

Effect of Soil Moisture Stress Duration on the Growth Characteristics and Yield of Rice Cultivars

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Abstract

Soil moisture stress is a major constraint to the productivity of rice under rain-fed conditions. A study was conducted to establish the effect of moisture stress duration on the growth characteristics and grain yields of rice cultivars, namely Namche-1, Namche-3 and Agoro. Rice plants were subjected to moisture stress at tillering and a thesis in the screen house. Moisture stress at tillering stage caused significant leaf rolling in Agoro than in Namche-3, but at a thesis Agoro was the least ($P \leq 0.05$) affected. Moisture stress at tillering and a thesis significantly reduced the number of tillers in Agoro, but not in Namche cultivars. The growth period of Agoro was significantly longer than that of the control when it was stressed at tillering for 15 days, but stressing Agoro at a thesis didn't affect its maturity period. Stressing Namche cultivars at tillering and a thesis increased ($P \leq 0.05$) their maturity periods, though these periods were shorter ($P \leq 0.05$) than that of Agoro. Grain yields for all the cultivars at tillering and a thesis decreased as the stress period was prolonged. Grain yields of Namche cultivars were higher ($P \leq 0.05$) than that of Agoro. Therefore, the growing of Namche cultivars in areas with insufficient moisture for rice production would be appropriate.

Keywords: Cultivar, growth stages, soil moisture stress, rice cultivars, yield components

1. Introduction

Rice is the most important food grain for more than a third of the world's population, and provides 35-60% of the calories consumed (Zhao *et al*, 2011). The world planted area with rice is about 150 million hectares, while production stands at 500 million metric tons (MT). In recent years, rice production has been expanding at the rate of 6% per annum, with 70% of the production increase being mainly due to land expansion and only 30% being attributed to an increase in productivity (Fagade, 2000). According to OSIRIZ, CIRAD's Observatory of International Rice Statistics (2008), Africa cultivated about 9 million hectares of rice in 2006 and production, which surpassed 20 million MT for the first time, was expected to increase by 7% per annum in future.

Despite the upward trends in international and domestic rice prices, domestic rice consumption is increasing at the rate of 8% per annum, surpassing domestic rice production growth rates of 6% per annum. The production-consumption gap in many African countries is being filled by imports, valued at over US\$ 1.4 billion per year. The share of rice imports rose from 43% in 1991 – 2000 to 57% in 2002 – 2004 (WARDA, 2007). Africa's emergence as a big rice importer is explained by the fact that during the last decade rice has become the most rapidly growing food source in sub-Saharan Africa (Solh, 2005).

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Indeed, due to high population growth rate of 4% per annum, rising incomes and a shift in consumer preferences in favour of rice especially in urban areas, the relative growth in demand for rice has been higher in Africa than anywhere in the world (Balasubramanian *et al.*, 2007). Rice production in Uganda started in 1942 mainly to feed the World War II soldiers. However, due to a number of constraints, production remained minimal until 1974 when the government established commercial farms in Kibimba, Doho and Olweny. Apart from these government rice schemes, rice growing in Uganda is still dominated by rural small-scale farmers living in areas adjacent to wetlands. Major rice growing regions are eastern and western Uganda due to the presence of lowland areas with high moisture content throughout the growing season. Rice production in these regions has steadily increased in the recent past due to a number of factors including the introduction and promotion of upland rice growing. Currently, the area under upland rice growing in Uganda constitutes 71% of the total area under rice production (Gitau, *et al.*, 2011).

In spite of the release of newly developed high yielding upland rice cultivars, the average rice yields for Ugandan farmers are still low, around 1.5 MT ha⁻¹ as opposed to 3.5 MT ha⁻¹ under irrigated conditions (Usman, 2013; Odogoola *et al.*, 2006). This has been largely attributed to both biotic and abiotic stresses, namely pests and diseases, and insufficient soil moisture in areas receiving low rainfall amounts (Briggs and Twomlow, 2002). The occurrence of moisture stress affects many of the physiological processes such as photosynthesis and transpiration resulting in reduced growth and eventual yield loss. Drought has a global dimension in that about 18 million MT of rice worth US\$3.6 billion are lost each year (Conway, 2004). Yield losses of up to 15 – 20% have been reported in most parts of Africa, especially in rain-fed production environments (Odogoola, 2006; Lafitte *et al.*, 2004). These losses affect food availability, resulting in higher malnutrition rates among the population in the affected areas.

In Uganda, a large portion of smallholder farmers depend on rain-fed agriculture where water supply is unpredictable. Some studies have been carried out to identify upland rice cultivars that are tolerant to soil moisture stress (drought) in Uganda. However, little has been done to determine the length of drought period these rice cultivars can withstand. Therefore, this study seeks to determine the effect of soil moisture stress duration on the growth characteristics and yield components of selected upland rice cultivars.

2. Materials and Methods

2.1 Experimental site

The study was conducted at the National Crops Resources Research Institute (NaCRRI), Namulonge located in central Uganda, (32° 34'E, 0° 32'N) at 1200m above sea level. The area has an average annual rainfall of approximately 1300 mm, temperature of 22 °C, and annual minimum and maximum temperatures of 16 and 28 °C, respectively. The soils are dark, reddish brown, sandy loams, with a pH range of 5.5 to 6.2.

2.2 Experimental design and treatments

The experiment was conducted in the greenhouse. Three rice cultivars (Namche-1, Namche-3 and Agoro) were subjected to seven irrigation regimes, using a Completely Randomized Design (CRD), with three replications. Rice was planted in an experimental concrete box 8 m long and 3 m wide, divided into twenty one plots, each measuring 1×1.14m. The spacing used was 30 cm between rows and 15 cm between hills, and three seeds were planted per hill. Nitrogen fertilizer was applied at the rate of 80 kg N ha⁻¹ in split doses, 50% basally and 50% as topdressing. Uniform irrigation was applied in all the plots after planting until tillering stage when some of the plots were subjected to moisture stress treatments by withholding irrigation for prescribed periods. Treatment 1 (T1) served as a control where irrigation was continuous till harvest; treatments T2, T3 and T4 comprised withholding irrigation at maximum tillering for 15, 25 and 30 days respectively; while treatments T5, T6 and T7 comprised withholding irrigation at 50% flowering (anthesis) for 15, 25 and 30 days respectively. Moisture content of the soil from the surface up to 15 cm depth in each plot was measured at the time of planting and before subjecting some of the plots to moisture stress treatments. Maximum tillering was considered to have occurred 30 days from planting date, while anthesis was considered to have occurred after 60 days from planting date.

2.3 Soil analysis

The soil used in the experiment was collected from the farm at NaCRRI, air-dried, grounded and sieved through a 2 mm sieve to remove debris. The soil was analyzed for physical (silt, sand and clay) and chemical (N, available P and K) contents and pH (Table 1) following standard methods described by Okalebo *et al.* (2002). Soil pH was measured in a soil water solution ratio of 1:2.5. Organic matter content was analyzed using the potassium dichromate wet acid oxidation method. Total N was determined by Kjeldhal digestion method, extractable P by Bray P1 method and exchangeable K from an ammonium acetate extract by flame photometry. Particle size distribution (texture) was determined using the Bouyoucos (hydrometer) method.

Table 1: Characteristics of soil (on DM basis)

pH	OM	N	Available P	Exchangeable K (g kg ⁻¹)	Sand	Clay	Silt
5.4	23.5	1.5	0.011	0.183	690	180	130

2.4 Data collection

This commenced 30 days from planting date and was done before and after every stress period till the end of the experiment. Data was collected on leaf rolling, number of tillers per hill, days to maturity, number of panicles per hill, biological yield (kg/ha) and grain yield (kg/ha). Four plants from the middle of each plot were randomly selected for data collection. Leaf rolling was determined visually on the basis of the degree of folding (O'Toole *et al.*, 1979). Plants were scored for leaf rolling after 15, 25 and 30 days of stress, using the scale of 0 – 9, the standard evaluation system for rice developed by IRRI (IRRI, 2002), where 0 (zero) represented healthy leaves, 1 represented leaves starting to fold along the margins, 3 for leaves folded into V- shape, 5 for leaves fully cupped, 7 for leaves folded to the extent that leaf margins touch each other (O – shaped), and 9 for leaves tightly rolled.

Tiller numbers per treatment were determined by counting and recording all emerging shoots per hill from 30 days after planting up to anthesis stage. Days to maturity were determined by counting the days from planting date to maturity date. Panicles were counted per hill. Biological yield (BY) was determined by weighing rice plants along with panicles obtained from each plot, while grain yield was determined by weighing the grain shelled from panicles obtained from each plot.

2.5 Statistical analysis of data

All the data collected were summarized in Microsoft excel and subjected to a two – way analysis of variance (ANOVA) using GENSTAT tenth Edition (VSN International Limited, 2011). Treatment means for the different parameters were separated using Fisher's least significant difference (LSD) procedure at 5 % level of significance.

3. Results

3.1 Leaf rolling at tillering stage

There were significant differences among the treatments ($P \leq 0.001$) and the cultivars ($P \leq 0.01$) (Table 2). All the three cultivars were significantly affected by the treatments when compared with the control (T1). However, the effect was severe when the cultivars were subjected to stress for 15 days. Among the three cultivars Agoro was significantly affected by the treatments than Namche-3, as revealed by the cultivar means (Table 2).

Table 2: Effect of soil moisture stress duration on plant leaf rolling at tillering stage

Treatments	Cultivar			Mean
	Agoro	Namche-1	Namche-3	
Continuous irrigation till harvest (control) (T1)	0.00 ^c	0.00 ^c	0.00 ^c	0.00
Stop irrigation at maximum tillering for 15 days (T2)	5.08 ^a	4.50 ^a	3.83 ^a	4.44
Stop irrigation at maximum tillering for 25 days (T3)	0.33 ^c	0.43 ^c	0.33 ^c	0.36
Stop irrigation at maximum tillering for 30 days (T4)	3.08 ^b	3.21 ^b	1.92 ^b	2.74
Cultivar means	2.12	2.03	1.52	
F- prob. Cultivar = <0.007, Treatment = <0.001, Cultivar × Treatment = 0.337				
LSD _(0.05) Cultivar = 0.36, Treatment = 0.55, Cultivar × Treatment = 0.96				

abc = Means within the same column having different superscripts are significantly ($P \leq 0.05$) different

3.2 Leaf rolling at a thesis stage

There were significant differences among the treatments ($P \leq 0.001$) and cultivars ($P \leq 0.05$) at an thesis stage (Table 3). Also the interaction between the cultivars and treatments was significant. All the cultivars were not significantly ($P > 0.05$) affected when they were subjected to moisture stress for 15 days (T5) as compared with the control (T1). However, they succumbed to stress when the stressful conditions were prolonged to 25 and 30 days. According to the cultivar means, leaf rolling was significantly different in all the varieties, and was highest in Namche-1 followed by Namche-3 and lastly Agoro. When the results of subjecting the three rice cultivars to moisture stress at tillering stage are compared with those of an thesis stage, Agoro which was severely affected at tillering stage was the least affected at an thesis stage.

Table 3: Effect of moisture stress duration on plant leaf rolling at an thesis stage

Treatments	Cultivar			Mean
	Agoro	Namche-1	Namche-3	
Continuous irrigation till harvest (control) (T1)	0.38 ^g	1.00 ^c	0.42 ^g	0.59
Stop irrigation at an thesis for 15 days (T5)	0.42 ^{bc}	0.42 ^c	0.33 ^c	0.79
Stop irrigation at an thesis for 25 days (T6)	1.17 ^{ab}	2.83 ^b	2.17 ^b	2.06
Stop irrigation at an thesis for 30 days (T7)	1.79 ^a	4.08 ^a	3.33 ^a	
Cultivar means	0.9	2.08	1.56	
F prob. Cultivar = <0.029, Treatment = <0.001, Variety × Treatment = <0.008				
LSD _(0.05) Cultivar = 0.46, Treatment = 0.70, Variety × Treatment = 1.21				

abc = Means within the same column having different superscripts are significantly ($P \leq 0.05$) different

3.3 Number of tillers

There were significant differences ($P \leq 0.001$) among the treatments, the cultivars as well as the interaction between treatments and cultivars (Table 4). Subjecting Agoro to moisture stress at tillering significantly reduced the number of tillers, as compared to the control (T1). The effect was severe when Agoro was stressed for 15 (T2) and (T4) 30 days. Subjecting Agoro to moisture stress at an thesis also affected tiller numbers, as compared to the control. However, tiller numbers were higher as compared to those that were produced when Agoro was subjected to moisture stress at tillering stage. However, the tiller numbers were significantly lower in treatment 5 when Agoro was subjected to stress for 15 days (T5) than when it was subjected to stress for 25 (T6) and 30 (T7) days. For the case of Namche-1, tiller numbers for all the treatments at tillering and an thesis were similar to those of the control (Table 4). For Namche-3, subjecting it to moisture stress at tillering caused significant reduction in tiller numbers as compared to the control. The reduction was more when subjected to stress for 15 days (T2).

However, subjecting Namche-3 to stress at an thesis stage only significantly reduced tiller numbers for the stress period of 15 days (T5) as compared to the control. According to the cultivar means, Agoro cultivar performed better with higher tiller number as compared with Namche cultivars.

Table 4: Effect of moisture stress duration and growth stage at which it occurs on tillering

Treatments	Cultivar			Mean
	Agoro	Namche-1	Namche-3	
Continuous irrigation till harvest (control) (T1)	23.33 ^a	8.47 ^{ab}	9.50 ^{ab}	13.77
Stop irrigation at maximum tillering for 15 days (T2)	13.89 ^f	7.86 ^{ab}	5.92 ^e	9.22
Stop irrigation at maximum tillering for 25 days (T3)	18.00 ^d	8.89 ^a	8.17 ^{cd}	10.69
Stop irrigation at maximum tillering for 30 days (T4)	12.83 ^f	8.50 ^{ab}	7.36 ^d	9.56
Stop irrigation at anthesis for 15 days (T5)	15.47 ^e	7.53 ^b	7.25 ^d	9.56
Stop irrigation at anthesis for 25 days (T6)	19.39 ^c	7.81 ^b	8.50 ^{bc}	11.90
Stop irrigation at anthesis for 30 days (T7)	20.81 ^b	7.94 ^{ab}	9.72 ^a	12.82
Cultivar means	17.67	8.06	8.06	

F- prob. Cultivar = <0.001, Treatment = <0.001, Cultivar × Treatment = <0.001
LSD_(0.05) Cultivar = 0.701, Treatment = 1.071, Cultivar × Treatment 1.85

abc = Means within the same column having different superscripts are significantly ($P \leq 0.05$) different

3.4 Days to maturity

There were significant differences among the three cultivars ($P \leq 0.001$) and treatments ($P \leq 0.01$) in the number of days to maturity, but their interactions were not significant (Table 5). Irrigation regimes affected the number of days taken by the rice plants to reach maturity. When moisture stress was imposed on Agoro at tillering stage for 15 days (T2), the number of days to maturity increased significantly as compared to the control. However, extending the stress period to 25 and 30 days (T3 and T4) did not significantly ($P > 0.05$) increase the number of days to maturity. Subjecting Agoro to stress at anthesis stage did not affect the maturity period, apart from T6 which prolonged ($P \leq 0.05$) the maturity period when compared with the control (Table 5). When Namche-1 and Namche-3 were subjected to moisture stress at both tillering and anthesis stages, the maturity periods were significantly increased when compared with their control treatments. For Namche-1, there were no significant differences between the stressful treatments at tillering stage (T2 – T4) and at anthesis stage (T5 – T7). For Namche-3, a significant ($P \leq 0.05$) difference in the maturity periods of stressful treatments was only observed between T2 and T3. According to the cultivar means, maturity periods of Namche-1 and Namche-3 were similar ($P > 0.05$) but shorter ($P \leq 0.05$) than that of Agoro (Table 5).

Table 5: Effect of moisture stress duration and growth stage at which it occurs on days to maturity

Treatment	Cultivar			Mean
	Agoro	Namche-1	Namche-3	
Continuous irrigation till harvest (control) (T1)	130.0 ^b	98.7 ^c	96.0 ^c	108.2
Stop irrigation at maximum tillering for 15 days (T2)	135.7 ^a	108.3 ^a	103.3 ^b	114.4
Stop irrigation at maximum tillering for 25 days (T3)	132.7 ^{ab}	108.3 ^a	108.7 ^a	116.6
Stop irrigation at maximum tillering for 30 days (T4)	131.3 ^b	105.3 ^{ab}	105.0 ^{ab}	113.9
Stop irrigation at anthesis for 15 days (T5)	131.3 ^b	103.7 ^b	105.3 ^{ab}	113.4
Stop irrigation at anthesis for 25 days (T6)	137.0 ^a	107.7 ^{ab}	107.0 ^{ab}	117.2
Stop irrigation at anthesis for 30 days (T7)	134.3 ^{ab}	107.7 ^{ab}	108.0 ^a	116.7
Cultivar means	133.2	105.0	104.9	

F- prob. Cultivar = <0.001, Treatment = 0.002, Cultivar × Treatment = 0.856
LSD_(0.05) Cultivar = 2.81, Treatment = 4.29, Cultivar × Treatment = 7.43

abc = Means within the same column having different superscripts are significantly ($P \leq 0.05$) different

3.5 Number of panicles

The effect of moisture stress on the number of panicles was highly significant ($P \leq 0.001$) among the treatments (Table 6). Subjecting Agoro to moisture stress at tillering stage significantly reduced the number of panicles, and the effect was more severe in T4, when compared to the control. During the anthesis stage, Agoro cultivar performed according to the duration of the stress period. When stressed for 15 days at anthesis (T5), panicle numbers were similar to those of the control, but significantly reduced when stress period was extended to 25 and 30 days.

When moisture stress treatments were imposed on Namche-1 at tillering and anthesis stages for 15, 25 and 30 days, the number of panicle obtained were not significantly different from each other, except for T7 where panicle number was lower than that of the control. For Namche-3, when subjected to moisture stress at tillering, treatments 3 and 4 had similar panicle numbers as compared to the control, while for T2, panicle numbers were significantly lower than that of the control as well as other stressful treatments (T3 and T4). At anthesis stage, when Namche-3 was subjected to moisture stress, panicle numbers for treatments T5 and T7 were significantly lower than that of the control. Treatments 5 and 6 had panicle numbers that were not significantly different, while for T6 the panicle number was significantly higher than that of T7. According to the performance of the treatment means, Namche cultivars performed better on the number of panicles than Agoro. However, the cultivar means of panicle number of Namche-1 and Namche-3 were not significantly different (Table 6).

3.6 Biological yield

There were significant ($P \leq 0.001$) differences among the cultivars of the biological yield (BY), but the interactions between cultivars and the treatments were not significant (Table 6). In the case of Agoro at tillering stage, T2 performed better than the control (T1) while the rest of the treatments performed poorer than the control. Exposing Agoro to stress at anthesis stage for 15 days did not make any significant difference on the BY as compared to the control. However, when the stress was prolonged to 25 and 30 days, BY significantly reduced. When the moisture stress was imposed on Namche-1, there were no significant differences in BYs for all treatments as compared to the control. For Namche-3 cultivars, exposure to stress for 15 days at tillering resulted in significant reduction in BY. However, no significant change occurred when stress period was increased to 25 and 30 days (Table 6). Subjecting Namche-3 to stress at anthesis stage did not significantly affect BY for all the treatments.

Table 6: Effect of moisture stress duration and growth stage at which it occurs on the yield components of selected rice cultivars

Treatments	Cultivar	Panicle numbers	Biological yield (kg/ha)	Grain yield kg/ha
T1	Agoro	12.50 ^a	6219 ^b	463.0 ^{efg}
T2	Agoro	10.75 ^b	7504 ^a	393.6 ^{ghi}
T3	Agoro	7.83 ^{bcd}	3137 ^{efgh}	214.8 ^{hij}
T4	Agoro	4.92 ^{gh}	3367 ^{defg}	200.0 ^{ij}
T5	Agoro	12.67 ^a	5185 ^{bc}	529.6 ^{efg}
T6	Agoro	5.25 ^{gh}	4489 ^{cd}	163.0 ^j
T7	Agoro	3.25 ^h	3993 ^{cde}	89.9 ^j
T1	Namche-1	7.58 ^{bcd}	2537 ^{fgh}	944.4 ^b
T2	Namche-1	6.92 ^{cdefg}	3052 ^{efgh}	869.3 ^b
T3	Namche-1	6.08 ^{efg}	2430 ^{gh}	411.1 ^{fgh}
T4	Namche-1	6.50 ^{defg}	3378 ^{defg}	833.3 ^{bc}
T5	Namche-1	6.42 ^{defg}	2748 ^{fgh}	785.2 ^{bcd}
T6	Namche-1	6.92 ^{cdefg}	2811 ^{efgh}	400.0 ^{fgh}
T7	Namche-1	5.67 ^{gh}	2330 ^{gh}	193.6 ^{ij}
T1	Namche-3	9.00 ^{bc}	3667 ^{def}	1659.3 ^a
T2	Namche-3	4.83 ^{gh}	2333 ^{gh}	240.7 ^{hij}
T3	Namche-3	7.50 ^{bcd}	2796 ^{efgh}	607.4 ^{def}
T4	Namche-3	7.42 ^{bcd}	2548 ^{fgh}	963.0 ^b
T5	Namche-3	6.42 ^{defg}	2019 ^h	648.1 ^{cde}
T6	Namche-3	8.33 ^{bcd}	2293 ^{gh}	500.0 ^{efg}
T7	Namche-3	5.25 ^{gh}	2207 ^{gh}	218.5 ^{hij}
F- prob.	Cultivar	0.154	<0.001	<0.001
	Treatment	0.002	0.084	<0.001
	Treatment × Cultivar	0.014	0.095	<0.001
LSD _(0.05)	Cultivar	1.46	791.0	136.8
	Treatment	2.22	1208.3	209.0
	Treatment × Cultivar	3.85	2092.9	362.1

abc = Means within the same column having different superscripts are significantly ($P \leq 0.05$) different

3.7 Grain yield

Comparison of the means on the grain yield showed that the effects of treatments, cultivar and their interactions were significant ($P \leq 0.001$) (Table 6). Among the Agoro treatments at tillering stage, the grain yield for the 15 days' stress was not different ($P > 0.05$) from that of the control. But as stress period increased to 25 and 30 days the grain yield significantly reduced. At anthesis stage, when stress was imposed, the 15 days' stress (T5) had the grain yield similar to that of the control, while T6 and T7 produced lower ($P \leq 0.05$) grain yield as compared with the control. In the case of Namche-1, at tillering stage, grain yields for T2 and T4 were similar to that of the control, but that of T3 when the plants were stressed for 25 days was significantly lower. At anthesis stage, grain yield at 15 days' stress period (T5) was the same as that of the control. When stress period was extended to 25 and 30 days, the yield significantly reduced.

For Namche-3, when it was exposed to moisture stress, there was significant reduction in grain yield for all the treatments as compared with the control. At tillering stage, the decline was greatest at stress period of 15 days (T2) while at stress period for 30 (T4) days grain yield was significantly higher than that of the 25 days (T3) stress. At anthesis, the yield decreased with the increase in soil moisture stress. Stressing Namche-3 at anthesis stage for 15 and 25 days did not because a significant change in grain yields between the two treatments, but when stress period was extended to 30 days, grain yield significantly reduced when compared with that of T5 and T6.

According to the cultivar means, grain yields of Namche-1 and Namche-3 were not significantly different but were higher ($P \leq 0.05$) than that of Agoro (Table 6). Therefore, the results indicated that Namche-1 and Namche-3 cultivars had the highest performance in terms of grain yield under moisture stress. For Agoro, the yield performance greatly declined under stressful conditions as compared with the cultivar means.

4. Discussion

4.1 Leaf rolling at tillering and anthesis

At tillering stage, leaf rolling was greatest where rice plants were subjected to stress for 15 days due to shock. Leaf rolling reduced when the stress was prolonged to 25 days indicating that plants tried to adjust and recover from stress. However, extending the stress period to 30 days again affected the rice plants. Leaf rolling in treatments T2 and T4 was attributed to the decrease in water contents within the leaf tissues leading to cells losing turgidity. Leaf rolling can reduce further loss of water by ensuring that the air trapped by the rolled leaf becomes saturated so as to reduce the water potential gradient between the water in the leaf and in air trapped by the leaf. In some plant, leaf rolling is a morphological feature associated with soil water deficit, and is an effective mechanism that enables plants in tropical and arid areas to avoid moisture stress (Street and Helgi, 1984). Rolling reduces the leaf area and consequently the rate of transpiration. Kadioglu and Terzi (2007) reported that leaf rolling is a hydronastic mechanism that reduces light interception, transpiration and leaf dehydration. Fischer *et al.* (2007) observed a correlation between leaf rolling and the internal water status of the leaf tissue. Leaf rolling is also related with the stomatal closure, which reduces transpiration from leaves, and also plays a role in osmotic adjustment to maintain internal plant water status (Subashri *et al.*, 2005).

According to the cultivar means, Namche 3 was less affected by moisture stress at tillering stage than Agoro. The degree of leaf rolling of rice plant is dependent on the ability of the cultivar to adjust osmotically. In plants, osmotic adjustment refers to the maintenance of turgor by lowering the tissue osmotic potential, arising from the net accumulation of solutes in the cell sap in response to the water potential of the cell's environment. Under moisture stress conditions the cells and tissues of some crop plants increase their solute concentration. This leads to maintenance of cell turgor, because water is drawn back in to the cell rather than flowing out (Kramer and Boyer, 1995). The maintenance of turgor pressure as the plant water potential declines is essential for cell enlargement, growth, stomatal opening and related physiological and morphological processes (Morgan, 1997). Osmotic adjustment has been identified as a physiologically important moisture stress tolerance characteristic (Turner *et al.*, 2001) and it aids the productivity of grasses under soil moisture stress by delaying leaf rolling response, although it may reduce transpiration, light interception and photosynthesis.

Osmotic adjustment also delays leaf senescence which is undoubtedly important in recovery of canopy photosynthetic activity and crop productivity after moisture stress is relieved. In mature tissues, the decline of turgidity might affect the properties of cellular membranes, such as permeability and enzymatic properties of the cell membranes and the tonoplast. With severe desiccation, death of the plant cells occurs due to structural disorganization of the protoplasm. When cells dry out, the protoplasts will be subjected to tension resulting from contraction in volume and their adherence to the cell walls – stress which might tear cell membranes. At finer level, there is structural damage to the macromolecules, such as denaturation of nucleic acids (Salisbury and Ross, 1992). Leaf rolling has been used as a reliable index of turgor loss in cereal crops which occurs as a result of the reduction in leaf water potential (Williams *et al.*, 1992). Under moisture stress conditions, cultivars with low osmotic adjustment may show early leaf rolling because of loss of turgor in response to low water potential while cultivars with higher osmotic adjustment may show delayed leaf rolling because of turgor maintenance. Osmotic adjustment has been demonstrated to maintain stomatal opening and photosynthesis during soil moisture stress conditions (Seeman *et al.*, 1999). Leaf rolling can thus be used as a visual score to select for moisture tolerance in rice (Fischer *et al.*, 2007; Lafitte *et al.*, 2004). A smaller degree of leaf rolling is taken as indicative of a greater degree of dehydration avoidance.

4.2 Effect of moisture stress duration and growth stage at which it occurs on tillering

In Agoro and Namche-3, moisture stress at tillering and anthesis stages resulted in significant ($P \leq 0.001$) variation in the number of tillers as compared with the control. Differences in tiller production under soil moisture levels and growth stages might be due to the fact that under moisture stress conditions, plants were not able to produce enough assimilates because of inhibited photosynthesis. It could also be attributed to reduced amount of water uptake that led to inhibition of cell division in the meristematic tissues. The results agreed with those of Castillo *et al.* (2006) and Rahman *et al.* (2002) who also attributed differences in tiller numbers to moisture stress. The higher numbers of tillers in Agoro than in Namche cultivars is mainly due to genetic differences.

4.3 Effect of moisture stress duration and growth stage at which it occurs on days to maturity

Under moisture stress conditions, Namche-1 and Namche-3 took longer to reach maturity, while for Agoro there were no significant differences between the maturity periods of stressful treatments and the control, except for treatments T2 and T6. Significant increases in the number of days to maturity in Namche cultivars meant that moisture stress retards the growth of these cultivars, which exposes their susceptibility. However, since they are quick maturing they can be planted early, since in severe moisture stress conditions, early maturity feature is an important mechanism for escaping drought (Jongdee *et al.*, 2006; Lafitte *et al.*, 2004).

4.4 Effect of moisture stress duration and growth stage at which it occurs on the number of panicles, and biological and grain yields of selected rice cultivars

The findings on the number of panicles are in agreement with those of RRD (1999) who reported that moisture stress at or before panicle initiation reduced panicle number regardless of the crop growth stage at which stress occurred. This might be due to the fact that moisture stress reduces the rate of cell division and growth of individual cells. The differences in BY could have resulted from the decline in the ability of different cultivars to absorb nutrients, and compose and transfer assimilates due to water shortage within the plants. The increase in BY of plants under favorable soil moisture conditions can also be attributed to the expansion of leaf area and its higher durability. It has been reported that usually the cultivars which have longer growing season have higher BY (Ehdaei, 1998). Moisture stress especially at the anthesis stage, reduces chances of grain filling resulting in reduced numbers of fertile panicles, and consequently low grain yields (Maisura *et al.*, 2014; Guolan *et al.*, 2010). Slow grain filling, reduction in 1000-grain weight, and an increase in spikelet sterility under moisture stress conditions was also reported by Raman *et al.* (2012) and Botwright Acuña *et al.* (2008). Moisture stress can also reduce grain yield by disrupting leaf gaseous exchange properties especially CO_2 assimilation rates and stomatal conductance, limiting the sizes of source and sink tissues, impairing phloem loading and assimilate translocation, and reducing the activities of sucrose and starch synthesis enzymes (Farooq *et al.*, 2009; Anjum *et al.*, 2011).

It has also been reported that the magnitude of grain yield loss depends on the length of moisture stress, the phase of crop growth at which it occurs and the severity of stress (Kumar *et al.*, 2014). The results of this study have shown that grain yield reduction indeed is more closely related to the duration of stress than to the stage at which the stress occurs (Table 6). This is also confirmed by the mean grain yields obtained at each stage when the stress treatments were applied (Table 7). Although there are large percentage reduction between mean yields obtained at the control and stressful treatments, differences between the percentages of stressful treatments are very low (Table 7).

Table 7: Summary of the effect of moisture stress duration and growth stage at which it occurs on the grain yields of selected rice cultivars

Cultivar	Growth stage	Mean grain yield (kg/ha)	% yield reduction
Agoro	Control (T1)	463.0	
	Tillering stage	269.5	42
	An thesis stage	260.8	44
Namche-1	Control (T1)	944.4	
	Tillering stage	414.8	56
	An thesis stage	395.1	58
Namche-3	Control (T1)	1659.3	
	Tillering stage	603.7	63
	An thesis stage	455.5	73

5. Summary, conclusions and recommendation

The study revealed that:

Moisture stress at tillering stage causes significant leaf rolling in Agoro than in Namche-3. But subjecting the cultivars to stress at a thesis showed that Agoro which was severely affected at tillering stage was the least ($P \leq 0.05$) affected. Agoro portrayed a very high tillering ability than Namche cultivars. But subjecting Agoro to stress both at tillering and a thesis significantly reduced the number of tillers, as compared to the control, which was not the case with Namche cultivars. However, basing on the cultivar means, Agoro had higher tiller numbers than Namche cultivars. Agoro had a significantly longer growth period as compared to the control when it was stressed at tillering for 15 days; but subjecting it to stress at an thesis did not affect the maturity period. Stressing Namche-1 and Namche-3 at both tillering and an thesis stages, increased ($P \leq 0.05$) their maturity periods when compared with their controls, though their maturity periods were similar but shorter ($P \leq 0.05$) than that of Agoro.

Subjecting Agoro to stress at tillering significantly reduced the number of panicles when compared with the control. When stressed for 15 days at an thesis panicle numbers were similar to those of the control, but reduced ($P \leq 0.05$) when stress period was extended. For Namche-1, stress at tillering and an thesis stages did not affect the number of panicles. For Namche-3, panicle numbers at tillering stage did not vary much from that of the control, while at an thesis stage, panicle numbers for treatments T5 and T7 were lower ($P \leq 0.05$). Basing on the treatment means, Namche cultivars performed better on the number of panicles than Agoro. For Agoro at tillering stage, BY values for all the treatments were lower ($P \leq 0.05$) than the control, except treatment T2. Exposing Agoro to stress at an thesis resulted in BY reduction when the stress was prolonged to 25 and 30 days. For the case of Namche-1, there were no significant differences in BYs for all treatments as compared to the control. For Namche-3 cultivars, exposure to stress for 15 days at tillering resulted in BY reduction, but no significant change occurred when stress period was prolonged.

Generally, grain yields for all the cultivars both at tillering and an thesis decreased as the stress period was prolonged. Basing on the cultivar means, grain yields of Namche-1 and Namche-3 were similar but were higher ($P \leq 0.05$) than that of Agoro. Therefore, the results indicated that Namche-1 and Namche-3 cultivars performed better in terms of grain yield under moisture stress than Agoro.

Therefore, the following conclusions were made basing on the findings.

The occurrence of soil moisture stress (drought) at the tillering and anthesis growth stages of rice cultivars significantly affects the growth characteristics and yield components of the cultivars leading to reduced grain yields. Grain yield reduction is more severely affected by the duration of stress than by the stage at which the stress occurs.

In spite of having higher tillering ability, Agoro was the most affected by moisture stress, probably due to longer maturity period and being more vegetative with low grain yield. Therefore, it was recommended that the growing of Namche cultivars should be promoted in areas with insufficient soil moisture for rice production.

Acknowledgements

The authors express sincere gratitude to the West Africa Agriculture Productivity Project – Liberia (WAAPP) for supporting this research. We also extend our thanks and appreciation to the management and technical staff of the National Crops Resources Research Institute (NaCRRI), Namulonge for their assistance during the research.

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