Global Journal of Science Frontier Research
Agriculture & Biology
Volume 12 Issue 3 Version 1.0 March 2012
Type : Double Blind Peer Reviewed International Research Journal
Publisher: Global Journals Inc. (USA)
Online ISSN: 2249-4626 & Print ISSN: 0975-5896

Yield Components and Gas Exchange Responses of Nerica Rice Varieties *(Oryza Sativa L.)* to Vegetative and Reproductive Stage Water Deficit

By Sikuku P.A., Onyango J.C. & Netondo G.W.
Maseno University, Maseno, Kenya

Abstract – Kenya has got a rapidly increasing population which was estimated to be 36 million in the year 2009 with a growth rate of 2.7 per annum hence the need for diversified food production. Water deficit is one of the most environmental stresses affecting agriculture productivity. Drought may affect crop yield and gas exchange at any developmental stage while early reproductive stage is found to be one of the most susceptible phases of a crop to drought stress. NERICA (New Rice for Africa) are high yielding rainfed rice varieties with early maturity and has shown high potential to revolutionize rice farming even in Africa's stress afflicted ecologies. However, NERICA varieties vary in their response to water deficit. A pot experiment was conducted in 2009 at the Maseno University Botanic garden, to evaluate the responses of five NERICA varieties (NERICA1, NERICA 2, NERICA 3, NERICA 4 and NERICA 5) to water deficit during their vegetative or reproductive stage of their development. The response pattern of crop yield and gas exchange parameters to water deficit imposed at different growth stages might provide basis for selecting the most tolerant variety to water deficit in order to stabilize yield and solve food crisis.

Keywords : NERICA rice, relative water content, transpiration, stomatal conductance, Photosynthesis, flowering and yield.

GJSFR-D Classification : FOR Code: 820402, 620103

Strictly as per the compliance and regulations of :

Yield Components and Gas Exchange Responses of Nerica Rice Varieties (*Oryza Sativa* L.) to Vegetative and Reproductive Stage Water Deficit

Sikuku P.A.[α], Onyango J.C.[σ] & Netondo G.W.[ρ]

Abstract - Kenya has got a rapidly increasing population which was estimated to be 36 million in the year 2009 with a growth rate of 2.7 per annum hence the need for diversified food production. Water deficit is one of the most environmental stresses affecting agriculture productivity. Drought may affect crop yield and gas exchange at any developmental stage while early reproductive stage is found to be one of the most susceptible phases of a crop to drought stress. NERICA (New Rice for Africa) are high yielding rainfed rice varieties with early maturity and has shown high potential to revolutionize rice farming even in Africa's stress afflicted ecologies. However, NERICA varieties vary in their response to water deficit. A pot experiment was conducted in 2009 at the Maseno University Botanic garden, to evaluate the responses of five NERICA varieties (NERICA1, NERICA 2, NERICA 3, NERICA 4 and NERICA 5) to water deficit during their vegetative or reproductive stage of their development. The response pattern of crop yield and gas exchange parameters to water deficit imposed at different growth stages might provide basis for selecting the most tolerant variety to water deficit in order to stabilize yield and solve food crisis. The treatments were; T_1-irrigating the pots with a litre of water after every two days (Control), T_2 -water deficit at vegetative stage in which water was withheld by irrigating the plants using one litre of water after every six days from 30-50 days after planting; T_3-water deficit at reproductive stage in which water was withheld by irrigating the plants using one litre of water after every six days from 51-71 days after planting. Water deficit caused a significant reduction in gas exchange parameters and yield more at the reproductive stage as compared to water deficit at vegetative stage. The results indicate that NERICA 2 and 4 were tolerant as compared to NERICA 1, 3 and 5 to water deficit occurring at vegetative stage or reproductive stage because their leaf relative water content, transpiration, stomatal conductance, photosynthesis and yield components were least affected.

Keywords : NERICA rice, relative water content, transpiration, stomatal conductance, Photosynthesis, flowering and yield.

I. Introduction

Agriculture is the mainstay of Kenya's economy and 80% of the rural population depends on agriculture (Irungu, 2009). Kenya has got a rapidly increasing population which was estimated to be 36 million in the year 2009 with a growth rate of 2.7 per annum hence the need for diversified food production (MOA, 2008). Water deficit is one of the most environmental stresses affecting agriculture productivity. Drought may affect crop yield and gas exchange at any developmental stage while early reproductive stage is found to be one of the most susceptible phases of a crop to drought stress (Liu *et al.*, 2003). Rice's susceptibility to water deficit is more pronounced at the reproductive stage and causes the greatest reduction in grain yield when stress coincides with the irreversible reproductive processes. According to Lanceras *et al.* (2004) stable and high yields of rainfed rice under drought conditions can be obtained by having appropriate phenology to avoid late season drought and Fukai *et al.* (1999) observed that ontogenic characters especially appropriate flowering time play an important role in drought avoidance of rainfed rice. Jongdee *et al.* (2002) pointed out that phenology is the most important factor. Timing, intensity and occurrence of water deficit have been associated with the delay of heading or flowering (Fukai *et al.*, 1999).

Water deficit during the vegetative stage may have relatively little effect on grain yield, perhaps owing to the compensatory growth or changed partitioning of dry matter after the stress is relieved. Kaurk *et al.* (2007) reported that water deficit during the reproductive stage in corn increases the interval from silking to pollen shed and reduce kernel number or weight while water deficit at seed set may result in a low number of seeds and after seed set may result in a high percentage of small seeds. In other cases severe water deficit can cause emergence of ready differentiated floral buds (Tenhunen *et al.*, 1985) and drought during developmental stage prior to kernel filling causes formation of wizened undeveloped seeds. Occurrence of early stage moisture stress leads to poor crop establishment and increased seed mortality in rice.

There are genotypic variations in the maintenance of leaf water potential and expression of osmotic adjustment among rice varieties with diverse backgrounds and environments of origin. The species adapted better to dry environments have higher relative

Author σ : Department of Botany, Faculty of Science, Maseno University, Maseno, Kenya. E-mail : phoebenyangi@yahoo.com

water content at given water potential. The maintenance of leaf water potential is indicative of drought tolerance that minimises the impact of stress on grain yield mainly by reducing the effect of stress on spikelet sterility (Jongdee *et al.*, 2002). Leaf water status is intimately related to several leaf physiological variables such as leaf turgor, growth, stomatal conductance, transpiration and photosynthesis (Penuelas *et al.*, 1993).

The maintenance of leaf water potential is indicative of drought tolerance that minimises the impact of stress on grain yield mainly by reducing the effect of stress on spikelet sterility (Jongdee *et al.*, 2002). Leaves normally present a large surface area to the surrounding air to facilitate CO_2 assimilation. Simultaneously evaporation of water from the moist cell walls is inevitable and thus transpiration must be replaced by water absorption from the soil. The availability of soil water to the roots of a plant and the efficiency of its absorption has a profound influence on the rate of transpiration. Absorption of water by the plant may lag behind the release of water via transpiration without noticeably affecting the plant for a short period, if the condition is prolonged, water deficit develops and the plant will wilt. Some plants avoid water deficit by water conservation and have a adaptations that limit the rate of water loss thus prevent the development of detrimental plant water deficits by conserving soil water for an extended period thus maintaining soil and plant water potential suitably high over a sufficient period for seed ripening (Jones, 1996). Plants can rapidly regulate their water loss through stomatal closure in order to maintain their water status despite decrease in water availability limiting transpiration to diffusion through the cuticle. Closure of the stomata improves water use efficiency under water deficit conditions. However, any structural feature which restricts water loss such as reduced leaf surface area inevitably decreases carbon assimilation due to reduction in physical transfer of CO_2 molecules. It also leads to increased leaf temperature, which reduces the rate of biochemical processes. Under water deficit conditions the leaf gas exchange of plants is reduced and this leads to a lower biomass accumulation and grain yield. It has been reported that over a wide range of crops, maize (Ray and Sinclair, 1997), soybean (Vadez and Sinclair, 2001) and rice (Serraj *et al.*, 2008) show genotypic differences in how leaf gas exchange responds to water deficit, with certain genotypes being capable of sustaining plant transpiration until soil becomes dry whereas others react with a decline in transpiration when the soil is relatively wet. Higher stomatal conductance increases CO_2 diffusion into the leaf and favours higher photosynthetic rates which consequently favour higher yields. The effect of water deficit on photosynthesis depends on the plants adaptations to water deficit and the intensity and duration to which the plant is exposed to water deficit. According to Kaiser (1987), the intensity of this effect influences the capacity of different species to cope with the drought which also depends on the plant genetic background. Water deficit in plant tissue develops under drought conditions and the ability to maintain photosynthetic machinery functional under water deficit is a major importance for drought tolerance (Zlatev and Yordanov, 2004). According to Richards (2000), high photosynthetic rate (Pn) is considered to be one of the most important breeding strategies for crop improvement. At the whole plant level, limited soil water supply may have a strong effect on development, activity and duration of various sources and sink organs. The aim of this work was to study the response pattern of crop yield and gas exchange parameters of five NERICA (NERICA1, NERICA 2, NERICA 3, NERICA 4 and NERICA 5) varieties to water deficit occurring at vegetative stage or reproductive stage of their development which might provide basis for selecting the most tolerant variety to water deficit in order to increase rice yields and help in poverty alleviation.

II. Materials and Methods

The study was carried out at Maseno University Botanic Garden in the green house between January 2009 and August 2009. The green house was naturally illuminated and the light, CO_2 concentration and temperature conditions were not controlled. Conditions during the study were: day temperature ranged from 22 - 34^{0}C, relative humidity from 50 – 90% and photon flux density (PPFD) from 400 – 600 μmol photons $m^{-2}s^{-1}$. Seeds of five New Rice for Africa (NERICA) rainfed rice varieties namely NERICA 1, 2, 3, 4 and 5 coded as N-1, N-2, N-3, N-4 and N-5 were obtained from the NERICA adaptability trials in Maseno University Botanic garden. The soil was dug from the garden, solarized for one week then filled into 20 litre plastic pots up to ¾ full. The soils at Maseno are classified as acrisol being well drained, deep clay with pH ranging between 4.6 and 5.4 (Sikuku *et al.*, 2010).The seeds were soaked in water at 30^{0}C for 72 hours prior to planting to facilitate germination. The pots were laid out in a Randomized Complete Block Design (RCBD). The seeds were sown at the rate of four seeds per hill and there were 4 hills per pot with a spacing of 15 x 25 cm and planting depth of 3cm. The treatment combinations consisted of three levels of water regimes, viz. T_1 - well watered throughout the life cycle in which the plants were watered with one litre of water after every two days throughout the growing period, T_2 - water deficit at vegetative stage in which water was withheld by irrigating the plants using one litre of water after every six days from 30-50 days after planting, T_3 - water deficit at reproductive stage in which water was withheld by irrigating the plants using one litre of water after every six days from 51-71 days after planting. One litre of water was used to irrigate all the pots after every two days for 28 days to maintain optimum moisture before initiating experimental treatments. Plants were irrigated after every six days from 30 to 50 days after planting to impose water deficit at vegetative stage and from 51 to 71 days after planting to impose water deficit at reproductive stage. After water deficit period, plants were irrigated after every two days. Three replications were performed for each treatment and each variety. The experiment was repeated twice.

a) Parameters measured

i. Relative leaf water content

Relative leaf water content was determined on the flag leaf of twelve plants per treatment for all replications at 28, 42, 56, 70 and 84 days after sowing. The leaves to be harvested were rinsed with distilled water to eliminate surface accumulation of salts two hours before harvesting. The sampled leaves were cut at the base of the lamina and one gram of each weighed immediately to get the fresh weight (W_f). The leaf disks were then placed in a test tube containing distilled water for 24 hours at room temperature to get the turgid weight (W_t). The disks were dried in an oven at 80°C until a constant weight was obtained to get the oven dry weight (W_d). The relative water content was calculated using the formula of Coombs *et al.* (1985) as follows: Relative water content $(R) = (W_f - W_d)/(W_t - W_d) \times 100$ Gas **Exchange.**

Leaf transpiration, stomatal conductance and net photosynthesis were determined on day 28, 42, 56, 70 and 84 after sowing by use of a portable infrared gas analyser system connected to a plant leaf (CIRAS-1, PP Systems Ltd.,Herts, U.K.) on 0.7 cm^2 of leaf surface. The measurements were carried out between 0930 and 1300 hours on fully sun exposed top leaf of twelve plants per treatment for all replications. The photosynthetically active radiation ranged from 400 – 600 μmol photons $m^{-2}s^{-1}$, leaf temperature varied from 22°C to 30°C, relative humidity varied from 35% to 40% and vapour pressure deficit was between 1.6 -1.9 kPa.

ii. *Panicle lengths*

This was determined using a metre rule. Measurements were done from the panicle base to the tip of twelve plants per treatment and per replication.

iii. *Days to flowering*

This was determined every day after the plants had started heading. This was done by counting the flowering plants per pot and expressing them as a percentage of the total plants in the pot. The data was obtained by scoring for the percentage of flowering plants in each pot when the first inflorescences were observed and when half of all the plants in each pot had flowered.

iv. *Days to maturity*

This was done by counting the days taken by plants from planting to harvesting date. The rice were harvested when the panicles had turned down and were yellowish in colour according to Chatterjee and Maiti (1988).

v. *Yield at 14% moisture content*

This was determined by measuring the moisture content of the grains immediately after harvesting using a grain moisture tester (model number AF 34086, Japan) and then converting the yield of the grains to 14% moisture content.

vi. *Filled grain Ratio percentage*

Grains harvested from all the hills in the pots were put in different buckets of water and the poorly filled together with empty grains floated while the well filled grains settled at the bottom. Filled grains were then separated from empty and poorly filled grains. The grains were dried and later weighed but each was handled separately. The percentage of empty grains was obtained as follows;

Grain loss = (Weight of well filled grain –weight of empty grain) / Weight of well filled grains.

vii. *Grain yield*

The grain yield was determined at harvesting from an area of 0.038m^2 in the pots. The number of grains per 5g, and filled grains per panicle were determined. The yield was extrapolated in kilograms per hectare.

viii. *Statistical analysis of data*

Analysis of variance (ANOVA) was carried out on the data for the variables measured during the study period to test for differences between the treatments and the varieties using a statistical computer package (SAS). The treatment and variety means was separated using the least significant differences (LSD) test at 5% level.

III. Results

a) Leaf Relative water content

There was a highly significant difference ($P \leq 0.05$) among the varieties, treatments and DAS. Water deficit caused a significant reduction in leaf water content and the highest reduction among the varieties was at water deficit treatment during reproductive stage as compared to vegetative stage. NERICA 2 and 4 recorded higher leaf water content as compared to NERICA 1, 3 and 5 at water deficit treatments during vegetative (Fig.1a) and reproductive stage (Fig.1b).

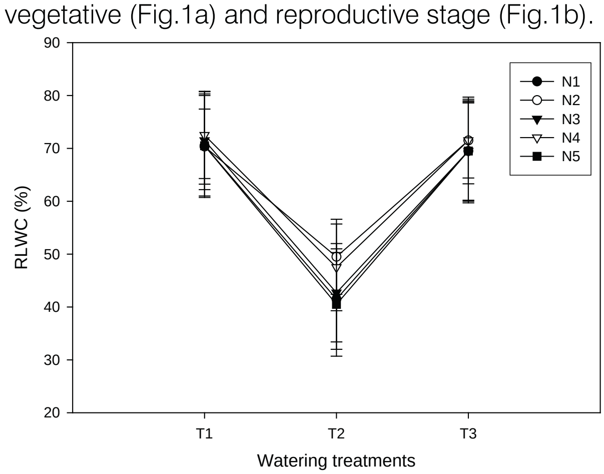

Fig.1a : Relative leaf water content (%) at DAS 42 (Vegetative stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ±SE). LSD (0.05) =0.4385 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

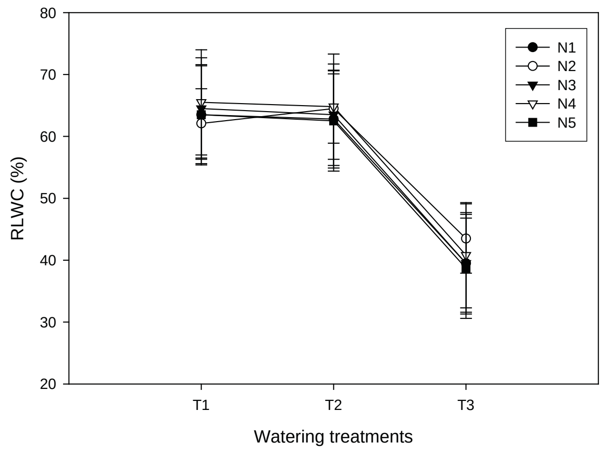

Fig.1b : Relative leaf water content (%) at DAS 70 (Reproductive stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) =0.4385 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

b) *Transpiration*

There was a significant interaction between the varieties and the treatments ($P \leq 0.05$) in transpiration rate. Transpiration rate was significantly affected due to imposition of water deficit with the varieties recording slightly higher transpiration rates during water deficit at vegetative stage compared to water deficit at reproductive stage as shown in Figure 2a and b. The varietal effect was also significant ($P \leq 0.05$) with NERICA 1, 3 and 5 having higher transpiration rates compared to NERICA 2 and 4 at water deficit treatments.

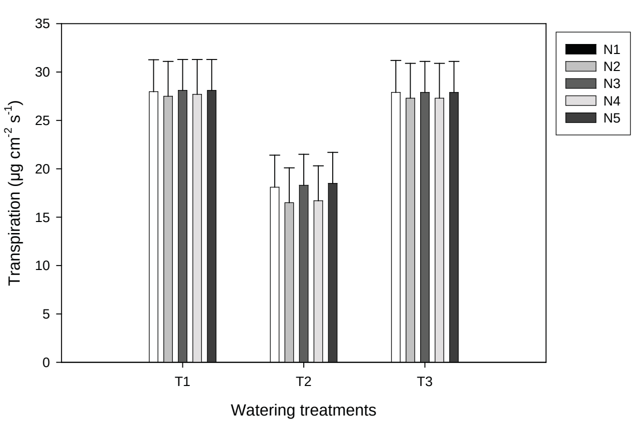

Fig. 2a : Transpiration rate at DAS 42 (Vegetative stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 0.2675 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

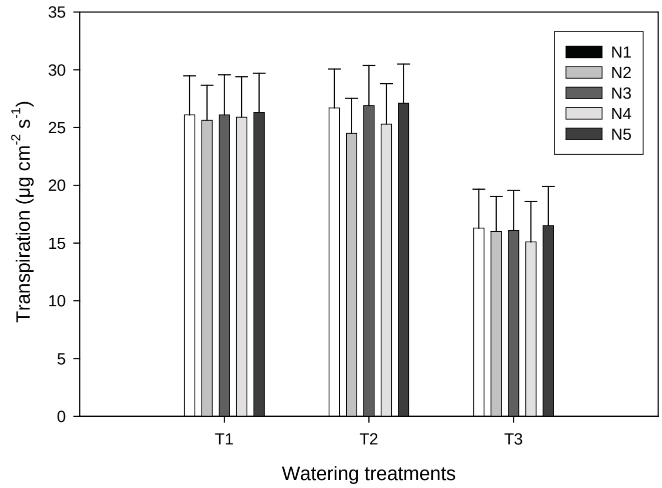

Fig. 2b : Transpiration rate at DAS 70 (Reproductive stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 0.2675 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

c) *Stomatal conductance*

A reduction in stomatal conductance (gs) was observed in all NERICA varieties due to water deficit. There was a significant effect ($P \leq 0.05$) among the varieties. Water deficit treatment imposed during reproductive stage caused more reduction in stomatal conductance among the varieties compared to water deficit treatment at the vegetative stage as shown by Figure 3a and 3b. The varietal effect was also significant with N-2 demonstrating the most tolerance to water deficit at reproductive stage due to lower reduction (23%) from the control in stomatal conductance compared to N-4 (29%), N-5 (32%), N-3 (37%) and N-1(38%).

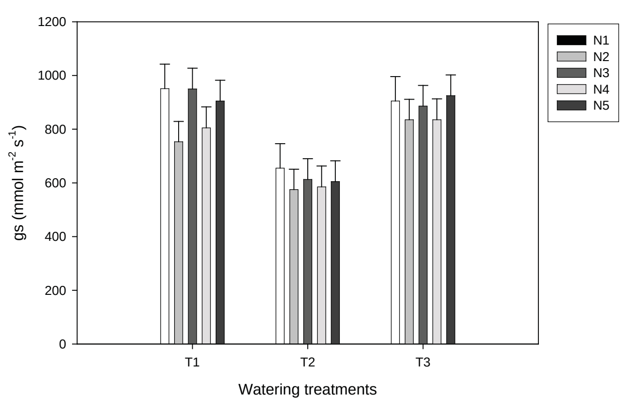

Fig. 3a : Stomatal conductance at DAS 42 (Vegetative stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 12.44 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

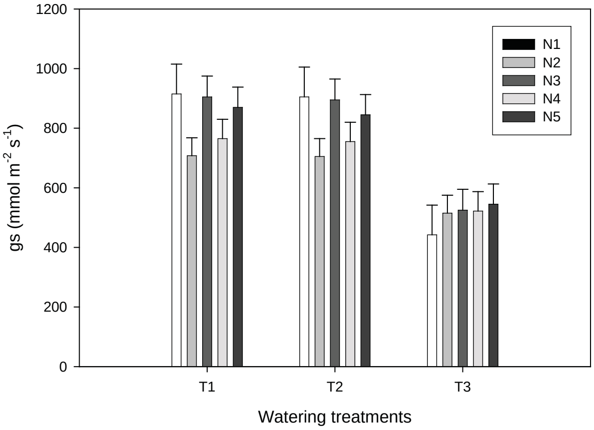

Fig. 3b : Stomatal conductance at DAS 70 (Reproductive stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 12.44 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

d) Net photosynthesis

Results indicate that water deficit had a significant inhibitory effect on net photosynthesis of all the NERICA varieties. The highest reduction in photosynthesis was found at the reproductive stage as compared to vegetative stage in all varieties as shown by Figure 4a and 4b. There was a significant interaction ($P \leq 0.05$) between the varieties and the treatments and a highly significant interaction ($P \leq 0.05$) between treatments and DAS. N-4 had the highest photosynthetic rate at water deficit during vegetative stage while N-2 had highest at reproductive stage.

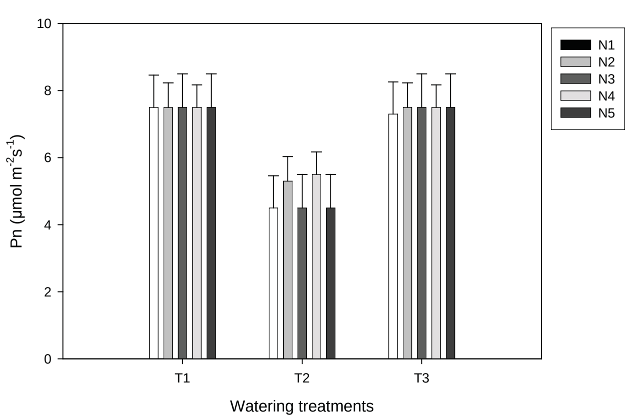

Fig. 4a : Net Photosynthesis (Pn) at DAS 42 (Vegetative stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 0.2215 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

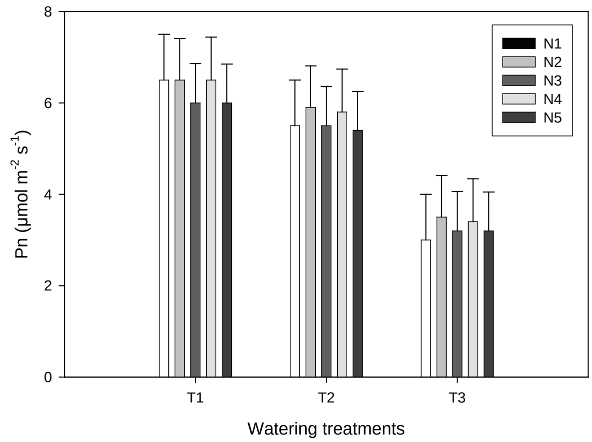

Fig. 4b : Net Photosynthesis (Pn) at DAS 70 (Reproductive stage) of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 0.2215 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

e) Days to 50% flowering

There was a significant effect ($P \leq 0.05$) in days to flowering among the treatments. There was also a significant varietal difference ($P \leq 0.05$) in days to 50% flowering. Water deficit caused a delay in flowering in all the varieties with the well watered plants flowering significantly early compared to plants exposed to water deficit. Plants that were exposed to water deficit at the reproductive stage flowered slightly earlier than plants stressed at vegetative stage. NERICA 2 and 4 took the least number of days to attain 50% flowering both at water deficit treatment and well watered treatments while NERICA 1, 3 and 5 flowered almost at the same time (Fig. 6a).

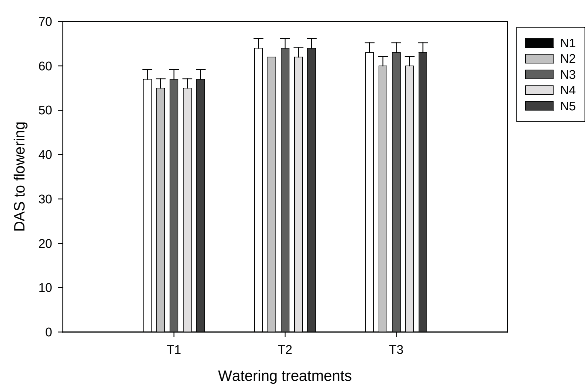

Fig. 5a : Effects of three levels of watering treatments on Days to flowering of five NERICA rice varieties. (Means of three replicates ± SE) LSD (0.05) = 1.2886 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

f) Days to harvesting

There was a significant difference ($P \leq 0.05$) among the treatments with the non water stressed plants maturing significantly early as compared to the plants exposed to water deficit. The plants exposed to water deficit at vegetative stage took slightly longer to mature compared to well watered plants. Plants exposed to water deficit at reproductive stage took the longest time to mature in all the varieties. The varietal difference was also significant ($P \leq 0.05$) with NERICA 2 and 4 maturing slightly early followed by N-3 while NERICA 1 and 5 took the longest time to mature as shown by Fig. 6b.

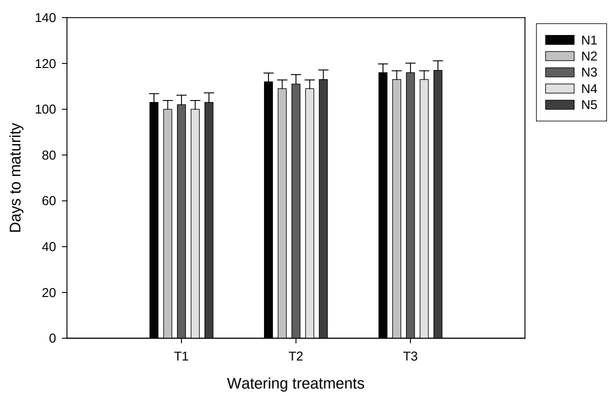

Fig.5b : Effects of three levels of watering treatments on Days to harvesting of five NERICA rice varieties. (Means of three replicates ± SE) LSD (0.05) = 1.272 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

g) Panicle length

There was a significant effect ($P \leq 0.05$) in panicle length among the varieties and among the treatments. Water deficit at reproductive and vegetative stage caused a reduction in panicle length with the plants exposed to water deficit during reproductive stage being the most affected hence had the shortest panicle lengths (Fig. 5). The well watered plants had significantly higher panicle lengths compared to plants exposed to water deficit. N-2 had the highest panicle length both at the control and at water deficit treatments while N-3 had the lowest length at water deficit treatment during reproductive stage.

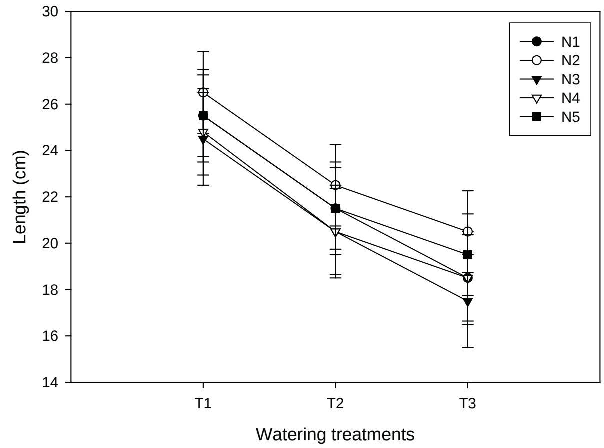

Fig. 6 : Panicle length of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 0.5665 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

h) Yield at 14% moisture content

The yield at 14% moisture content was significantly reduced by water deficit both at vegetative and reproductive stages of plants growth. There was a highly significant ($P \leq 0.05$) varietal effect in yield with N-2 having significantly higher yield at water deficit treatments followed by N-4 (Figure 7a). NERICA 3 and 5 were the most affected and recorded the highest percentage reduction in yield relative to the control at water deficit during vegetative and at reproductive stage. The treatments had a highly significant difference ($P \leq 0.05$) with the well watered plants producing higher yields followed by plants exposed to water deficit treatment at vegetative stage. However, the plants exposed to water deficit at reproductive stage were the most affected.

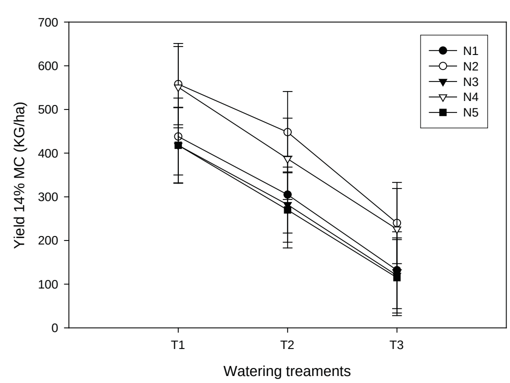

Fig. 7a : Yield at 14% moisture content of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 14.088 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

i) Filled grain ratio (%)

There was a highly significant difference ($P \leq 0.05$) between the NERICAS and the treatments. Water deficit significantly reduced the filled grain ratio percentage with plants exposed to water deficit at the vegetative stage having a slight reduction from the control while those exposed to water deficit at reproductive stage had a significant reduction. The varietal difference was also highly significant ($P \leq 0.05$) with the varieties having almost the same filled grain ratio percentage at the well watered treatment, slight difference in treatment 2 and a marked difference in plants exposed to water deficit at reproductive stage with NERICA 2 and 4 registering the highest filled grain ratios while NERICA 3 and 5 had the lowest percentage ratios (Fig.7b).

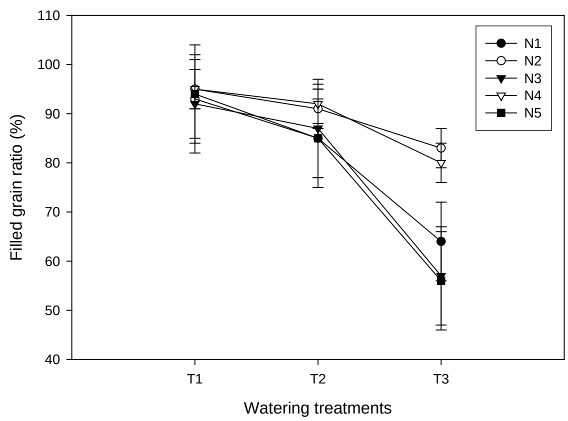

Fig. 7b : Filled grain ratio percentage of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 1.4724 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

j) Yield components

Significant reduction in yield was observed in all NERICA varieties due to water deficit. There was a highly significant difference ($P \leq 0.05$) among the treatments with the well watered having higher yield compared to plants exposed to water deficit treatments. The reproductive stage imposed water deficit had a significant effect on yield. Varieties also differed significantly ($P \leq 0.05$) with NERICA 2 and 4 recording higher yields both at well watered and at water deficit treatments and N-5 registering the lowest yield under water deficit treatment at reproductive stage (Fig. 7c). NERICA 2 had the least yield reduction relative to the control under water deficit both at vegetative and reproductive while N-3 and 5 had the highest percentage reduction when water deficit was imposed at the reproductive stage.

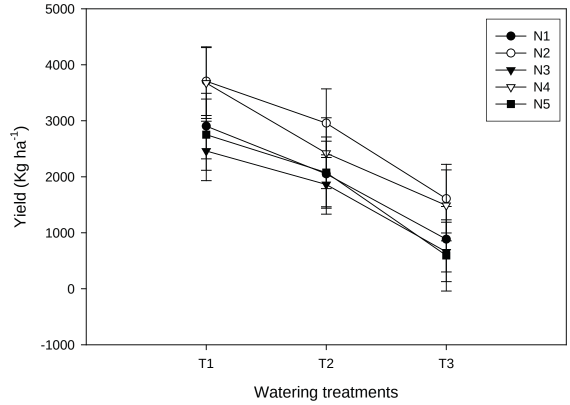

Fig. 7c : Yield of five NERICA rice varieties grown at three levels of watering treatments (Means of three replicates ± SE). LSD (0.05) = 140.87 (T1- Well watered control, T2- water deficit at vegetative, T3- water deficit at reproductive).

IV. Discussion

Relative water content decreased significantly at water deficit treatments (Fig. 1a and b). Similar observations were made by Cruz *et al.* (1986) in rice and Siddique *et al.* (2000) in wheat. Decrease in leaf water content may be attributed to water loss through evapotranspiration and decreased water absorption by the roots when the soil water was limiting. Relative water content is a key indicator of the degree of cell and tissue hydration which is crucial for optimum physiological functioning and growth processes. In the present study, low relative water content due to water deficit inhibited growth and plant function which were reflected in lower transpiration, decreased photosynthesis and lower yield. When the soil dries, water uptake by the roots becomes more difficult and uptake declines. The reduction in water uptake eventually resulted in the development of water deficit in the shoot hence the decrease in relative water content. According to Sah and Zamora (2005), relative water content is an integrated measure of plant water status. Higher relative water content is necessary for proper growth and function of plant. During drought stress the water balance of a plant is disrupted and as a result of which the relative water content decreases (Sikuku *et al.*, 2010). The varietal difference was significant but only at water deficit treatments. N-2 was able to maintain the highest water content at reproductive stage and it had the lowest percentage reduction from the control (25%) while N-5 had the highest reduction (39%). The higher relative water content recorded by NERICA 2 and 4 at water deficit treatments may be attributed to their ability to absorb more water from the soil and the ability to control water loss through stomata. According to Sinclair and Ludlow (1985), under water deficit conditions, the varieties that are tolerant to drought have more relative water content and relative water content can be used to select high yielding genotypes that maintain cell turgor under water deficit environments and give relative high yield. Transpiration rate decreased significantly in the plants under water deficit at reproductive and vegetative stage as compared to control. Similar results have been reported in wheat (El Hafid *et al.,* 1998) and soy bean (Sionit and Kramer, 1983). The severity of moisture deficit was most felt by plants at the reproductive stage as compared to vegetative stage hence plants had lower transpiration rates at water deficit treatment at reproductive as compared to vegetative stage. The lower rate of transpiration was possibly a result of moderate stomatal conductance. The varietal difference was significant but only at water deficit treatments. During vegetative stage, the plants recorded almost similar transpiration rates at well watered treatments but at water deficit treatment NERICA 2 and 4 had slightly lower transpiration rate as compared to NERICA 1, 3 and 5 (Fig 2a). At water deficit during reproductive stage, NERICA 2 and 4 had slightly lower transpiration rate compared to NERICA 1, 3 and 5 (Fig. 2b). This may suggest that NERICA 2 and 4 are fairly tolerant being able to minimize water loss in response to water deficit (Casadebaig *et al*., 2008). Previous studies by El Jaafari (2000) have shown that the ability of the plant to survive water deficits depends on its ability to restrict water loss through the leaf epidermis after the stomata have attained minimum aperture. While this physiological response to increasing water deficit can help prevent development of lethal water deficit it can also lead to lethal temperatures under warm sunny conditions as observed by Silva *et al*. (2007), hence tolerant genotypes like NERICA 2 and 4 maintain a more favourable leaf water status therefore more open stomata and sustained transpirational cooling. As a consequence CO_2 influx towards chloroplasts may be sustained longer thus allowing greater photosynthetic rates and ultimately crop yield (Silva *et al.*, 2007). Stomatal conductance generally decreased with the imposition of water deficit (Fig. 3a and b). This tendency of reduction of stomatal conductance underwater deficit is consistent with observations made by Collinson *et al*. (1997) in bambara groundnuts. The reduction in the leaf water potential though not measured in this experiment may have led to the development of water deficit in the leaves causing guard cells to loose turgor hence reduced stomatal pores which apparently led to reduced CO_2 diffusion through the stomata (Flexas *et al*., 2004). In addition, the increased stomatal resistance may have led to reduced water transport in the leaves further causing a decrease in stomatal conductance (Silva *et al*., 2007). Reduction in stomatal conductance decreases transpiration and also limits photosynthesis (Sikuku *et al,* 2010). The varietal effect was significant and at water deficit during reproductive, N-2 (27%) recorded the lowest reduction from the control followed by N-4 (32%) while N-1 with 52% had the highest reduction. This shows that NERICA 2 and 4 were water deficit tolerant hence the lower deviation from the control at water deficit treatment during reproductive stage. It was also observed that stomatal conductance decreased with age of the leaves (Siddique *et al*., 2000). The results are in general agreement with those of Upretty and Bhatia (1989), who reported that stomatal resistance in the leaves of mungbean increased with water deficit. Plants exposed to water deficit during the vegetative and reproductive stage recovered their stomatal conductance after rewatering. Recovery of stomatal conductance may have resulted in increased CO_2 diffusion into the leaves to attain higher photosynthetic rates which favoured higher biomass (Siddique *et al*., 2000). Photosynthetic rate was inhibited by water deficit both at vegetative and reproductive stage. A reduction in photosynthesis was found at reproductive stage as compared to vegetative stage in all the varieties. The results are in agreement with observations of Siddique *et al*. (2000), and Bogale *et al*. (2011) on wheat. Decreased photosynthetic rate could have resulted from stomatal and non stomatal (biochemical) limitations. The apparent decrease in the photosynthetic rates in the varieties can be explained by the clear decline in the stomatal conductance and can also be related to the metabolic limitations (Lawlor, 2002) whereby Tezara *et al*. (1999) proposed that the decline in ATP synthesis was the main reason for the low photosynthesis rates under water deficit conditions. However, Cornic and Fresneau (2002) strongly supported the stomatal closing to be the main reason in reducing the photosynthesis rates as a result of water deficit. This is because the maximum value of photosynthesis can be recovered by supplying sufficient amount of CO_2 to the leaves. Thus the causes of low photosynthesis under water deficit depend not only on the stress and plant variety but also on the complex interaction between the age of the plant and the leaves, the light intensity (Flexas *et al.,* 2004). Significant varietal difference in net photosynthesis was observed both at vegetative and reproductive stage. At the vegetative stage NERICA 2 and 4 showed higher photosynthetic rate compared to NERICA 1, 3 and 5 (Fig. 4a). This shows that NERICA 2 and 4 are fairly more tolerant to moisture deficit than NERICA 1, 3 and 5 and can photosynthesize under certain levels of soil moisture deficit. Plants subjected to water deficit at the vegetative stage apparently recovered quickly to show a greater rate of photosynthesis at reproductive stage hence plants stressed at vegetative but not stressed subsequently gave similar photosynthesis rates at reproductive to the well watered control plants. This shows that the photosynthetic apparatus was not affected by water deficit. Water deficit had a significant effect on days to flowering and maturity of the five NERICA rice varieties (Fig.5a and b). Days to maturity among rice varieties ranged from 100 to 117. Plants exposed to water deficit took longer to reach flowering and maturity. Similar results have been reported in rice (Fukai *et al*., 1999). The results may have been due to the fact that when plants are exposed to water deficit, their carbohydrates metabolism is affected, in turn the disorder slows down growth rate and delays development stages in stressed plants thus affecting maturity period (Atera *et al*., 2011). Plants that were exposed to water deficit at the vegetative stage took slightly longer to reach flowering as compared to plants stressed during reproductive stage. However, plants exposed to water deficit at reproductive stage took the most number of days to reach maturity. This may imply that the plants exposed to water deficit at vegetative stage had slow growth hence the delay in heading and flowering but recovered after rewatering to attain maturity earlier compared to plants exposed to water deficit during reproductive season. NERICA 2 and 4 took slightly fewer days to attain maturity compared to NERICA 1, 3 and 5. This shows that NERICA 2 and 4 may be able to evade moisture deficit that may develop late in the season. The variation for days to maturity was attributed to genetic constituent. The delay in flowering observed in NERICA 1 and 3 under water deficit is deleterious and indicates poor adaptation to water deficit. Plants exposed to water deficit at reproductive stage had lower panicle lengths as compared to plants stressed at vegetative stage (Fig.6). This may have been caused by the fact that under water deficit at the early reproductive stages, spikelet water potential as well as leaf water content decreased which inhibited cell growth or carbohydrate metabolism in the floral organ hence the reduction in panicle length (Boyer and Westgate, 2004). In addition, even a small decrease of photosynthates could be a cause for the insufficient development of young panicles because young panicles compete with vegetative organs for available photosynthates during meiosis stage. NERICA 2 and 5 had the highest panicle lengths while N-3 had the least. Water deficit at vegetative and reproductive stages of growth and development of NERICA rice significantly reduced 1000grain weight. The plants stressed during the vegetative stage had a reduced seed number per plant. This is because water deficit during this stage reduced plant growth therefore may have delayed and reduced appearance of nodes and so resulting in plants with fewer inflorescence and seed numbers per plant after rewatering (Vurayai *et al*., 2011). Yield at 14% moisture content was significantly reduced by water deficit. NERICA 2 and 4 had higher yields at 14% moisture content, higher filled grain ratio percentages (Fig.7b), higher 1000 grain weight and had the least yield reduction relative to the control as compared to NERICA 1, 3 and 5. Water deficit at vegetative and reproductive stage reduced yield by 26% and 67% respectively as compared to well watered plants. Similar results have been reported in maize (Sah and Zamora, 2005). The low yield might have been as a result of decreased filled grains per panicle caused by inhibition of sufficient translocation of assimilates to the grains as the plants competed for moisture. The lowest yield was recorded at water deficit during reproductive stage as compared to water deficit during vegetative stage (Fig.7c). This may be due to the fact that water deficit at reproductive stage accelerated the leaf senescence, inhibited photosynthesis, reduced the assimilate supply and thus decreased the rate and duration of grain filling (Sah and Zamora, 2005). Reproductive stage water deficit can cause asynchrony between pollen shedding and silk emergence and thus results failure of pollination. Lower water potential at early reproductive stage reduces the assimilate supply because of inhibition of photosynthesis which may cause low seed number (Westgate and Boyer, 1985). Among the NERICA varieties there was clear varietal diversity in the performance under water deficit and early maturing varieties performed better at water deficit treatments. Low growth rate of plants is one of the limiting factors of yield under water deficit conditions. Therefore varieties with greater growth rate under water deficit conditions provide the highest grain yield (Bogale *et al*., 2011). As observed by Gupta *et al.* (2001), favorable conditions during growth may permit an expansion of the last internodes as well as higher yield. Carbohydrates are also remobilized from the peduncle and flag leaf to the grain during grain filling period. NERICA 1, 3 and 5 were more sensitive to water deficit than NERICA 2 and 4 hence NERICA 2 and 4 had the highest yield and also the least reduction in yield relative to control at water deficit treatment during reproductive stage. Grain yield of rice may be limited by the supply of assimilates to the developing grain (source limitation) or by the capacity of the reproductive organ to accept assimilates (sink capacity).

V. Conclusion

In the present study, low relative water content due to water deficit inhibited growth and plant function which were reflected in lower transpiration, decreased photosynthesis and lower yield of the five NERICA rice varieties. The effect was more pronounced at water deficit during reproductive stage as compared to vegetative stage. The study shows appreciable differences among the NERICA rainfed rice varieties in respect to their response to vegetative or reproductive stage water deficit. It has shown that the production of yield by NERICA varieties under water deficit may be linked to maintenance of leaf water content and a relatively high photosynthetic rate during water deficit. It can also be linked to NERICAS' ability to recover in gas exchange parameters after rewatering. Water deficit at vegetative and reproductive stage has cumulative effect ultimately manifested by reduction in yield. The various amounts of NERICAS' yield (Kg ha^{-1}) obtained on different treatments showed that NERICA rice is capable of producing worthwhile yield even if it has been affected by water deficit at any stage of growth. The overall results indicate that there is genetic variability present in the NERICA varieties studied. NERICA 2 and 4 were tolerant to water deficit occurring at vegetative stage or reproductive stage as compared to NERICA 1, 3 and 5 because their gas exchange parameters and yield was less affected. The authors recommend that where possible adequate water should be available to NERICA varieties at all developmental stages in order to obtain an optimum yield.

VI. Acknowledgements

The authors are grateful to Japan International Co- operation Agency (JICA) and African Institute for Capacity Development (AICAD) for providing the NERICA seeds for adaptability trials through Prof. J.C. Onyango.

References Références Referencias

1. Atera, E.A., Onyango, J.C., Azuma, T., Asanuma, S., and Itoh, K. 2011. Field evaluation of selected NERICA rice cultivars in western Kenya. *African Journal of agricultural research* 6(1): 60-66.
2. Bogale, A., Tesfaye, K., Galeto, T. 2011. Morphological and physiological attributes associated to drought tolerance of Ethiopian durum wheat genotypes under water deficit conditions. *Biodiversity and Environmental Sciences* 1(2): 22-36.
3. Boyer, J.S. and Westgate, M.E. 2004. Grain yields with limited water. *Experimental Botany* 55: 2385-2394.
4. Casadebaig, P., Dabaeke, P. and Lecoeur, J. 2008. Thresholds for leaf transpiration and transpiration response to soil water deficit in a range of sunflower genotypes. *Agronomy* 28: 646-654.
5. Collinson, S.T., Clawson, E.J., Azam-Ali, S.N. and Black, C.R. 1997. Effects of soil moisture deficits on the water relations of Bambara groundnuts. *Experimental Botany* 48: 877-884.
6. Coombs, J., Hind, G., Leegood, R.C., Tieszen, L.L. and Vonshak, A. 1985. Analytical Techniques, In: Techniques in Bioproductivity and photosynthesis 2nd edition. (Eds) J. Coombs, D.O. Hall, S.P. Long and J.M.O. Scurlock, Pp 219-220, Pergamon Press 1985.
7. Cornic, G. and Fresneau, B. 2002. Photosynthetic carbon reduction and carbon oxidation cycles are the main electron sinks for PSII activity during mild drought. *Annals Botany* 89:887-894.
8. Chatterjee B.N. and Maiti, S. 1988. Principles and practices of rice growing, 2nd edition, Oxford, New Delhi Pp11-235.
9. Cruz, R.T., Turner, N.C. and Dingkuhn, M. 1986. Responses of seven diverse rice cultivars to water deficits, Osmotic adjustment, leaf elasticity, leaf extension, leaf death, stomatal conductance and photosynthesis. *Field Crop Research* 13: 273 – 286.
10. El-Jaafari, S. 2000. Durum wheat breeding for a biotic stresses resistance. Defining physiological traits and criteria. *Options Mediterranean* 40:251-256.
11. El-Hafid, R., Smith, D.H., Karrou, M. and Samir, K., 1998. Physiological response of spring durum wheat cultivars to early season drought in a Mediterranean environment. *Annals of Botany* 81: 363-370.
12. Flexas, J., Bota, J., Loreto, F., Cornic, G. and Sharkey, T.D. 2004: Diffusive and metabolic limitations to photosynthesis under drought and salinity in C_3 plants. *Plant Biology* **6**: 1-11.
13. Fukai, S. Pantuwan, G., Jongdee, B. and Cooper, M. 1999. Screening for drought resistance in rainfed lowland rice. *Field Crop Research* 64: 61- 74.
14. Gupta, N.K., Gupta, S., Kumar, A. 2001. Effects of water stress on physiological attributes and their relationship with growth and yield of wheat cultivars at different stages. *Agronomy and Crop Science*. 186:55-62.
15. Irungu Johnson 2009. Kenya national rice development strategy. Ministry of Agriculture Annual Report Pp 1-7.
16. Jones, G.H. 1996. Plants and microclimate, 2nd edition, Cambridge USA. Pp 72 – 108.
17. Jongdee, B., Fukai, S. and Cooper, M. 2002. Leaf water potential and osmotic adjustment as physiological traits to improve drought tolerance in rice. *Fields Crop Research* 76: 153-163.
18. Kaiser, W.M. 1987. Effects of water deficit on photosynthetic capacity. *Plant physiology* 71:142 – 149.
19. Kaurk, K., Gupta, A.K. and Kaur, N. 2007. Effects of water deficit on carbohydrate status and enzymes of carbohydrate metabolism in seedlings of wheat cultivars. *Biochemica and Biophysica* 44: 223- 230.
20. Lanceras, J.C., Pantuwan, G., Jongdee, B., Toojinda, T. 2004. Quantitative trait Loci associated with drought tolerance at reproductive stage in rice. *Plant Physiology* 135: 384-399.
21. Liu, F., Andersen, M.N. and Jensen, C.R. 2003. Loss of pot set caused by drought stress is associated with water status and ABA content of reproductive structures in soybean. *Functional Plant Biology* 30: 271-280.
22. MOA 2008. Kenya National strategic rice development plan; Crop development division. Annual report Pp 1-10.
23. Penuelas, J., Pinol, J., Ogaya, R. and Filella, I. 1993. Estimation of plant water concentration by the reflectance water index. *International Journal of Remote Sensing* 18: 2869-2879.
24. Ray, J.D., Sinclair, T.R. 1997. Stomatal closure of maize hybrids in response to soil drying. *Crop Science* 37: 803-807.

25. Richards, A. 2000. Selectable traits to increase crop photosynthesis and yield of grain crops. *Experimental Botany* 51:447-458.
26. Sah, S.K. and Zamora, O.B. 2005. Effects of water deficit at vegetative and reproductive stages of Hybrid open pollinated variety and local, maize (*Zea mays* L.). *Agriculture and Animal Science* 26: 37- 42.
27. Serraj, R., Kumar, A., McNally, K.L., Slamet, I., Bruskiewich, R., Macleon, R., Cairns, J.K. and Hijmans, R.J. 2009. Improvement of drought resistance in rice. *Advances in Agronomy* 103: 41-99.
28. Siddique, M.R., Hamid, A. Islam, M. 2000. Drought stress effects on water relations of wheat. *Plant Physiology* 41: 35-39.
29. Sikuku P.A., Netondo G.W., Onyango J.C.,Musyimi D.M., 2010. Effects of Water Deficit on Physiology and Morphology of three varieties of NERICA rainfed rice (*Oryza sativa* L.). Journal of Agricultural and Biological Science 5(1): 23-28.
30. Sinclair,T. and Ludlow, M. 1985. Who taught plants thermodynamics?. The unfulfilled potential of plant water potential. *Australian Journal of Plant Physiology* 12:213-217.
31. Silva, A.M., John, L.J., Jorge, A.G and Sharma, V. 2007. Use of physiological parameters as fast tools to screen for drought tolerance in sugarcane. *Brazilian Journal Plant Physiology* 19(3): 193-201.
32. Sionit, N. and Kramer, P.J. 1983. Effects of water stress during different stages of growth of Soya bean. *Agronomy Journal* 67: 274 – 278.
33. Tenhunen, J.D., Cantario, F.M., Lange, O.L. and Oechel, W.C. 1985. Plant responses to stress. Functional Analysis in Mediterranean Ecosystems, *Ecological Sciences*.15: 28 – 40.
34. Tezara, W., Mitchell, V.J., Driscoll, S.D. and Lawlor, D.W. 1999. Water stress inhibits plant photosynthesis by decreasing coupling factor and ATP. *Nature* 5: 914-917.
35. Upretty, D.C. and Bhatia, R. 1989. Effect of water stress on photosynthesis, productivity and water status of Mung bean. *Crop Science* 163:115-123.
36. Vadez, V., Sinclair, T.R. 2001. Leaf Ureide degradation and Nitrogen fixation tolerance to water deficit in Soybean. *Experimental Botany* 52: 153-159.
37. Vurayai, R., Emongor, V. and Moseki, B. 2011. Physiological responses of Bambara groundnut to short periods of water stress during different development stages. *Asian Journal of Agriculture Science* 3(1): 37-43.
38. Zlatev, S.Z., and Yordanov, I.T. 2004. Effects of soil drought on photosynthesis and chlorophyll fluorescence in bean plants. *Bulgarian Journal of Plant Physiology* 30: 3-18.

This page is intentionally left blank