under drought. Altered biomass partitioning that favor the corm confers a survival advantage in perennials like enset for such reserves are later re-mobilized and utilized in leaf initiation after a period of dry spell. Moreover, it also increased the Harvest Index (HI) of the corm which is the harvestable part of the plant. The practical significance of our finding is that such a trait could be used as a selection criterion in screening enset clones for drought prone areas.

Relative Growth Rate (RGR) of enset plants of both clones was significantly reduced by prolonged drought and the morphological (SLA) and physiological components (NAR) are positively correlated with RGR. The observed response in RGR of droughted enset plants could predominantly be ascribed to the reduction in physiological processes with a lesser influence of the morphological component. Present findings are in line with the observations in different plant groups (Poorter and Nagel, 2000) but disagree with Galmes *et al*. (2005) where the morphological component (SLA and LMR was the strong determinant for the reduction in RGR of perennial herbs under water stress). However, the relationship among the growth parameters depend on the species, growth form (Poorter *et al*., 1990; Ryser and Wahl, 2001) and most importantly, growth conditions (Ryser and Wahl, 2001; Shipley, 2002).

Leaf water status, gas exchange and chlorophyll a fluorescence: Leaf water status (as estimated by RWC) of droughted enset plants was little affected by prolonged drought. The RWC values measured for droughted enset plants in this study were by far higher than what should be expected from depleted soil water and require further scrutiny. Despite little change in leaf RWC, prolonged drought markedly reduced Pn, gs and E in droughted plants. The reduction in stomatal conductance in response to depleted soil moisture could partly be responsible for the reduced photosynthetic rate in droughted plants. Maximum photosynthetic rates in droughted plants were attained in the early morning hours. This could possibly be a means of maximizing carbon uptake while minimizing water loss during hours of high evaporative demand.

On the other hand, the reductions in P_n of droughted plants not only closely associated with F′v/F′m diurnal course but the lowest F′v/F′m diurnal values coincided with diurnal peaks in air temperature and irradiance levels. Photo-inhibition in stressed leaves has been observed as a parallel decrease in CO_2 uptake and quantum yield of PS II (F′v/F′m) of sun exposed leaves, as the latter reflects the fraction of light absorbed by PSII antennae that is utilized in PSII photochemistry at a given PFD (Demmig-Adams *et al*., 1996; BjÖrkman *et al*., 1988). Similar observations were reported for Mediterranean ever green trees exposed to summer drought in the field (Faria *et al*., 1998). This down-regulation of photosynthesis resulted from the thermal dissipation of excess excitation energy in the chloroplasts (Chaves *et al*., 2002) as shown by the increase in non-photochemical fluorescence quenching (NPQ). The response of photosynthesis to PAR is indicative of the existence of regulatory and/or photo-inhibitory processes, differences in physiological state of the two groups and also their photochemical efficiency. These further explain the possible role of regulatory processes that led to higher NPQ values in droughted plants. Under severe water deficit, the photosynthetic capacity is reduced which could be reflected as an increase in the C_i (Aniya and Herzog, 2004) as observed for different plant species (Guan *et al*., 2004; Tezara *et al*., 2005). It can be deduced from the significant decline in F′v/F′m that the higher Ci in droughted *Ameratye* plants could possibly be attributed partly to a non-stomatal limitation. In summary, we can conclude that the decline in carbon assimilation rate of droughted enset plants could be a combination of both stomatal and non-stomatal factors. Except for total dry matter production, there was no significant difference in performance between the two clones under drought and/or irrigation. Future investigations should consider looking into the P_n-C_i (A-C_i curve) relations under controlled and field conditions. Moreover, the mechanism by which stomata in droughted enset plants respond to changes in soil water, in the absence of large changes in RWC remains to be determined.

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