Journal of Plant Breeding and Crop Science

Volume 7 Number 6 June 2015

ISSN 2006-9758

Academic Journals

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Journal of Plant Breeding and Crop Science

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Vol. 7(6), pp. 163-169, June 2015
DOI: 10.5897/JPBCS2014.0450
Article Number: A8E7C2D53630
ISSN 2006-9758

http://www.academicjournals.org/IPBCS

Journal of Plant Breeding and Crop Science

Full Length Research Paper

Generation mean analysis to estimate genetic parameters of some traits for rice–weed competitiveness

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Received 6 March, 2014; Accepted 11 December, 2014

Weeds are the most widespread biotic production constraint of rice in Africa and one of the major factors limiting grain yield. An efficient breeding strategy could be particularly important for improving weed management in sub-Saharan Africa (SSA) because most smallholder rice farmers use few external inputs. To understand rice weed competitiveness, experiments on reciprocal interspecific crosses derived from FKR19 (*Oryza sativa*) and CG20 (*Oryza glaberrima*) were carried out to estimate gene effects and heritability of traits: plant height at five leaves, plant height 30 days after transplanting, plant height at maturity, number of tillers at 30 and 60 DAT, number of fertile tillers, width of leaves at 80 DAT and at maturity, and length of leaves at 80 DAT and at maturity for rice–weed competitiveness. Six generations – P_1, P_2, F_1, F_2, BC_1F_1 and BC_2F_1 – were raised and subjected to generation mean analysis. The lowest heterosis of F_1 was obtained in both crosses (CG20/FKR19 and FKR19/CG20), except for plant height at 30 days after transplanting and leaf width at maturity in the CG20/FKR19 cross. The majority of traits displayed higher dominance gene effects (H_{5_L}, H_{30} and $L_{\_80}$ for CG20/FKR19; $W_{\_mat}$ and $L_{\_mat}$ for FKR19/CG20) than additive gene effects; the latter were slight and non-significant for the majority of traits. Duplicate epistasis was observed for the number of tillers 30 days after transplanting and leaf length at maturity and plant height at maturity. Additive genetic variance values were higher in CG20/FKR19, revealing that the CG20 variety can be used as a donor parent. Plant height at maturity, length of leaves at 80 DAT and at maturity showed high narrow-sense heritability (h_n^2>0.70), influencing weed competitiveness.

Key words: Additive, dominance, heritability, rice, variance components, weed competitiveness.

INTRODUCTION

Rice (*Oryza sativa* L.) is one of the most important crops in the world. It is the fifth most important cereal in Africa in terms of area harvested, and fourth in terms of production (FAO, 2008). In sub-Saharan Africa (SSA), 80% of rice is produced by smallholder farmers (WARDA, 2004, personal communication). Weeds are the most widespread biotic production constraint of rice in Africa and one of the major factors limiting grain yield (Halidou

et al., 2006). Screening assessments have revealed a selection of rice varieties that provide a superior level of weed competitiveness in African production systems. These include IG10 (Johnson et al., 1998; Fofana and Rauber, 2000), CG14 (Dingkuhn et al., 1998; Jones et al., 1996) and CG20 (Jones et al., 1996; Sarla and Mallikarjuna, 2005; Moukoumbi et al., 2011). Understanding the dynamics of crop genetic resources facilitates access to the diversity of traits – including weed competitiveness – that can be exploited. An efficient breeding strategy could be particularly important for improving weed management in SSA because most smallholder rice farmers use few external inputs (Rodenburg and Johnson, 2009).

The choice of an effective rice breeding approach to select for a particular characteristic depends substantially on the knowledge of the genetic system controlling these characteristics (Azizi et al., 2006). The value of each parameter depends on a combination of its genotypic effects and environmental effects. Genotypic variance can be divided into genetic additive variance (V_A), dominance (V_D), interactive additive–dominance (V_{AD}) and environmental (V_E) components. Determining these components contributes to a better understanding of the action of genes involved in the expression of the trait (Wolf and Hallauer, 1997). Generation mean analysis (Mather and Jinks, 1971) or scaling tests have been widely used for genetic analysis (Fall, 1994; Kearsey and Pooni, 1996; Möhring and Piepho, 2010). This approach was used in the present research to estimate genetic parameters such as additive gene effects, dominance gene effects and narrow-sense heritability. This leads to an understanding of the inheritance of traits and the nature of the epistatic gene effects (Fall, 1994).

Breeding weed-competitive cultivars requires an easily used protocol for selection under weed regimes. Competitiveness is an interaction between members of the same population for limited quantities of the same essential resource. The weed competitiveness of a crop has two components: weed tolerance, the ability to maintain high yields despite weed competition; and weed-suppressive ability, the ability to reduce weed growth (Jannink et al., 2000). Rice–weed competitiveness is controlled by a mixture of qualitative and quantitative genes (Azizi et al., 2006), but there are few existing studies that assess its genetic effects. However, some previous studies of the genetic effects of wheat–weed competitiveness have shown that it is possible to combine high grain yield with high competitiveness in a single genotype (Gibson and Fischer, 2004). Applying this approach to rice has the potential to generate new knowledge about the nature and magnitude of gene effects and their contribution to the control of rice–weed competitive traits, and to assist in formulating an efficient breeding program. In addition, main rice characteristics were reported to be associated with weed competitiveness include plant height (Caton et al., 2003); higher tiller number (Fisher et al., 2001); droopy leaves (Dingkuhn et al., 1999); high biomass accumulation at the early stage (Ni et al., 2000); high leaf area index and high specific leaf area (Dingkuhn et al., 1999) during vegetative growth stage.

The present research investigated genetic effects and heritability in reciprocal interspecific crosses for weed-competitiveness. It measured ten main quantitative traits: plant height at five leaves (H_{5_L}), plant height 30 days after transplanting (DAT) (H_{30}), plant height at maturity (H_{mat}), number of tillers at 30 DAT (T_{30}) and 60 DAT (T_{60}), number of fertile tillers (T_{fert}), width of leaves at 80 DAT ($W_{\_80}$) and at maturity ($W_{\_mat}$), and length of leaves at 80 DAT ($L_{\_80}$) and at maturity ($L_{\_mat}$).

MATERIALS AND METHODS

Experiments were conducted for a preliminary germplasm screening (Moukoumbi et al., 2011) and selected CG20 (*Oryza glaberrima*) as tolerant variety and FKR19 (*O. sativa*) as susceptible parent. F_1 seeds and their parents were planted to generate second filial generations (F_2), BC_1F_1 (CG20/2*FKR19 and FKR19/*2CG20) and BC_2F_1 (CG20/3*FKR19 and FKR19/*3CG20) backcross generations according to the reciprocal interspecific crosses. The populations BC_1F_1 and BC_2F_2 were developped using hand pollination. The experiment was conducted at the Africa Rice Center in Benin (6°25′N, 2°19′E and 15 m altitude) during the 2009/2010 wet season. Six generations derived from two crosses were transplanted in a randomized block design in three replications. Each generation was transplanted on 1.5 m long plot with spacing of 0.20 m between and within rows. For the F_1, BC_1F_1 and BC_2F_1 generations, the number of plants per block varied according to plant material availability: 15 F_1, 200 F_2, 39 BC_1F_1 and 38 BC_2F_1 with CG20 as female and FKR19 as male; 14 F_1, 137 F_2, 29 BC_1F_1 and 32 BC_2F_1 for a reciprocal cross (FKR19/CG20); GC20 and FKR19 plants. Fertilizers were applied at the rate of 200 kg ha^{-1} of $NPK_{15\text{-}15\text{-}15}$ (vegetative stage) and 50 kg ha^{-1} urea (reproductive stage). Ten quantitative agro-morphological data were collected at the appropriate growth stage, following the Standard Evaluation System for rice (INGER–IRRI, 1996) and descriptors for rice (*Oryza* spp.) from Biodiversity International–IRRI–AfricaRice (2007).

A formula explaining gene effects, first proposed by Mather and Jinks (1971), then by Kearsey and Pooni (1996) and finally by Möhring and Piepho (2010), was used: $\mu_i = m + [a]x_{i1} + [d]x_{i2} + [aa]x^2_{i1} + [dd]x^2_{i2} + [ad]x_{i1}x_{i2,}$ where μ = mean of each generation, m = phenotypic mean of both parents, [a] = additive gene effect, [d] = gene effect of residual dominance, [aa], [dd] and [ad] = epistasic (interaction between loci), and x_{i1} and x_{i2} = assigned coefficients for each generation (Table 1). The type of epistasis was determined only when the dominance effect [d] was significant and when these effects had the same sign, the epistasis was complementary while the different sign indicated duplicate epistasis (Dvojković et al., 2010).

Following Möhring and Piepho (2010), an ANOVA mixed model was applied to estimate mean values, standards errors and to test

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Table 1. Linear models for means, genetic variances and total within-plot variance of six generations for generation mean analysis using the additive–dominance model of Kearsey and Pooni (1996).

Mean parameter						Variance parameter
Generations	**[a] (coefficient x_{i1})**	**[d] (coefficient x_{i2})**	**σ^2_a**	**σ^2_d**	**σ_{ad}**	**$V_{(fijk)} = V_{(gijk + eijk)}$**
P_1	1	0	0	0	0	$\sigma^2_1 = \sigma^2_e$
P_2	-1	0	0	0	0	$\sigma^2_1 = \sigma^2_e$
F_1	0	1	0	0	0	$\sigma^2_1 = \sigma^2_e$
F_2	0	0.5	1	1	0	$\sigma^2_2 = \sigma^2_e + \sigma^2_a + \sigma^2_d$
BC_1F_1	0.5	0.5	0.5	1	-1	$\sigma^2_3 = \sigma^2_e + 1/2(\sigma^2_a) + \sigma^2_d - \sigma_{ad}$
BC_2F_1	-0.5	0.5	0.5	1	1	$\sigma^2_4 = \sigma^2_e + 1/2(\sigma^2_a) + \sigma^2_d + \sigma_{ad}$

[a] : additive effect ; [d] : dominance effect ; [ad] : interaction between loci = epistasis; xi1 et xi2 coefficients affected to each generation ; V(fijk) : Phenotypic variance ; V(gijk) : genotypic variance ; V(eijk) : Environmental variance ; i =generation ; j =Block number and k =plant number tested

homogeneity of the genetic components of variance (V_A, V_E, V_{AD} and V_E) and genetic effects (additive, dominance and additive × dominance). A lack of fit test was added to check the adequacy of the model for estimating genetic effects. In addition, a Wald f-test, based on the mixed model and equivalent to the joint scaling test proposed by Mather and Jinks (1971), was used to confirm the model.

The variance components were determined following two formulae: $V_P = V_G + V_E$, where V_P = phenotypic variance, V_G = genotypic variance, and V_E = environmental variance; and: $V_G = V_A + V_D + V_{AD}$, where V_A = additive variance, V_D = dominant variance, and V_{AD} = epistasis. V_D and V_{AD} values were set to zero when estimated variance turned out to be negative. Broad-sense heritability was estimated using $h^2_b = V_G/(V_G + V_E)$ and narrow sense heritability using $h^2n = V_A/(V_G+V_E)$. All statistical analysis was carried out using SAS 9.1 (2003) software.

RESULTS

Mean values and their standard errors for the ten traits of the two crosses are presented in Table 2a and b. The parents used in the reciprocal interspecific cross showed significant difference (P ≤0.0001) with all traits except for H_{30}. The mean values of the ten traits for the F_1 generation derived from the CG20/FKR19 cross were lower than the mean values for either parent, except for the trait $W_{\_mat}$, where it was higher than the mean value of both parents. The mean values for the traits $L_{\_80}$ and $L_{\_mat}$ were the highest when FKR19 was the female parent. Of the F_1 generation derived from the FKR19/CG20 cross, the mean value was also generally lower than the mean value for either parent, except for H_{30} where it was greater than the donor parent, and for the trait $W_{\_mat,}$ where it was greater than both parents. The mean values of the second filial generation F_2 derived from the CG20/FKR19 cross were better than the parental lines for the traits H_{mat}, $W_{\_mat}$ and $L_{\_80}$. In addition, with the second cross (FKR19/CG20), the values obtained with H_{mat} (donor parent) and $W_{\_mat}$ were higher than their parents.

The differences between generations obtained were analyzed using generation mean analysis following the additive–dominance model, and all tests were found to be significant at 0.05. Dominance gene effects (Table 3) were found to be more important for H_{mat}, T_{30}, T_{60}, T_{fert}, $W_{\_80}$, $W_{\_mat}$ and $L_{\_mat}$ in the CG20/FKR19 cross, and for H_{5_L}, H_{30}, H_{mat}, T_{30}, T_{60}, T_{fert}, $W_{\_80}$ and $L_{\_80}$ in the FKR19/CG20 cross. Superdominance and epistatic gene effects were predominant in controlling inheritance with the CG20/FKR19 cross for five traits: H_{mat}, T_{30}, T_{60}, T_{fert} and $W_{\_80}$. In addition, the negative values of the dominance gene effect were found for H_{30}, H_{mat} and $L_{\_mat}$ in the reciprocal cross, and for $W_{\_80}$ in the FKR19/CG20 cross. In the CG20/FKR19 cross, additive gene effects were significant and important for H_{30}, H_{mat}, T_{30} and $L_{\_mat}$. In the FKR19/CG20 cross, additive gene effects were also significant but moderate for H_{30}, H_{mat}, $W_{\_80}$, $L_{\_80}$ and $L_{\_mat}$.

The analysis of the gene effects revealed that additive and dominance effects were involved in the inheritance of most traits. Dominance gene effects were non-significant and negative in the CG20/FKR19 cross for $H_{5\text{-}L}$, H_{30} and $L_{\_80}$, and in the FKR19/GC20 cross for $W_{\_mat}$ and $L_{\_mat}$. The additive–dominance model used cannot explain the variation between generations, which may be the result of the complexity of the mechanisms of genetic control of these traits. The dominance gene effects on H_{mat}, T_{30}, T_{60}, T_{fert} and $W_{\_80}$ (CG20/FKR19 and FKR19/CG20), $L_{\_mat}$ and $W_{\_mat}$ (CG20/FKR19) and H_{5_L}, $W_{\_mat}$ and $L_{\_mat}$ (FKR19/CG20) were significant. In this case, the variation in generation revealed a digenic epistatic model between generations.

V_E component values were higher for all traits analyzed, with the exception of $W_{\_80}$ and $L_{\_80}$ in both crosses. Estimated V_A component values were highest for all analyzed traits except for H_{30} and T_{fert} in the CG20/FKR19 cross and H_{5_L} and $W_{\_80}$ in the FKR19/GC20 cross. In accordance with the results shown in Table 4a and b, estimated values of broad-sense heritability (h^2_b) ranged from 0 ($W_{\_80}$) to 0.86 (H_{5_L}) in FKR19/CG20, and from 0.23 (T_{30}) to 0.86 (H_{mat}) in CG20/FKR19. For narrow-sense heritability (h^2_n), the highest estimated value was 0.79 (H_mat and L_80) in CG20/FKR19, while the range in FKR19/CG20 was 0.72

Table 2a. Generation means and standard errors for ten quantitative traits using CG20 and FKR19 as female and donor parents.

Generations	Traits (Mean ± SE)									
	H_{5_L}	H_{30}	H_{mat}	T_{30}	T_{60}	T_{fert}	$W_{\_80}$	$W_{\_mat}$	$L_{\_80}$	$L_{\_mat}$
P_1: CG20	30.40±1.04^{ab}	53.13±1.12^{a}	135.40±1.72^{a}	17.32±1.23^{a}	37.10±1.99^{a}	32.48±1.78^{a}	1.51±0.03^{b}	0.82±0.06^{c}	41.81±0.89^{ab}	43.73±0.85^{a}
P_2: FKR19	27.37±1.01^{ab}	57.20±1.08^{a}	118.12±1.65^{b}	14.9±1.18^{a}	38.22±1.91^{a}	36.62±1.71^{a}	1.67±0.03^{a}	0.93±0.05^{bc}	42.44±0.85^{ab}	39.57±0.82^{ab}
F_1: CG20/FKR19	26.93±1.64^{ab}	53.93±1.76^{a}	95.66±2.70^{c}	5.37±0.65^{c}	20.2±3.12^{b}	11.53±2.79d	1.18±0.05^{c}	1.11±0.08^{ab}	38.36±1.39^{ab}	29.96±1.34^{c}
F_2:CG20/FKR19 (*self pollinisation*)	26.67±0.61^{b}	52.96±0.92^{a}	133.72±2.35^{a}	10.56±0.45^{b}	24.26±0.8^{b}	20.88±0.87^{bc}	1.26±0.02^{c}	1.17±0.01^{a}	42.95±1.03^{ab}	42.20±0.98^{ab}
BC_1F_1: CG20/2*FKR19	28.20±1.13^{ab}	54.96±1.53^{a}	108±2.25^{bc}	6.31±0.82^{c}	18.20±1.37^{b}	16.68±1.22^{c}d	1.18±0.02^{c}	1.10±0.02^{ab}	44.61±1.61^{a}	44.16±1.18^{a}
BC_2F_1: CG20/3*FKR19	32.12±1.44^{a}	55.87±3.63^{a}	105.16±6.68^{bc}	5.37±0.65^{c}	21±2.18^{b}	26.62±3.83^{b}	1.13±0.06^{c}	1.12±0.05^{ab}	36.65±1.50^{b}	37.13±1.28^{b}

Table 2b. Generation means and standard errors for ten quantitative traits using FKR19 and CG20 as female and donor parents.

Generations	Traits (Mean ± SE)									
	H_{5_L}	H_{30}	H_{mat}	T_{30}	T_{60}	T_{fert}	$W_{\_80}$	$W_{\_mat}$	$L_{\_80}$	$L_{\_mat}$
P_1: FKR19	27.38±0.89^{ab}	57.1±0.95^{a}	118.25±1.62^{b}	14.90±1.23^{ab}	38.23±1.87^{a}	36.63±1.69^{a}	1.67±0.03^{a}	0.93±0.05^{bc}	42.44±0.92^{b}	39.57±0.82^{b}
P_2: CG20	30.41±0.93^{ab}	53.13±0.99^{a}	135.40±1.68^{a}	17.32±1.23^{a}	37.11±1.95^{a}	32.49±1.76^{a}	1.51±0.03^{b}	0.85±0.05^{c}	41.81±0.95^{b}	43.79±0.85^{ab}
F_1: FKR19/CG20	25.14±1.51^{ab}	55.71±1.61^{a}	111.41±2.74^{bc}	8.36±2.01^{cd}	11.79±3.17^{c}	13.70±2.86^{b}	1.22±0.05^{c}	1.17±0.08^{ab}	42.48±1.55^{b}	41.29±1.38^{b}
F_2: FKR19/CG20 (*self pollinisation*)	24.31±1.06^{b}	53.07±2.21^{a}	137.03±4.03^{a}	10.35±0.84^{bc}	22.35±1.42^{b}	19.54±1.35^{b}	1.28±0.03^{c}	1.15±0.03^{ab}	41.36±1.86^{b}	39.02±1.58^{b}
BC_1 F_1: FKR19/2*CG20	31.25±3.26^{a}	54.37±4.7^{a}	103±4.91^{c}	4.38±0.82^{d}	13.38±1.13^{c}	10.88±1.05^{b}	1.26±0.08^{c}	1.22±0.06^{ab}	41.31±1.57^{b}	38.56±1.97^{b}
BC_2 F_1: FKR19/3*CG20	29.45±3.67^{ab}	51.27±2.12^{a}	107.81±4.91^{bc}	3.45±0.47^{d}	20.18±2.39^{bc}	17.55±1.85^{b}	1.34±0.03^{c}	1.34±0.05^{a}	50.16±2.10^{a}	47.88±2.63^{a}

($H_{\_mat}$).

DISCUSSION

The variations depended on the cross and on the associated trait. Variation in the generation means did not, in most cases, fit a simple epistatic model, as also reported by Dvojković et al. (2010). This indicates that improvement in the traits studied would be more difficult to achieve in comparison with simpler models of inheritance such as additive–dominance and digenic epistatic models, which are considered best from a breeder's point-of-view. These results are in accordance with the literature, and were validated through genetic analysis of the ten traits following the technique reported by Möhring and Piepho (2010).

The unexpectedly low F_1 values obtained could be explained by the regression of heterosis reported by Lefort-Busson (1985), personal communication who mentions that the dispersion of alleles from the parents can occur when a cross is carried out between two genetically opposed parents, such as a rice–weed competitive variety and rice-weed non-competitive variety. On the other hand, the moderate heterosis values obtained suggest the genetic gain in the performance of some traits, but this depends on the cross carried out. In addition, maternal effect might explain some of the disparities between the crosses for T_{30}, T_{60}, T_{fert}, $L_{\_80}$ and $L_{\_mat}$. For the first and second backcrosses and reciprocal

Table 3. Estimation of gene effects for quantitative traits with standard errors and p-*value* of lack of fit (m = constant; a = additive gene effects; d = dominance gene effects and ad: epistasis; * = significant at 0.05; ** = significant at 0.01-0.001; *** = significant at 0.0001; ns = non-significant at 0.05).

Traits	Parameter (Mean ± SE) using CG20 and FKR19 as female and donor parents				Lack of fit
	m	a	d	ad	(α=0.05)
H_{5_L}	28.89± 0.72**	-1.51± 0.72^{ns}	-4.44± 1.89^{ns}	24.84± 6.43*	0.07
H_{30}	55.16± 0.77*	2.03± 0.77**	-4.39± 2.41^{ns}	7.55± 15.07^{ns}	0.50
H_{mat}	126.76± 1.19**	-8.64± 1.19***	13.92± 5.27***	-96.96± 28.44***	0.01
T_{30}	16.11± 0.85**	-1.21± 0.85**	-11.09± 1.93***	-18.34± 3.61***	0.68
T_{60}	37.66± 1.38**	0.55± 1.38^{ns}	-26.79± 3.28***	-14.18± 9.84***	0.04
T_{fert}	34.55± 1.23**	2.06± 1.23^{ns}	-27.33± 3.03***	18.81± 15.93*	0.04
W_{80}	1.59± 0.02*	0.08± 0.02^{ns}	-0.66± 0.07***	-0.66± 0.28***	0.02
W_{mat}	0.89± 0.04**	0.05± 0.04^{ns}	0.59± 0.08***	-0.32± 0.23^{ns}	0.01
L_{80}	42.12± 0.61**	0.31± 0.61^{ns}	1.65± 2.40^{ns}	-25.86± 7.41^{ns}	0.01
L_{mat}	41.68± 0.59**	-2.11± 0.59**	1.05± 2.3***	16.06± 6.58**	0.01

Traits	Parameters (Mean ± SE) using FKR19 and CG20 as female and donor parents				Lack of fit
	m	a	d	ad	(α=0.05)
H_{5_L}	28.89± 0.64**	-1.51± 0.64^{ns}	-9.16± 2.49*	-17.55± 15.34^{ns}	0.04
H_{30}	55.16± 0.68**	2.03± 0.68**	-4.18± 4.63*	3.15±12.36^{ns}	0.10
H_{mat}	126.76± 1.17*	-1.21± 0.85***	-11.53± 2.41***	118.16± 25.53^{ns}	0.01
T_{30}	16.11± 0.85**	0.55± 1.35^{ns}	-30.64± 3.93**	29.99± 4.24**	0.01
T_{60}	37.66± 1.35**	-8.64± 1.17^{ns}	12.54± 8.39**	7.54± 11.47^{ns}	0.01
T_{fert}	34.55± 1.23*	2.06± 1.22 ^{ns}	-30.03± 3.64***	3.83± 9.50***	0.01
W_{80}	1.59± 0.02*	0.08± 0.02***	-0.61± 0.08***	-0.37± 0.21^{ns}	0.04
W_{mat}	0.89± 0.03*	0.04± 0.03^{ns}	0.52± 0.10^{ns}	-0.84± 0.26**	0.01
L_{80}	42.12± 0.66**	0.31± 0.66*	-1.62± 3.41***	-36.02± 10.59^{ns}	0.07
L_{mat}	41.68± 0.59*	-2.10± 0.59***	-5.32± 3.39^{ns}	-31.21± 12.36*	0.19

Table 4a. Estimation of genetic variance component and heritability for ten quantitative traits using CG20 and FKR19 as female and donor parents.

Parameter	Traits (Mean ± SE)									
	H_{5_L}	H_{30}	H_{mat}	T_{30}	T_{60}	T_{fert}	W_{80}	W_{mat}	L_{80}	L_{mat}
V_E	40.43	46.71	109.76	56.43	146.64	117.49	0.05	0.11	29.38	27.31
V_A	18.37	0	644.76	16.55	61.15	0	0.07	0.02	109.39	135.74
V_D	0	44.45	0	0	0	0	0	0	0	0
V_{AD}	0	18.72	60.37	0	0	37.16	0.01	0	0	0
V_G	18.37	63.18	705.13	16.55	61.15	37.17	0.07	0.03	109.40	135.74
V_P	58.80	109.90	814.89	72.98	207.79	154.65	0.12	0.14	138.78	163.05
h^2_b	0.312	0.57	0.86	0.23	0.29	0.24	0.59	0.18	0.80	0.83
h^2_n	0.21	0	0.79	0.22	0.28	0	0.56	0.18	0.79	0.72

backcrosses, the differences found come from the parent's contribution during the crosses.

These results indicate that improving these traits would be difficult, as reported by Dvojković et al. (2010) in their genetic analysis for yield and yield traits associated for two winter wheat crosses. The present research showed a preponderance of dominance gene effects over additive gene effects in the expression of the ten traits (7/10 in CG20/FKR19 and 8/10 in FKR19/CG20), as already reported by Akhatar and Muhammad (2006), Fethi and El Mohamed (2010) and Hasib et al. (2002) regarding tillering ability and plant height. Highly significant dominance gene effects could explain the phenomenon of great dominance indicated by Akhatar and Muhammad (2006), resulting from the strong accumulation of dominant genes from parents of all generations, and indicating that the parents were dispersing genes (Dhanda and Sethi, 1996; Fethi and El Mohamed, 2010).

Table 4b. Estimation of genetic variance components and heritability for ten quantitative traits using FKR19 and CG20 as female and donor parent.

Parameter	Traits (Mean ± SE)									
	H_{5_L}	H_{30}	H_{mat}	T_{30}	T_{60}	T_{fert}	$W_{\_80}$	$W_{\_mat}$	$L_{\_80}$	$L_{\_mat}$
V_E	32.25	36.58	105.56	56.78	141.10	115.25	0.05	0.10	33.97	26.96
V_A	0	21.63	405.13	29.38	32.99	48.38	0	0.01	47.34	23.68
V_D	171.59	69.21	0	0	0	0	0	0	0	15.01
V_{AD}	31.60	0	45.21	0	26.34	14.44	0	0	10.43	22.50
V_G	203.19	90.85	450.34	29.38	59.34	62.82	0	0.01	57.77	61.19
V_P	235.44	127.43	555.90	86.17	200.44	178.08	0.04	0.10	91.74	88.15
h^2_b	0.86	0.71	0.81	0.34	0.29	0.35	0	0.01	0.62	0.69
h^2_n	0	0.16	0.72	0.31	0.16	0.27	0	0.01	0.51	0.26

On the other hand, genetic recombination during the crossing process could explain the significant negative dominance gene effects obtained in generations, with the high degree of dispersion of increasing alleles between parents contributing to a slight and non-significant additive gene effect.

In most cases the variation between generation means did not fit a simple epistatic model, but the additive–dominance model was accurate for the main gene effects for $H_{mat,}$ T_{30} and $L_{\_mat}$ in the CG20/FKR19 cross and for H_{30}, H_{mat}, $W_{\_80}$ and, $L_{\_80}$ in the FKR19/CG20 cross. Epistatic affects following an additive–dominance interaction were more important with the CG20/FKR19 cross than with the FKR19/CG20 cross. Duplicate epistasis was observed for H_{mat}, T_{30} and $L_{\_mat}$ and means that the model was adequate for both crosses. However, a better explanation of this duplicate epistasis, offering greater precision on rice–weed competitiveness (Griffiths et al., 2006; Cuguen, 2010), could be obtained by estimating the substitution effects of additive–additive (aa), dominance–additive (da) and dominance–dominance (dd).

V_A was high, despite some variations noted in CG20/FKR19, revealing that the variety CG20 can be used as donor parent in a breeding strategy to develop a weed-competitive rice variety. The negative, nil and non-significant estimates obtained with V_D could be due to environmental variation, sampling errors and/or the fact that basic generations are inefficient for determining dominance variance (Dvojković et al., 2010). In addition, the inheritance of quantitative traits has been described as a 'moving target' (Lewis and John, 1999 cited by Benjdi and El Gazzah, 2010), since it is affected not only by the actions of multiple individual genes, but also by the interactions between genes and environmental factors. The estimates values of narrow-sense heritability were lower than broad-sense heritability and are in accordance with those reported by Robinson et al. (1949) who identified three levels of heritability, low (h^2<0.2), moderate (0.2<h^2<0.4) and high (h^2>0.4). Reported estimates of heritability indicate that these agro-morphological traits influence the weed-competitiveness of the variety. But for traits where estimates of heritability were low to moderate, further analysis of rice–weed competitiveness is needed, ensuring that the breeding population is wide and that selection for rice–weed competitiveness in later generations is exercised under controlled conditions (Saha and Amirul, 2008).

The initial expectations of this research were met and the study provided estimations of additive and dominance gene effects. Additive–dominance interaction effects enabled an explanation of the gene effects involved in the rice–weed competitiveness. The additive components of variance were higher with H_{mat}, T30 and $L_{\_mat}$. Dominance gene effects were high and significant, and epistasis was more important than additive gene effects, which were slight and non-significant for the majority of traits. The contribution of environmental component variance in governing weed competitiveness cannot be elucidated without estimates of the other substitution effects such as additive–additive (aa), dominance–additive (ad) and dominance–dominance (dd). These could confirm the nature of epistasis and offer new opportunities for genetic improvement of rice–weed competitiveness.

Conflict of Interest

The authors have not declared any conflict of interest.

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academicJournals

Vol. 7(6), pp. 170-176, June 2015
DOI: 10.5897/JPBCS2015.0505
Article Number: 23B6E5253633
ISSN 2006-9758

http://www.academicjournals.org/IPBCS

Journal of Plant Breeding and Crop Science

Full Length Research Paper

Climatic conditions requirements of maize germplasm for flowering in the rainforest Agro-ecology of Nigeria

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Received 11 February, 2015; Accepted 9 June, 2015

The number of days from planting to flowering in maize (*Zea mays* L.) is of interest to maize breeders because of its importance in the selection of appropriate hybrid parents. Highly significant interaction of planting dates with varieties for flowering traits have been observed during the early and late cropping seasons in the rainforest agro-ecology of South West Nigeria. This makes the use of flowering dates as indicators of maturity unreliable. Therefore the objectives of this study were to evaluate 100 maize varieties for flowering traits and determine the climatic factors influencing the interaction of the environments with days to flowering (GxE) in the rainforest ecology of South West Nigeria. One hundred maize varieties were evaluated during the late and early cropping seasons of 2007/2008 and 2008/2009. Significant differences were observed among the varieties for flowering traits (days to 50% tasseling, anthesis and silking). There was also significant variety x season interaction mean squares. In the early season, TZEE-WSRBC$_5$, TZEEPOPSTRCo and 97TZEE-Y-2C1 with 47-53 days to full flowering were the earliest to flower while Oba-Super II and ACR96DMR-LSR W with 64-71 days to flowering were the latest to flower. In the late seasons, 2004TZEE-WPOPSTRC4, TZEEPOPSTRCo, SINETEE-WSR and TZE-WPOPDTSTRC4F2 were the earliest to flower (42-47 days) while BUSOLA STR, TZLCOMPCO, 9021-18STR and Oba super II were the latest (61-68 days). Flowering interval was shorter in the late than the early season regardless of the maturity group with temperature as main climatic factor influencing flowering in this ecology.

Key words: Maize, germplasm, climatic condition, rainforest, agro-ecology.

INTRODUCTION

Maize (*Zea mays* L.) is the second most important food crop, behind cassava (*Manihot esculenta* Crantz) in Africa, and is grown in a wide range of environments ranging from Niger's northern Sahel to Ethiopia's highlands and the converted forest lands of Sierra Leone. The popularity of maize among African farmers grew slowly until the early part of the 20th century after which it has increased rapidly (African Crops, 2000). The reproductive

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stages of maize are based on appearance of the male flower (tassel producing anthers), female flower (silk) and developmental changes in the kernels. Therefore, time to flowering commonly used in research include days to 50% tasseling, anthesis and silking. The number of days from planting to flowering is a trait of interest to maize breeders because of its importance in selecting appropriate hybrid parents and for its role in the utilization of unadapted germplasm (Koester et al., 1993).

The environments found in the tropical and sub tropical locations are extremely diverse (Whiteman, 1985) with highly variable effects on flowering in maize.. Bonhomme et al. (1994) reported that anthesis rather than silking was more stable and reliable among the flowering traits because of more pronounced environmental stress effects on silking. Oluwaranti et al. (2008) observed highly significant interaction of planting dates with varieties for flowering traits in maize during the early and late cropping seasons at Ile-Ife, a typical tropical rainforest location in Nigeria.

Temperature is one of the most important factors that determine plant growth, development, and yield. Accurate summary of plant temperature response in plants is a prerequisite to successful crop systems modelling and application of such models to crop management (Wiekai and Hunt, 1999). Thermal models involving a framework of three cardinal temperatures were used to study crop development with particular reference to maize (Xinyou et al., 1995). The cardinal temperatures were the base (T_b), the optimum (T_o) and the ceiling (T_c). Maize is a warm weather crop and is not grown in areas where the mean daily temperature is less than 19°C or where the mean of the summer months is less than 23°C (Jean, 2009). Dauda (1992) reported that Crop Heat Unit (CHU) closely predicted days to silking than other flowering traits in a study conducted at Obafemi Awolwo University Teaching and Research Farm.

Photoperiodicity has been defined as physiological reaction of organisms to the length of day or night and was found to occur in plants and animals (Photoperiodism, 2009). Photoperiodic flowering plants are classified as long-day plants or short day plants, although the regulatory mechanism is actually governed by the hours of darkness, not the length of the day. A long-day plant requires fewer than a certain number of hours of darkness in each 24 h period to induce flowering while a short day plant flowers when the night is longer than a critical length. There are also day-neutral plants that do not initiate flowering based on photoperiodism at all, they flower regardless of the length of the night. The day-neutral plants may initiate flowering after attaining a certain overall developmental stage or age, or in response to alternative environmental stimuli, such as vernalization (a period of low temperature), rather than in response to photoperiod (Photoperiodism, 2009). Russell and Stuber (1983) observed that in maize photoperiod effect on days to tassel initiation (DTI) and total leaf number (TLN) was considerably greater than that of temperature. Photoperiod x temperature interactions were significant only for DTI. Total leaf number (TLN) was concluded to be better than DTI for measuring effects of photoperiod on the duration of vegetative growth in maize.

The role of photoperiod x temperature interaction in controlling flowering processes has been one of the key research problems in the understanding of the growth of some crops such as maize and soybean [Glycine max (L). Merr] (Jean, 2009; Cregan and Hartwig, 1984; Egli et al., 1989; Mcblain et al., 1987; Sinclair et al., 1991; Wang et al., 1987). Therefore the objectives of this study were to evaluate 100 maize varieties for flowering traits and determine the climatic factors influencing the interaction of the environments with days to flowering (GxE) in the rainforest ecology of South West Nigeria.

MATERIALS AND METHODS

One hundred maize varieties of different maturity groups were evaluated for flowering traits (days to 50% tasseling, anthesis and silking) at the Teaching and Research Farm (TRF) of Obafemi Awolowo University (7°28'N 4°33'E and 244 m above sea level), Ile-Ife during late and early cropping seasons of 2007/2008 and 2008/2009. These maize varieties were supplied by the Maize Breeding Programme of IITA, Ibadan, Nigeria. The climatic data used for this study were supplied by Nigerian Meteorological Agency (NIMET), Oshodi Lagos and the Geo-Spatial Laboratory of IITA, Ibadan.

In all plantings, a tripple lattice design with three replications and ten incomplete blocks in each replication was used. Plots were two rows, 5 m long each, with intra- and inter-row spacings of 0.5 and 0.75 m, respectively. Each plot was bordered by a common variety. Three seeds were planted per hill and the plants were thinned to two at the three-leaf stage, giving a population of 53,333 plants/ha. Seeds were treated with Apron plus prior to planting to control damage by soil-borne diseases and insect pests. Apron plus, a systemic fungicide and insecticide also controls downy mildew which is endemic at the site**.** Ploughing and harrowing were done before laying out of the experimental field. Fertilizer NPK was applied at a total rate of 180 kg N, 90 kg P_2O_5 and 90 kg K_2O/ha in two splits; first at three weeks after planting and finally at five weeks after planting. Weeds were controlled with primextra, which contained atrazine (2-chloro-4-(ethyl amino)-6-isopropylamino-s-triazine) and alachlor (N-(1-methyl-2-methoxy-ethyl)-2-ethyl-8-methyl-chloroacetanilide) as active ingredients. The herbicide was applied the day after planting at the rate of 5 L/ha. Weeds were also controlled by hand weeding as necessary after the crop had established. Dates when 50% of the plants in a plot attained tasseling (TS), anthesis (ANTH) and incipient silk extrusion (SILK) were recorded and expressed as days after planting (DAP).

Analysis of Variance (ANOVA) using the General Linear Model (GLM) procedures of SAS version 9.2 (SAS Institute, 2003) was computed for each flowering trait recorded in each trial and combined trials for all cropping seasons. Means of the days to flowering traits for the varieties were separated with Least Significant Difference at 0.05 level of probability. Furthermore, correlation between each flowering trait and climatic factors (temperature, photoperiod and heat units) was carried out for all the trials and the combined trials. This was followed by simple linear, multiple linear and quadratic regressions of mean values the varieties (N=100) for each trait on temperature, heat units and

Table 1. Mean squares from the analysis of variance for the flowering traits of 100 maize varieties evaluated at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, during the late and early cropping seasons of 2007/ 2008 and 2008/2009.

Sources of variation	DF	Tasseling	Anthesis	Silking
Environment	3	1859.85**	2424.0767**	8846.009**
Variety	99	202.647**	207.567**	20712.0017**
Rep	2	144.5908**	303.818**	1046.6461**
Block/Rep	27	9.839*	9.354*	346.2133*
ENV x VAR	297	18.237**	17.842**	5376.9075**
CV		4.46	4.34	4.52
R^2		0.88	0.89	0.88

*, ** Significant at 0.05 and 0.01 levels of probability respectively.

photoperiod.

RESULTS

In the ANOVA combined across four environments, significant (p=0.01) mean squares were obtained for environment, variety, replication, block within replication and environment x variety interaction (Table 1). The CV was about 4 to 4.5% while the R^2 was about 88 to 89% for each flowering trait. Means of days to silking for five earliest and latest varieties in this study are presented in Table 2. The five earliest varieties in 2008 early cropping season took between 47 and 50 days after planting to full flowering while it took 50 to 54 days after planting for the earliest varieties to full flowering in 2009 early cropping season. Varieties TZEE-WSRBC$_5$ was the earliest to silk with 47 days after planting in 2008 early season while TZEEPOPSTRC$_0$ was the earliest to show silk extrusion in 2009 early season. TZEE-WSRBC$_5$, TZEEPOPSTRC$_0$ and 97TZEE-Y-2C$_1$ were observed to be among 5 earliest varieties to full flowering in both 2008 and 2009 early cropping seasons. Similarly, in the late seasons of 2007 and 2008, TZEEPOPSTRC$_0$, 97TZEE-Y-2C1 and TZEE-WSRBC$_5$ were also observed to be among the five earliest to silk with 45-57 days after planting. TZPB-SRPROL.F1C3, BR9943-DMRSR and TZLCOMP.1C$_6$ were among the latest varieties to silk with 66 - 71 days after planting in 2008 and 2009 early seasons while in the late seasons of 2007 and 2008, Oba Super II, TZB-SR and MASYN VAR3F2 were among the latest to silk with 64 -71 days after planting (Table 2).

Effects of temperature, heat units and photoperiod on flowering traits of maize

Correlation analysis

Highly significant positive correlation coefficients (r-values) were observed between all the flowering traits and the climatic factors (temperature, photoperiod and heat units) in the individual trials except for the correlation between photoperiod and days to 50% tasseling which was negative but not significant in the 2007 late season trial (Table 3). The correlation between days to silking and heat units was also negative but highly significant in this trial. Therefore, increases in the values of these climatic factors delayed the expression of each of the flowering traits.

Regression analysis

In 2007 late season trial, the regression analyses of days to flowering on the climatic factors for the 100 varieties consistently indicated that the variations observed in days to flowering were explained by the variation in temperature (Table 4). For the three types of regression models performed for each flowering event, the coefficient of determination (R^2) for temperature per se or temperature plus photoperiod were above 90% (Table 4). However, there were no increases in the R^2- value due to the addition of photoperiod in the multiple regression models, indicating that the effect of photoperiod on flowering was negligible during this season. Similar trends were observed during the 2009 early cropping season (Tables 5). Although the other two climatic variables appeared to be as important as the temperature itself, the changes in R^2 values were not consistent. Addition of photoperiod in the multiple regression or quadratic term had little or no improvement for the fit of the temperature model.

DISCUSSION

There were significant differences among the hundred varieties of maize evaluated for flowering traits in this study. These results were expected because of the following reasons. First, the 100 varieties were of different maturity classes; extra-early, early, intermediate and late maturity. Second, they were bred for different purposes; tolerance to diseases such as downy mildew,

Table 2. Means of days to silking of 5 earliest and latest varieties evaluated at the Teaching and Research Farm of Obafemi Awolowo University, Ile-Ife, during the early and late seasons of 2008/2009 and 2007/2008 respectively.

			Earliest	
Early seasons	**2008**	**DAP**	**2009**	**DAP**
	TZEE-WSRBC$_5$	47	TZEEPOPSTRC$_0$	50
	EV.8766-SRBC6QPM	48	POOL18SRQPMx EVDTY2000STRC1	52
	TZEEPOPSTRC$_0$	49	TZEE-WSRBC$_5$	53
	TZEEPOPSTRC$_2$	50	97TZEE-Y-2C1	53
	97TZEE-Y-2C1	50	TZEE-WPOPSTRQPMCo	54
LSD$_{0.05}$		1.8		4.9
Late seasons	**2007**	**DAP**	**2008**	**DAP**
	TZEEPOPSTRC$_0$	54	TZEEPOPSTRC$_0$	45
	ACR88POOL16SD	55	2004TZEE-WPOPSTRC$_4$	47
	97TZEE-Y-2C1	56	TZEE-WPOPSTRQPMC$_0$	48
	TZEE-YPOPSTRC$_4$	56	SINETZEE-WSR	48
	TZEE-WSRBC$_5$	57	EVDT-W2000STRC$_0$	49
LSD$_{0.05}$		6.6		2.1
			Latest	
Early seasons	**2008**	**DAP**	**2009**	**DAP**
	TZPB-SRPROL.F1C3	71	TZPB-SRPROL.F1C3	71
	BR9943-DMRSR	70	BR9943-DMRSR	70
	DTSR-WC1	69	TZSR-W-1C4	69
	TZB-SR	67	TZLCOMP.1STRSYN-W	68
	TZLCOMP.1C6	66	TZLCOMP.1C6	67
LSD$_{0.05}$		1.8		4.9
Late seasons	**2007**	**DAP**	**2008**	**DAP**
	MASYN VAR3F2	71	TZLCOMP.CØ	68
	TZLCOMP.1STRSYN-W	70	9021-18STR	66
	TZB-SR	70	BUSOLA STR	66
	BR 9928-DMRSR	69	TZB-SR	64
	TZLCOMP.1C6	68	Oba Super II	64
LSD$_{0.05}$		6.6		2.1

streak, blight, and others, resistance to insect pests such as stem borer. Third, they were developed at different locations as indicated by their names. Four, the 100 varieties have different genetic backgrounds. Significant differences were also observed among the environments (seasons), where the varieties were evaluated in the early and late cropping seasons of this study. These results were also expected because the seasons are characterized by different temperature, sunshine hour, heat units received. The high coefficient of determination (R^2 values) obtained for all the flowering traits, in the combined trials is an indication of the reliability of the models. Likewise, low CVs obtained from this study showed that the observed days to flowering is quite stable and reliable.

Highly significant interactions of environments with varieties observed for the flowering traits were consistent with the findings of Oluwaranti et al. (2008), and this was the justification for this study. In other words, the use of flowering dates as indicators of maturity may not be reliable because of significant and relatively large GxE interaction. The results obtained for days to flowering in early and late cropping seasons of this study also corroborate with those of Fakorede (1985) in a study on the response of maize to planting dates at the Teaching and Research Farm of Obafemi Awolowo University. As part of a study carried out in 2001 late cropping season, days to 50% tasseling, anthesis and silking decreased from early planting to later plantings and increased thereafter because the amount of rainfall available for the crop decreased as planting was delayed (Oluwaranti et al., 2008). Likewise from the study, in 2002 the maize varieties flowered faster on planting dates that received larger amounts of rainfall than those which received smaller amounts. It was, therefore, concluded from the study that the higher the amounts of rainfall, the fewer the

Table 3. Pearson correlation coefficients (r-values) between the climatic factors and flowering traits for the individual and combined seasons of 2007 to 2009 at the Obafemi Awolowo University Teaching and Research Farm, Ile-Ife.

Climatic factors	Tasseling	Anthesis	Silking
	2007 late season		
Temperature	0.99**	0.99**	0.98**
Photoperiod	-0.03	0.33**	0.73**
Heat units	0.82**	0.29**	-0.62**
	2008 early season		
Temperature	0.96**	0.87**	0.87**
Photoperiod	0.79**	0.68**	0.70**
Heat units	0.96**	0.85**	0.86**
	2008 late season		
Temperature	0.84**	0.85**	0.86**
Photoperiod	0.82**	0.84**	0.85**
Heat units	0.68**	0.78**	0.76**
	2009 early season		
Temperature	0.88**	0.89**	0.99**
Photoperiod	0.86**	0.87**	0.97**
Heat units	0.32**	0.31**	1.00**

** significant at 0.01 level of probability.

Table 4. Simple linear, multiple linear and quadratic regression analyses of days to tasseling, anthesis and silking on temperature, photoperiod and heatunits of 100 maize varieties evaluated during the 2007 late cropping season at the Obafemi Awolowo University Teaching and Research Farm, Ile-Ife.

Trait and regression model	Climatic factors	Regression equation	R^2 values
Tasseling			
Simple Linear	**Temperature**	**(-2539.7)+(103.68)T**	**0.98**
	Photoperiod	(66.66)+(-1.96)P	0.01
	Heat units	(-3553.52)+(236.95)H	0.67
Multiple Linear	**Photothermal**	**(-2530.58)+(-2.01)P+(103.69)T**	**0.98**
	Photo-heat units	(-3564.39)+(1.45)P+(237.23)H	0.67
Quadratic	**Temperature**	$(-253.70)+(103.68)T+(0.0000001)T^2$	**0.98**
	Photoperiod	$(-5854.50)+(2596.07)P+(-284.94)P^2$	0.27
	Heat units	$(-3533.52)+(236.95)H+(0.0000001)H^2$	0.67
Anthesis			
Simple Linear	**Temperature**	**(-2579.71)+(105.29)T**	**0.98**
	Photoperiod	(-81.76)+3(1.10)P	0.16
	Heat units	(-1915.58)+(129.64)H	0.08
Multiple Linear	**Photothermal**	**(-2589.98)+(-1.99)P+(106.06)T**	**0.98**
	Photoheat units	(-4099.74)+(56.54)P+(255.97)H	0.36
Quadratic	**Temperature**	$(-2579.71)+(105.29)T+(0.000001)T^2$	**0.98**
	Photoperiod	$(-12533)+(5457.99)P+(-591.25)P^2$	0.24
	Heat units	$(-1915.57)+(129.64)H+(0.000001)H^2$	0.08
Silking			
Simple Linear	**Temperature**	**(-2488.35)+(101.64)T**	**0.98**
	Photoperiod	(-265.19)+(71.59)P	0.53

Table 4. Contd.

	Heat units	(3999.91)+(-258.31) H	0.34
Multiple Linear	Photothermal	(-2545.59)+(-3.69)P+104.59)T	**0.97**
	Photoheat units	2124.33+(55.85)P+(-152.06)H	0.64
Quadratic	**Temperature**	(-2488.35)+(101.64)T+(0.000001)T^2	**0.92**
	Photoperiod	(-292.94)+(2698.02)P+(-286.06)P^2	0.56
	Heat units	3999.91+(-258.31)H+(0.0000001)H^2	0.38

Table 5. Simple Linear, multiple linear and quadratic regression analyses of days to tasseling, Anthesis and silking on temperature, photoperiod and heatunits of 100 maize varieties evaluated during the 2009 Early cropping season at the Obafemi Awolowo University Teaching and Research Farm Ile-Ife.

Trait and regression model	Climatic factors	Regression equation	R^2 values
Tasseling			
Simple Linear	**Temperature**	**1286.93+(-48.36)T**	**0.78**
	Photoperiod	163.79+(-23.54)P	0.74
	Heat units	-86.94+(8.94)H	0.10
Multiple Linear	**Photothermal**	**1243.93+(-0.96)P+(46.50)T**	**0.78**
	Photo-heat units	111.76+(-22.78)P+(3.02)H	0.75
Quadratic	**Temperature**	1286.93+(-48.36)T+(0.00001)T^2	0.78
	Photoperiod	-440.64+(245.67)P+(-29.95)P^2	0.76
	Heat units	-22534+(2755.69)H+(-84.00)T^2	0.78
Anthesis			
Simple Linear	**Temperature**	**1297.75+(-48.68)T**	**0.79**
	Photoperiod	167.57+(-23.77)P	0.75
	Heat units	-78.29+(8.62)H	1.00
Multiple Linear	**Photothermal**	**1200.77+(-2.17)P+(-44.48)T**	**0.79**
	Photoheat units	122.45+(-23.11)P+(2.62)H	0.76
Quadratic	**Temperature**	1297.75+(-48.68)T+(0.00001)T^2	0.79
	Photoperiod	-478.13+(263.83)P+(31.99)P^2	0.78
	Heat units	-22701+(2776.77)H+(-84.65)H^2	0.79
Silking			
Simple Linear	**Temperature**	**1729.62+(-65.66)T**	**1.00**
	Photoperiod	205.26+(-32.09)P	0.95
	Heat units	1288.70+(-80.52)H	1.00
Multiple Linear	Photothermal	1574.58+(-3.47)P+(-58.95)T	1.00
	Photoheat units	1163.28+(-3.96)P+(-71.12)T	1.00
Quadratic	**Temperature**	1729.62+(-62.66)T+(0.00001)T^2	1.00
	Photoperiod	(-192.76)+(145.18)P+(-19.72)P^2	0.96
	Heat units	1288.70+(-80.52)H+(0.00001)H^2	1.00

number of days it takes the maize varieties to flower. The study by Oluwaranti et al. (2008), however did not consider other climatic factors and therefore did not report the effect of temperature on flowering. Studies by Fakorede (1985) and Fakorede and Opeke (1985) examined the effects of several climatic factors on grain yield of maize in this location but did not include flowering traits. Therefore, the findings in the present study on the GxE interaction of flowering dates is important and warrant the analysis of climatic factors responsible for the interactions.

Effects of temperature, heat units and photoperiod on flowering traits of maize

Correlation analysis indicated that temperature, photoperiod and heat units are the major climatic factors affecting days to flowering in maize at this location. Days to flowering increased as temperature, heat units and

photoperiod increased and decreased as these climatic factors decreased. Theoretically, delayed planting in the early season should reduce the number of days to flowering while in the late season, it should delay flowering. The trend observed in this study, however, showed that increased temperature, delayed the progress towards flowering thereby resulting in increased number of days to flowering. Regression models also indicated that photoperiod and heat units influenced flowering when considered singly. This is in corroboration with the findings of Shaykewich (1995) who observed that photoperiod and temperature had major effects on days to flowering in cereals and could be important sources of genotype × environment interaction. The combination of these variables with temperature was not important in determining flowering date of the maize varieties in the present study. Temperature was the main climatic factor contributing to the variation observed in the days to flowering in this study as addition of photoperiod and or heat unit did not increase this observed variation as shown by their R^2 values.

Conclusion

It was concluded that development rate from sowing to flowering (days to 50% tasseling, anthesis and silking) was affected mainly by temperature in the rainforest agro-ecology since use of photoperiod and accumulated heat units as additional parameters in predictive models did not improve goodness of fit of the models.

Conflict of Interest

The authors have not declared any conflict of interest.

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academicJournals

Vol. 7(6), pp. 177-184, June, 2015
DOI: 10.5897/JPBCS2014.0492
Article Number: 735ABA253637
ISSN 2006-9758

http://www.academicjournals.org/JPBCS

Journal of Plant Breeding and Crop Science

Full Length Research Paper

Genetic diversity and association of physio-morphological traits for drought resistance in wheat (*Triticum aesitivum*)

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Received 27 November, 2014; Accepted 10 March, 2015

Wheat (*Triticum aestivum* L.) occupied 17 percentage of the total cultivated land in the world whereas it has contributed major role to maintain the Nepalese agricultural gross domestic products (MOAC, 2012) but area of cultivation has been decreasing. Moreover, potential yield of popular varieties have reduced by the effect of drought. To combat from drought loss, tolerant variety is one of the major solutions to address that issue. From this point of view, an experiment was conducted in split plot design from November 2009 to May 2010. The result showed significant variations among both for genotypes as well as to both level of water management. The average leaf area were reduced by 8.80 cm^2, 0.2655 kg biomass yield, 6.64 g thousand kernel weight, 4.11 booting days, 3.23 heading days, 1.26 flag leaf senescence and 0.0706 kg yield in drought condition. Similarly, WK1123 has least drought susceptibility index for yield. However, relative water content and chlorophyll content were correlated significantly with yield. To conclude, genotypes WK1701, WK1444, WK1123, 3EBWYT513 and 3EBWYT512 considered as the most drought tolerant and might be used as a variety in drought prone area of Nepal.

Key words: Wheat, drought, stress chlorophyll content and relative water content.

INTRODUCTION

Wheat (*Triticum aestivum* L.) is the first important cereals crop in the world and staple food for 35% of the world's population and provides more calories and proteins in the world's diet than any other crop. In Nepal, total area of 765317 ha and 1846142 mt of production with productivity of 2412 kg/ha (MOAD, 2012/2013). Similarly, wheat has been grown both in irrigated and unirrigated conditions. However, 63.19% of wheat has been cultivated in completely irrigated condition with improved varieties but 34.44% of wheat grown in unirrigated Nepalese condition (MOAD, 2012/2013). Therefore, it will be wise to develop the drought tolerant varieties which would address the issue of yield loss through drought. The prevailing cropping system, rice after wheat would

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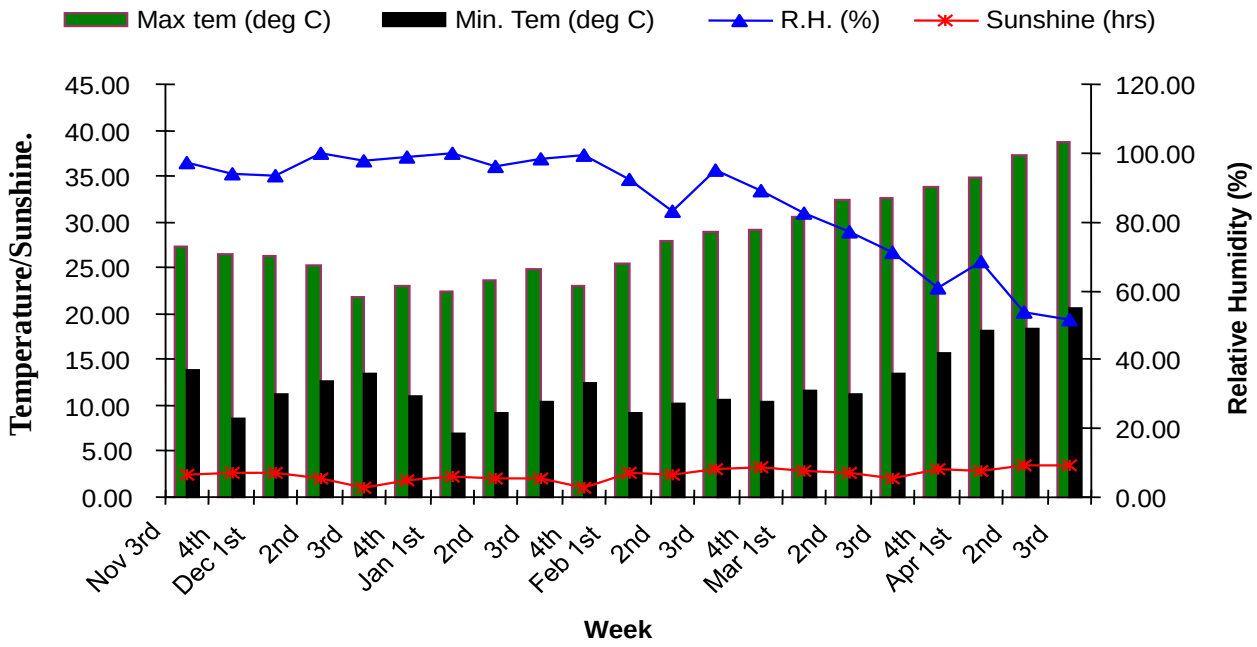

Figure 1. Agrometorological condition of the research site during 2009/2010.

enforced to the plantation of wheat in late sown condition that generally damaged the crop by combined effect drought and terminal heat stress. Drought stress has been recognized as one of the major abiotic factors limiting wheat production in Nepal (Sharma et al., 2008). Due to increasing summer temperature, uneven annual rainfall pattern and depleting water resource for irrigation, breeding wheat for drought tolerance will become an increasingly higher priority in this region (Joshi et al., 2007). Thus, wheat breeding for drought tolerance or higher water use efficiency is needed to supply food to the growing Nepalese population therefore, this study aimed to assess the genetic variability of drought adaptive traits and their association with drought tolerance which is vital for the development of drought tolerant wheat cultivars.

MATERIALS AND METHODS

The research site and experimental design

The field experiment was conducted at the research farm of the Institute of Agriculture and Animal Science (IAAS), Rampur, Chitwan, Nepal, from November 2009 to June 2010. The geography of this location is 27°64' N latitude and 84° 34' E longitude and at an altitude of 228 m above sea level, respectively. The research location is characteristics of subtropical climate and experiment was setup from November, 2009 to June, 2010 after that, field remained fallow until the next season, that is, November, 2010. Thirty genotypes were used in the research where most of the lines were Nepalese landraces and advanced lines derived from Agriculture Botany Division NARC, Khumaltar, Nepal and commercial varieties and check used was WK1204. The experiment was laid out in a split plot design with optimum moisture and moisture stressed environments as main plot factors and 30 wheat genotypes as sub-plot factors. Each plot was 0.75 m^2. The rain-out shelter (stress) plot was erected over the plot at the start of tillering where trench had been made around the main plot, provided with a 1 m deep and 0.5 m wide ditch around the edge to prevent rain coming off to the shelter from seeping into the plot. Other intercultural operations and cultivation practices were completed according to the national recommendation for wheat cultivation.

Each set of experiment was replicated three times where composite soil sample had been taken from the soil after land preparation from the field at different depth (0 to 30 cm). The soil texture class was determined sandy loam where moisture content was found 75% of the field capacity at the time of seeding for both condition. For moisture stressed experiment, soil moisture content was maintained at 35% of the field capacity from heading to flowering. The maximum temperature recorded was 40°C in the month of April. The Minimum- maximum, standard deviation and Coefficient of variation for the quantitative traits were being measured. Differentiation between populations was usually quantified using the difference in mean expression (t-test) (Spagnoletti Zeuli and Qualset, 1987) (Figure 1). The following were the traits measured in this experiment:

Canopy temperature depression

The canopy temperature depression was calculated by using the following formula.

Canopy Temperature Depression (CTD) = Ambient temperature – Canopy Temperature

Relative water content

RWC was calculated from the equation of Schonfeld et al. (1988) as:

Table 1. Flag leaf area, plant height, panicle length, TKW, Booting days, heading days, Anthesis days, and yield as affected by drought condition in IAAS, Rampur, (2009/2010).

Condition	Leaf area	Plant height (cm)	Panicle length (cm)	TKW (gm)	Booting duration (days)	Heading duration (days)	Anthesis duration (days)	Yield (kg/ha)
Drought(mean)	54.4063[a]	113.075[a]	11.088[a]	34.825[a]	67.644[a]	75.100 [a]	84.467 [a]	2926[a]
SEM+or-for drought	2.58301	4.25584	0.3934	1.6209	2.5595	2.793	3.0992	0.01334
Irrigated	59.6154[b]	121.35 [b]	11.765[b]	37.34 [b]	70.044[b]	78.333[b]	88.233[b]	3365[b]
SEM+or- flor Irrigated	1.73924	1.4126	0.43526	1.581	1.6399	1.9585	2.159	0.0156
t-value	3.021[**]	3.137[**]	4.6.6[**]	3.133[**]	2.043[*]	2.812[**]	3.096[**]	3.380[**]

Means within the column with same letters are not significantly different. t- Value obtained from paired t-test are significantly different at 5% level of significance (*) and highly significantly different at 1% level of significance (**).

$$RWC = \frac{\text{Fresh wt-Dry wt}}{\text{Turgid wt-Dry wt}} \times 100$$

Flag leaf duration, days of booting, days of anthesis, days of heading, Panicle length, seed weight per spike, leaf area, plant height, productive tiller per plot, thousand kernel weight (TKW) and drought susceptibility index (DSI).

Drought susceptibility indices for grain yield of each genotype were calculated as proposed by Fischer and Maurer (1992). DSI = [(1-Y/Yp)/D], Y = yield at normal sown condition, Yp = yield at drought sown condition, D = stress intensity = 1- X/Xp, X = mean Y of all genotypes, and Xp = mean Yp of all genotypes. Analysis of variance and calculation of means was done by using Cropstat 7.2. The main plot treatment comparison was done by paired t-test with SPSS. UPGMA clustering and PCA was done using Minitab-14.

RESULTS AND DISCUSSION

Days to booting and heading

The mean number of days to booting in irrigated normal sown condition was 70.044 where 67.6444 days for the stress conditions. Stress condition and normal condition were nonsignificant with dates to booting as seen by paired t-test (Table 1). In the irrigated conditions, WK1627 had minimum days to booting days (61) whereas WK1719 was identified as late booted (82). The decrease in heading days in stressed plants as compared to non stress was reported by Reynolds et al. (1993).

Days to flag leaf senescence

The mean number of days to flag leaf senescence differed non significantly for the main plot treatment as shown by paired t-test (Table 1) but significantly different was seen through the Analysis of Variance. The mean numbers of days to flag leaf senescence were found 117.3 days and 114.67 days for Irrigated and drought conditions respectively. In the drought condition, WK1627 was senesced as earliest with 109 days whereas WK1123 senesced in later with 123 days. Later on in the growth cycle, water stress reduces the green leaf duration (GLD) from accelerated senescence by Reynold et al. (1993) (Table 2).

Thousand kernel weight

There was significant difference in the mean thousand kernel weight for the Irrigated and drought condition as seen by paired t-test. The 37.34 and 34.825 g were mean thousand kernel weight (TKW) for irrigated and drought plot, respectively. The Godawari local had 20.847 g of thousand kernel weight which was found as minimum among the others and maximum (42.37 g) kernel weight was found to WK1700. However, genotypes WK1123 and WK1670 had least drought susceptibility index and considered as most useful for drought environment. Sharma et al. (2008) had identified reduction in kernel weight as a potential tool for indirect selection criteria for grain yield under drought stress.

Plant height

The drought and irrigated plots have had mean plant height of 113.07 and 121.35 cm respectively. The significant variations were shown among genotypes. In addition, shortest genotype was WK1204 (93.26 cm) where as Godawari local had been tallest among genotypes in drought condition. However, WK1912 was found as shortest (108.56 cm) and tallest was Godawari local with 134.4219 cm. Drought

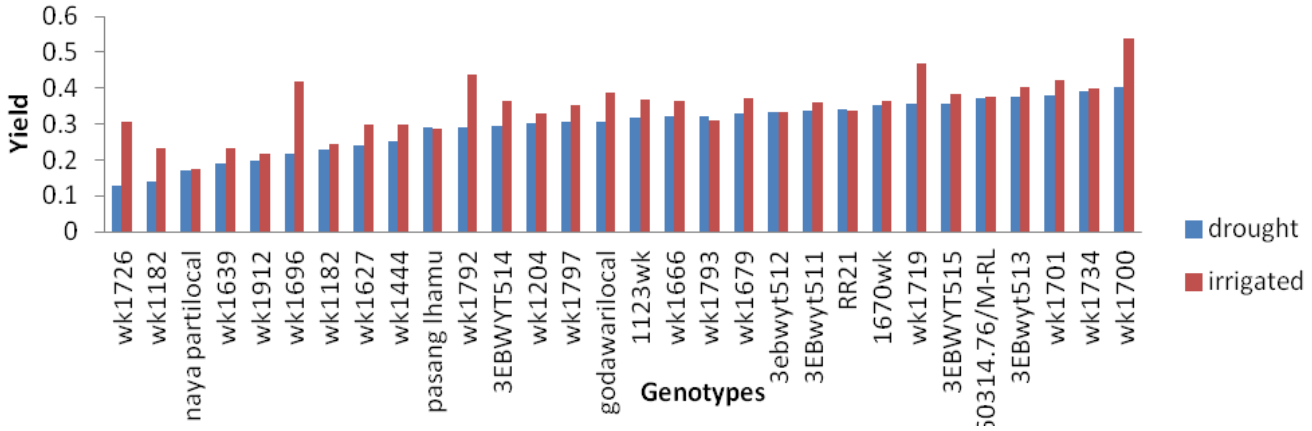

Figure 2. The effect of moisture level on the yield response of genotypes used in the experiment at IAAS, Rampur (2009/2010).

Table 2. Drought susceptibility index (DSI) for TKW, Yield/Plot, and Biomass/Plot of Five selected genotypes in IAAS, Rampur (2009/2010).

Genotypes	Biomass	Genotypes	TKW	Genotypes	Yield
WK1123	-7.017	WK1123	-0.4071	3EBwyt513	-10.198
F60314.76/M	-3.462	Wk1670	-0.1995	3ebwyt512	-8.195
Wk1912	-1.926	3EBwyt511	-0.0493	3EBwyt511	-5.324
Nayapartilocal	-0.4193	3EBwyt512	-0.003	WK1670	-0.0248
Wk1726	0.25625	3EBwyt513	0.0024	WK1123	0.254

significantly reduced internodes length and thus reduced the length of the main stem by Richards (1992). This decrease in plant height negatively correlated (-0.798) with high yield under stressed condition which guessed for the stem reserve mobilization might transferred towards the spikes.

Yield and yield component traits

There were significant differences between water management for mean per plot yield as seen by pair t-test (Table 1). In more clearly, mean per plot yield in drought and irrigated condition were 2563 and 3269 kg/ha. Moreover, highly significant yield differences among genotypes had been found for drought condition. In drought condition, WK 1701 and WK1700 had produced yield of 3737 and 3541 kg/ha respectively but, lowest yield found for Nayaparti local (1590.867 kg/ha). In contrast to drought condition, irrigated condition produced highest yield of 5504 kg/ha from WK1700 but least yield had been found from F60314.76/M-RL(1975 kg/ha) (Figure 2).

Drought susceptibility index

Drought susceptibility index was calculated for yield and yield related traits. This was important because we need to address higher yield potential against drought condition (Blum et al., 1989) (Table 3). Drought susceptibility indices are use either based on drought resistance or susceptibility of genotypes (Blum et al., 1989). Genotypes WK 1123, 3EBWYT513 and 3EBWYT512 were less influenced by the drought for biomass yield and thousand kernel weight.

Relative water content

Mean relative water content had valued for 1.370 in normal sown wheat while it was 1.244 in drought condition. Genotypes with highest RWC was WK1701 (2.19) but lowest was found to WK1123 (0.26) in drought therefore WK1701 might be more drought tolerance than rest of genotypes. Therefore genotypes which maintained higher RWC under stress conditions had maintained higher yield in spite of drought condition suggested for the existence of drought tolerance traits which has been supported by Araus et al. (1997) (Figure 3). The genotypic correlation between gain yield and RWC under water stress condition was positively significant (0.84^{**}) suggested that under drought condition higher relative water content in leaf might contributed with the better yield (Blum et al., 1989).

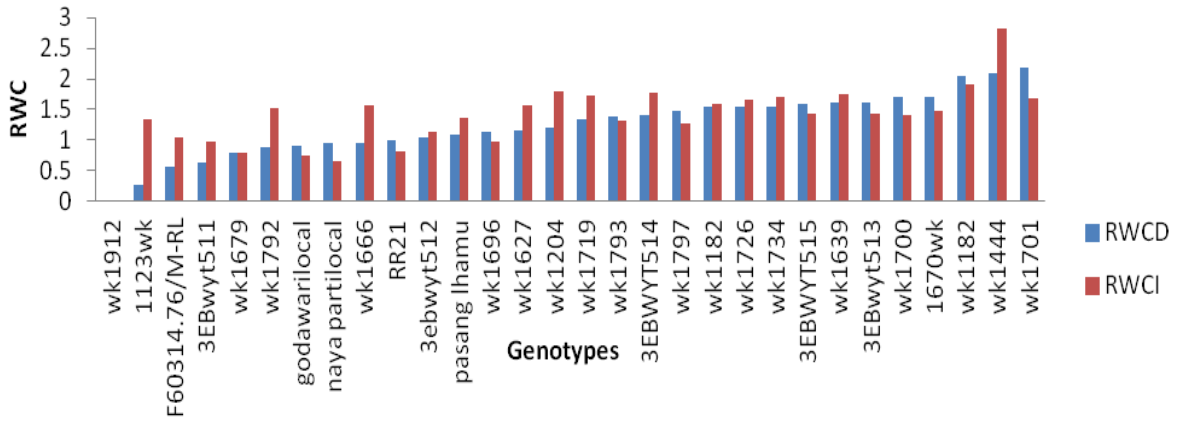

Figure 3. Wheat genotypes differing for RWC in both drought and irrigated condition (2009/2010).

Table 3. The correlation among different measured traits under drought conditions.

	Correlations								
	LA	**Plht**	**DOFS**	**TKW**	**Y/Plot**	**PL**	**DOB**	**DOH**	**DOA**
LA	1	0.372*	0.509**	0.583**	0.495**	0.693**	0.505**	0.452*	0.509**
Plht		1	0.903**	0.622**	-798**	-769**	0.836**	0.850**	0.857**
DOFS			1	0.693**	0.986**	0.886**	0.941**	0.949**	0.960**
TKW				1	0.720**	0.789**	0.537**	0.542**	0.602**
Y/Plot					1	0.884**	0.898**	0.915**	0.929**
PL						1	0.783**	0.793**	0.833**
DOB							1	0.992**	0.984**
DOH								1	0.988**
DOA									1

*. Correlation is significant at the 0.05 level (2-tailed), **. Correlation is significant at the 0.01 level (2-tailed).

Correlation studies

Yield had significant correlation with Thousand Kernel Weight and days to flag leaf senescence to each of drought and irrigated condition but negative correlation of plant height with grain yield was found under drought condition (Table 4) which was supported from Gill et al. (1989) and Patil and Jain (2002). On the other hand, spike length was positively correlated significantly with weight of grains per spike in both condition therefore selection based on panicle length would favor for the bold grain in drought condition. Similar findings supported by Shah et al. (1988). Briefly, highly significant positive association had been established for days to flag leaf senescence, thousand kernel weight, and panicle length, days of booting, days of heading and days to anthesis with higher yield per plot in drought condition. Ultimately, that would help to selection based on other traits rather than yield. The all the measured traits were significantly correlated with each other in irrigated condition (Table 5) suggested that selection based on other traits would beneficial for the indirect selection of genotypes as a variety for future use.

Canopy temperature depression (CTD)

Average CTD in stress at three growth stages recorded highest for WK1444, WK1639 and WK1701 and had maintained lower canopy temperature. Relatively lower canopy temperatures under stress indicate the better plant water status and CTD were positively correlated with yield in stress condition (Blum et al., 1989). Similar kind of research result had been observed for correlation between CTD with yield advantage in stress condition.

Soil physical analysis and development meter (SPAD)

There were significant differences of SPAD values between drought and irrigated condition to illustrate,

Table 4. The correlation among different traits measured under irrigated conditions.

Correlations									
	LA	**Plht**	**DOFS**	**TKW**	**Y/Plot**	**PL**	**DOB**	**DOH**	**DOA**
LA	1	0.530**	0.628**	0.587**	0.613**	0.740**	0.637**	0.450*	0.505**
Plht		1	0.32	0.639**	0.412*	-0.406*	0.431*	0.398*	0.495*
DOFS			1	0.506**	0.975**	0.749**	0.970**	0.851**	0.892**
TKW				1	0.531**	0.580**	0.446*	0.425*	-392*
Y/Plot					1	0.745**	-923**	0.763**	-813**
PL						1	0.768**	0.600**	0.663**
DOB							1	0.923**	0.946**
DOH								1	0.966**
DOA									1

*. Correlation is significant at the 0.05 level (2-tailed),**. Correlation is significant at the 0.01 level (2-tailed).

Table 5. Mean square from ANOVA of leaf area (LA), biomass (kg/Plot), plant height (cm), Flag leaf senescence (FLS), TKW, booting days, heading days, anthesis days as influenced by moisture stress of genotypes at IAAS Rampur (2009/2010).

Source	**DF**	**LA**	**Biomass**	**Plant height (cm)**	**FLS**	**TKW**
Water management	1	59.58	1.43	479.2	45.76	134.8
Repx WM	3	120.79	0.047	85.20	5.51	28.08
BlockxRepx WM	18	68.35	0.040	154.37	7.514	72.53
Genotypes	29	720.15**	0.50**	626.28**	85.24**	336.10**
Genotypesx WM	29	123.57*	0.017*	89.044*	6.46**	13.81**
Error	116	60.11	0.036	76.342	7.46	8.50
Total	196					

Source	**DF**	**Booting days**	**SPAD at boot**	**Anthesis days**	**SPAD at Anthesis**	**Grain (ton/ha)**
Water management	1	76.991	219.862	152.98	210.85	0.059
Repx WM	3	15.70	8.022	7.91	36.32	0.012
BlockxRepx WM	18	10.397	6.932	9.28	14.32	0.0070
Genotypes	29	289.18**	110.57**	340.90**	170.15**	0.0393**
Genotypesx WM	29	10.54*	9.96*	8.18**	11.38**	0.0088*
Error	116	7.24	10.24	6.066	11.43	0.0106
Total	196					

*, ** Significant at 0.05 and 0.01 probability levels, respectively. Water management (WM) refers to irrigated and drought conditions.

highest SPAD value had been found in normal irrigated condition with 24.82 and little less value was defined in drought condition worth 23.54. This decrease in value of SPAD was closely related with the decrease in value of chlorophyll and ultimately gave lower yield which has supported from Araus et al. (1997) (Table 6).

Multivariate analysis

UPGMA clustering

Four clusters were seen with a minimum of 50% similarity level in UPGMA clustering where Cluster 1 consist of 4 genotypes WK1123, WK1182, F60314.76/M-RL and WK1444. The member of this cluster were characterized by their lowest drought susceptibility index for Biomass, TKW, Yield /Plot, Number of tillers per plot and Number of seed per panicle therefore these were selected and categorized as the most drought resistance. Cluster 2 was developed by the use of Biomass yield/plot, number of tillers per plot. Genotypes consisted WK1670, WK1639, WK1700, WK1701, 3EBWYT511, Pasang lhamu, WK1679, WK1726, 3EBWYT515, RR21, WK1792, WK1793, WK1794, WK1204 and WK1627. The members of this cluster also have mild drought tolerance

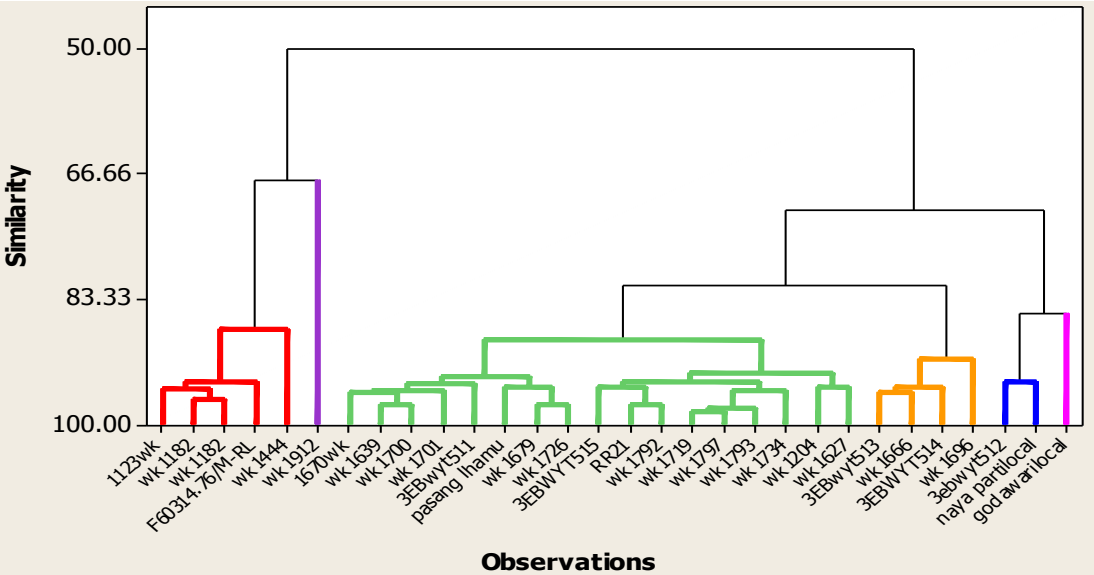

Figure 4. Different cluster groups in the dendogram while all the genotypes were grouped based on their average performance from irrigated environments.

Table 6. Eigen analysis and proportion of PCA to the different traits of the correlation matrix.

Eigenvalue	4.2937	1.8783	0.8686	0.6713	0.5034
Proportion	0.477	0.209	0.097	0.075	0.056
Cumulative	0.477	0.686	0.782	0.857	0.913
Variable	PC1	PC2	PC3	PC4	PC5

characters. Similarly, Cluster 3 consist of 3EBWYT513, WK1666, 3EBWYT514 and WK1696 which have categorized on the basis of similar type of plant height in addition to this, heights of these genotypes were highest among other and this group was also characterized on the basis of mild tolerance for drought adaptation on the basis of yield component traits. Cluster 4 was using the days to flag leaf senescence, days to booting, days to heading, days to anthesis, CTD at 13 February and CTD at 24th March. These clusters consist of 3EBWYT512, Nayaparti local and Godawari local (Figure 4).

Principle component analysis

The contribution of various parameters in the first three principle components is presented (Table 6). The first three principle component explained variation of 78.2% of the total variation. PC1 contributed 47.7% of the total variation and PC2 and PC3 contributed 20.9 and 9.7% of the total variation, respectively. Hence, the three components can be regarded the main contributing factors for the grouping of the genotypes across various groups. The PCA supported the results obtained by cluster analysis. It clearly separated the four major groups recognized by the cluster analysis. This PCA analysis clearly showed that there were presences of diversity between and within group of the cluster for many quantitative traits (Figure 5).

Conclusion

The mean per plot yield in drought condition was 2563 kg/ha whereas it was 3269 kg/ha in irrigated condition. To conclude, all the measured traits were correlated medium to high correlation coefficient in both environments. Accordingly, possibility of indirect selection would increase rather than as direct yield component. In summary, least drought sensitive index for yield per plot were found to 3EBWYT513, 3EBWYT512, WK1444 and WK 1701 therefore these genotypes could be used either directly as a variety or used as a parent for hybridization.

Conflict of Interest

The authors have not declared any conflict of interest.

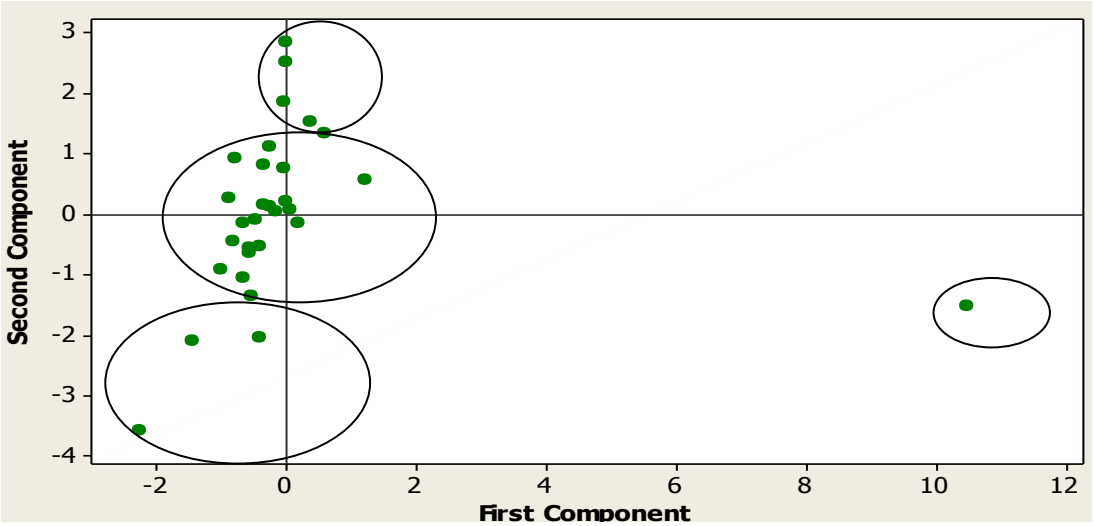

Figure 5. The score plot of first two components of 30 wheat genotypes in irrigated environment.

ACKNOWLEDGEMENTS

This research was possible due to the financial support from National Agricultural Research and Development fund, Government of Nepal. Similarly, seed materials were received from Agri-botany Division, Nepal Agricultural Research Council, and Government of Nepal. I hearty acknowledge to my major advisor Dr. Surya Kant Ghimire for his constant support and constant guidance throughout the whole research.

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academicJournals

Vol. 7(6), pp. 185-202, June 2015
DOI: 10.5897/JPBCS2015.0504
Article Number: 78DD42853683
ISSN 2006-9758

http://www.academicjournals.org/JPBCS

Journal of Plant Breeding and Crop Science

Full Length Research Paper

Analysis of phenotypic responses influencing leaf growth rate and harvest parameters in cassava (*Manihot esculenta* Crantz) under hydrothermal stress

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Received 10 February, 2015; Accepted 9 June, 2015

Plants under hydrothermal stress show a variety of responses aimed at reducing leaf growth and total leaf area, thereby reducing physiological processes such as transpiration and photosynthesis. The effects of hydrothermal stress on cassava plant growth parameters were thus investigated. Twenty cassava varieties representing a broad range of genetic diversity were used. Plants were grown in the field, physical measurements were made and percentage changes in growth parameters and biomass accumulation recorded bimonthly. Significant variation among varieties was found for the response to stress of leaf growth rate (losses of between 60 and 100% after stress) and duration (losses within 1 to 2 months) which equally resulted into reduction in leaf area. Variations were also observed in leaf retention (0 to 40%) and expansion rate (lamina width (25 to 33%) and length (14 to 58%) among different varieties. Differences were also observed for the time and rate of leaf loss during stress period. Based on observed differences, varieties were grouped under three distinct clusters including early recovering varieties, stay green varieties and the susceptible varieties. Alterations in leaf properties were highly correlated to harvest index where low harvest index (0.2 to 0.4) was observed for stay green and susceptible varieties compared to early recovering varieties (0.4 to 0.7). From the observation, different coping mechanisms, important in selection of drought stress tolerant genotypes were identified and pointed to specific genetic mechanisms for leaf retention/loss and biomass accumulation. The results suggest that rate of growth and duration differences are due to different physiological mechanisms, and can be combined to select for hydrothermal stress tolerant varieties.

Key words: Leaf expansion rate, leaf area, leaf development, recovery mechanisms.

INTRODUCTION

Plants respond to abiotic stresses, in part through the reduction of physiological processes (transpiration,

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photosynthesis and respiration) which can be can be achieved by morphological adjustments such as stomatal closure (Tardieu and Davies, 1993), leaf wilting and leaf rolling (O'Toole and Cruz, 1980). Understanding morphological trait adjustments during cassava growth is thus essential in elucidating how environmental stress affects plant growth and development components. In addition, common stress tolerance mechanisms involve reductions in leaf and shoots growth which are genetically determined, but are highly influenced by the environment (Kaplan, 2001). Therefore, their behavior can explain observed changes in plant structure in response to changes in environment. Notably, changes in leaf area under stress can be a consequence of reduced leaf number and/or reduced area of individual leaves (Aguirreza´bal, 2006; Kaplan, 2001) which in turn leads to reduction of leaf growth, a factor that is influenced by decreased cell division (Schuppler et al., 1998; Granier et al., 2000), cell wall hardening (Neumann, 1995), and decreased turgor (Hsiao et al., 1998).

The extent of leaf growth reduction in response to stress is an important factor in determining the adaptation of a certain plant or variety to an environmental scenario. As observed in some plants, prolonged drought leads to reduced leaf growth but plants are more likely to reach maturity with considerable yield. On the other hand, during short-term water deficits, a plant which maintains leaf growth is likely to have higher yields (Blum, 2005). This too is observed under thermal stress which results in total leaf morphology shift as observed by Guerin et al. (2012). Architectural changes during growths, which are related to such limitations as abiotic stresses or translocation of water and nutrients, can therefore decrease or, increase the effects of physiological changes on the functioning of entire plants (Valladares and Pearcy, 1999; Zotz et al., 2002). Such scenarios point to an internal genetic control mechanism that allows cassava to adapt to changes in environment. It also points to a well regulated gene expression network allowing plants to respond appropriately to hydrothermal stress.

Since the photosynthetic performance of vascular plants depends on plant and leaf size (Schmidt and Zotz 2001), changes in leaf related parameters such as leaf area, leaf size and leaf numbers are likely to influence net productivity of the plant and related plant processes such as cell expansion, physiology and development. Usually changes in plant size result into changes in leaf shape although changes in leaf sizes and leaf architecture may be mediated by the effects of the environment. In addition, changes in the leaf area index are not only affected by the age of the plant but by other environmental factors such as photosynthetic light flux and temperature (Zotz et al., 2002). This implies that occurrence of hydrothermal stress has a negative impact on leaf development and related processes such as nitrogen use efficiency and carbon partitioning which determine the photosynthetic potential of the leaf and hence its broad functioning (Katahata et al., 2007).

A plant can maintain its leaf area by maintaining its growth rate (Salekdeh et al., 2009; Blum, 2005) or by increasing the duration of leaf growth (Aguirreza´bal , 2006) both of which have the benefit of increasing the opportunity for recovery after offset of stress (Alves and Setter, 2004). However, changes in the moisture and temperature regimes over a certain period may result into failure of the plant to uphold its growth rate hence reducing the plant size. In a number of crops (Fasehun, 1979) low soil moisture results into dehydration or loss of cell water and hence cell death or inactivity (Osorio et al., 1998). Water deficits, important causes of dehydration, result into reduced branching, leaf production and leaf expansion which result into reduced biomass (Osorio et al., 1998) and reduced photosynthetic capabilities (Seyed et al., 2012). This could be attributed to dehydration that results into altered biomass allocation and changes in the translocation/evapo-transpiration processes. Thus, acclimatization to dehydration stress may trigger avoidance mechanisms which in turn protect the plant from dehydration stresses (Seyed et al., 2012). In particular, loss in turgor in the leaves results into surface area reduction hence reduced leaf size (Salekdeh et al., 2009), a stress tolerance/avoidance strategy. Hence, different plants will respond differently to such changes where the responses are mediated by the plants' genetic makeup. This genetic variability in leaf growth and development could be used to develop crop varieties adapted to specific stress scenarios. However, breeding for these traits is not a common approach for obtaining drought resistance in crop species because of a lack of well-characterized source of genetic variability. This study seeks to address this concern by providing relevant phenotypic information to explain the genetic variability observed.

In studies on the effect of temperature on leafy vegetative parts of the plants, it has been established that increase in temperature results into increased senescence of floral and leafy parts with more than 50% reductions observed in flowery parts compared to the leafy parts (Yin and Kropff, 1996). Temperatures slightly below the optimal growth temperatures result into increased leaf area, dry weight and thickness (Shin et al., 2001). For tropical plants, temperatures slightly above optimal growth temperatures may mean increased photosynthesis for the leaves although this may result into loss in dry weight (Boese and Huner, 1990) which later affects the plants ability to produce metabolites for storage or yield and accelerates aging. Thus, thermal stress negative effects on biomass and reductions observed are a result of modifications in the plants developmental organs which help the plant in offsetting the effects of the stress. This protects the plant from succumbing to cumulative stress as observed for most abiotic stresses (Salekdeh et al. 2009). In addition, when

there is an interaction between water and heat stress (hydrothermal stress), plant growth and development may be severely compromised.

The changes in plant growth respond to water deficit and high temperatures as discussed above have not been studied in cassava. At this point and with the changes in climate anticipated, it is required that the analysis of cell- and leaf-level responses to water deficit and increased temperature in regard to plant growth traits be understood. Since radiation interception, as well as photosynthesis and transpiration, are largely affected by water availability and temperatures, the effects of these factors on primary morphological sites for physiological process need to be understood. Thus, the objective of this work was to analyze the response of leaf growth to water deficit and increased temperature in several cassava genotypes in order to identify and quantitatively describe sources of phenotypic variability for these drought tolerance determinant traits.

MATERIALS AND METHODS

Twenty varieties of cassava were selected based on their dry matter content, resistance to Cassava Mosaic Disease (CMD) and farmer preference and established in a Randomized Complete Block Design (RCBD) in Kasese, Western Uganda. The varieties included local farmer preferred varieties such as Nyaraboke, Kwatamumpale, Mpologoma, Bao, Bukalasa, Mercury, Magana, Rugogoma and Gwalanda. These varieties have good eating qualities, are very amenable to processing, show a specific level of tolerance to cassava mosaic disease and are said to be adapted to dry conditions. The elite varieties selected included NASE 1, NASE 2, NASE 3, NASE 12, TME 204, I/92/00067, MH96/0068 which combine tolerance to drought with CMD resistance, high dry matter content and good processing traits. In particular, variety MH96/0068 was selected in a study by Turyagyenda et al. (2013) as one of the stay green varieties with high levels of tolerance to water stress. The newly released varieties NASE 13, NASE 14, NASE 16 and NASE 19 are farmer preferred elite varieties recently released and have shown some level of resilience to drought stress. These varieties combine high dry matter contents and high yield with resistance to CMD, tolerance to CBSD and a recommendable level of resistance to abiotic stresses. However, they have not been screened thoroughly for their resistance to hydrothermal stress and no recommendations so far can be made in this effect to the farmers using these varieties. The trial consisted of two experimental and two control blocks in $81M^2$ plots, with up to 81 plants per plot. The plant responses to available conditions were monitored on a bimonthly basis where changes in leaf properties and plant growth parameters were recorded. Weather and location characteristics were also recorded during the trial period.

Soil properties, water properties and weather characteristics of the trial site

Properties including soil pH, organic matter, and minerals such as Nitrogen, Phosphorus, Calcium, Potassium, Boron, Zinc, Copper, Manganese, Iron, and Magnesium were investigated in terms of their quantities. Soil components such as silt, sand and clay were determined. Properties of the irrigation water to be used such as salinity and pH were also determined.

Weather patterns for the trial site were monitored during the trial period. This allowed the forecasting and determination of periods of critical soil moisture stress and increased air temperatures and factors that affect changes in these two properties that make hydrothermal stress. Important parameters affecting the relative humidity and soil water availability were considered. Daily rain fall patterns were recorded in addition to hourly temperature regimes throughout the stress period. The relative humidity was also recorded on an hourly basis. These were averaged on a monthly basis and used to make inferences on how the plant reacted to different environmental changes during its growth cycle.

Description of planting date and developmental cycles of cassava with rainfall pattern

In order to synchronize the data collection schedule with impending forecasted weather conditions, a specific date for planting the trial was chosen. The choice of the planting date was dependent on the developmental cycle of cassava plants and considerations for parameters to be studied at different times in the crop growth cycle. Planting was carried out in the first season representing a time of maximal rainfall during April to allow the plant to fully establish in the high moisture regimes and favorable temperatures at that time. Initial hydrothermal stress was experienced in the low rainfall period (June to August), allowing studies into the effect of stress and how it affects plant growth and development. This was followed by favorable moisture and temperature conditions between September and November allowing unaltered crop growth and root bulking coupled to maximum canopy development for the crop. The final stage of root bulking fell into a hydrothermal stress period between December and March affecting the plants canopy and its stored reserves.

Determination of leaf properties

During the plant growth cycle, the rate of growth and development was determined by direct measurements of leaf related properties and the changes thereof used to compare differences in plant growth and developments. Leaf properties were determined by direct measurements on the 5^{th} most fully expanded leaf on each plant at a specific time. Leaf length, leaf width, petiole length, and plant height were measured using a measuring tape (Stanley 33-115, Power Lock, England) and the different measurements recorded in centimeters. For leaf lobe length and width, the centrally positioned leaf lobe on the 5^{th} leaf was considered. This was meant to harmonize the different measurements taken. Numerical counting was used for leaf lobe numbers of the 5^{th} fully expanded leaf and whole plant leaf numbers. Cumulative changes in leaf numbers and leaf characteristics were recorded over the 12 month growth period. These were compared across the three broad phenotypic manifestations observed during growth. In addition, changes in particular leaf properties with growth time were also recorded. Mean values for each property was determined from replicated observations on six plants per plot. Variations in these properties were then determined using the analysis of variance. Summary statistics (means, and standard deviations) were computed for leaf, soil and water properties. For each of the leaf properties, values for the fifteen replicate leaves in each replication were averaged to produce a mean for each of the varieties. Means were computed for cumulative changes in each leaf property to produce mean trends for each variety across the growing period. Subsequently, variables were averaged across all varieties and within each phenotypic class for trend evaluation. The significance ($P > 0.05$) of mean differences among variety groups was determined by analysis of variance (GenStat Discovery Edition, 2012).

Cumulative Leaf Percentage change (%CLP) in the different leaf

properties was calculated using the formulae below:

$$\%CLP = \frac{100(V2 - V0)}{V0}$$

Where V0 = Variety group leaf property at preceding data taking period; and V2 = Variety leaf property two months after the preceding data taking period.

The percentage progressive change in total leaf numbers (%PCL) was calculated from two months after planting using the formulae:

$$\%PCL = \frac{100(Ln2 - Ln0)}{Ln0}$$

Where: Ln0 = Number of leaves in the preceding month of data collection, and Ln2 = Number of leaves two months after the preceding month of data collection.

Progressive change in plant height (PCH) was calculated from two months after planting using the formulae:

$$\%PCH = \frac{100(Ph2 - Ph0)}{Ph0}$$

Where: Ph0 = Plant height in the preceding month of data collection, and Ph2 = Plant height two months after the preceding month of data collection.

Harvest index and related parameters

To determine the overall effect of the hydrothermal stress on cassava yield and the differences among the varieties of cassava used in this study, the harvest index and related yield parameters were investigated. Harvest index was determined as the ratio of the weight of the root to the weight of the shoot for six plants in each plot in three replications. Total root number for each plant was recorded and cortex thickness determined for at least six commercial roots from each plot. In addition, the branching length and stem diameter were also determined by measurement.

Statistical analysis

Mean values for each of the properties were generated from the analysis of results using Microsoft excel software. The standard deviations and standard error were used to compare the variety characteristics across a given parameter. Analysis of variance and correlations among study parameters for all the test varieties were computed using the GenStat software (Genstat, discovery edition, 2012) and used to study the effect of above plant biomass on the yield components of the plant. Regression analyses and correlation analyses were employed to determine overall relationships among leaf properties and harvest parameters.

RESULTS

Soil, water and weather characteristics

Soil and water properties were determined for the trial site to understand the suitability of the site for a hydrothermal stress screening experiment. It was also important in understanding the water retention properties of the soil, mineral and nutrient availability and the suitability of the water for irrigating the control plots.

These properties are presented in Table 1. Soil pH ranged from 6.5 to 6.7 and was in the required range for growth and development of cassava as earlier suggested by Alves and Setter (2004). The water pH was also at neutrality ranging from 7.01 to 7.07. The average percentage of sand (53.47%) was twice as much as the percentage of clay (21.9%) and silt (18.63%) showing that the soil at the trial site could be easily drained and with very low capacity to hold water for a long time appropriate for drought screening. A high organic matter content (3.5 to 4.8%) and Nitrogen content 0.2 to 0.25% was observed which was appropriate for vegetative growth. Other elements such as phosphorus, Calcium, Magnesium, Potassium, Boron, Zinc, Copper, Manganese, and Iron fell in the recommended range for plant growth. The electrical conductivity of the irrigation water ranged from 104 to 111 µs/cm while the water contained low amounts of minerals such as calcium, magnesium, and potassium which ranged from trace to 0.17 ppm. The water also did not contain either carbonates or bicarbonates hence the near neutral pH observed.

Weather characteristics

The main determinant weather characteristics were recorded to show the relationships between weather characteristics and how they varied during the experimental period. The values are presented in Figure 2F. The trial was planted in April at a time when a considerable amount of rainfall and hence humidity was available to allow for crop establishment. By June (at two months after planting), the experiment was established. Between August and October, high rainfall hence increments in humidity were realized allowing the trial to fully establish and the plants to root and bulk. By the onset of stress in the month of December, the plants had already developed roots and had substantial reserves in the storage roots. Stress was characterized by reductions in rainfall and humidity and increments in temperature for a period of 12 weeks between the month of December and March (Figure 2F). Peak stress was characterized by increased temperature and reduced humidity experienced mid-January up to beginning of March for a period of 7 to 8 weeks. This was reversed with increased rainfall and moisture experienced in March and April (Figure 2F).

Phenotypic grouping of the varieties

Based on observed phenotypic characteristics, varieties were ranked according to their ability to retain leaves or recover leaves during and after the hydrothermal stress period (Plate 1). The groupings included varieties that maintained a moderately high Leaf Area Index (LAI) during hydrothermal stress or stay green varieties (SGV).

Table 1. Properties of Soil at the trial site and characteristics of irrigation water used.

Property (soil)	Units	Content	Range
pH	-	6.53	6.4-6.7
Sand	%	53.47	49.8-59.8
Clay	%	21.90	24.9-30.9
Silt	%	18.63	15.3-21.3
Organic matter	%	4.01	3.5-4.8
Nitrogen	%	0.22	0.2-0.25
Phosphorus	ppm	23.80	6.0-55
Calcium	Ppm	4090.26	2316.4-7573
Magnesium	ppm	882.3	346.3-1467.5
Potassium	ppm	383.98	194.8-675.1
Boron	ppm	17.50	12.87-26.8
Zinc	ppm	0.58	0.2-1.1
Copper	ppm	10.23	8.2-13.8
Manganese	ppm	156.34	82.0-235.7
Iron	ppm	457.57	380.7-1786
Water properties			
Water pH	-	7.05	7.02-7.07
Electrical conductivity	Us/cm	107	104-111
SAR	Meq/L	2.0	1.2-2.9
Calcium	ppm	Trace	Trace
Magnesium	ppm	0.11	0.08-0.15
Pottasium	ppm	0.09	0.04-0.17
Sodium	ppm	0.05	0.2-0.9
Carbonates	ppm	0.00	0
Bicarbonates	ppm	0.00	0

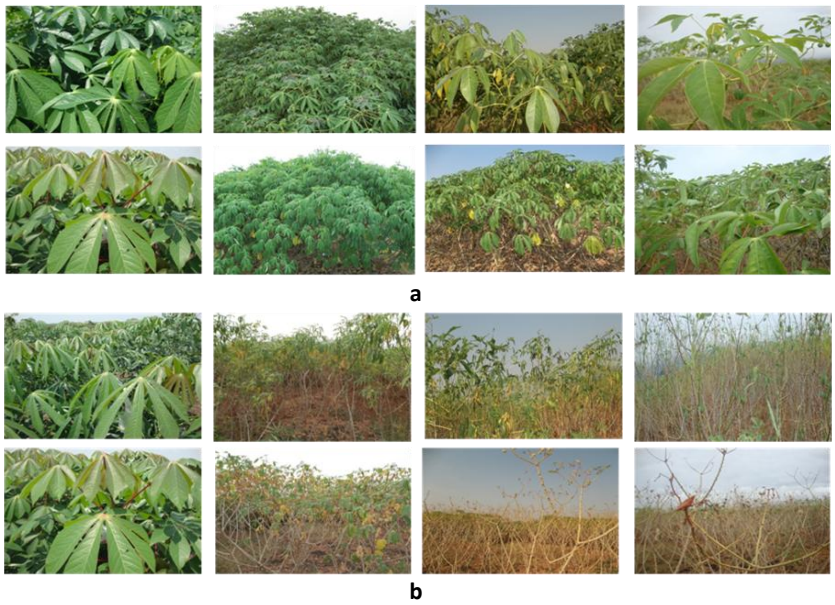

Plate 1. (a) Stay green varieties (NASE 3 [top] and 1/92/0067 [bottom]) as observed at 6 MAP, 8 MAP (on set of stress) and 9 to 10 MAP; (b) Some susceptible varieties (Mercury [top] and NASE 1 [bottom]) as observed 6 MAP, 8 MAP (on set of stress) and 9 to 10 MAP.

Plate 2. The early recovering trait observed in NASE 16, 19 and 12 two weeks before rains in response to increased relative humidity.

These included varieties such as NASE 2, NASE 3, MH96/0686, I/92/0067 and the local variety Magana. However, some varieties completely lost leaves as stress progressed and even the remaining leaves during stress were dechloropyllated and yellow signifying losses in chlorophyll and related pigments hence little or no capacity to photosynthesize. These varieties showed little or no capacity to recover easily after stress and they were labeled susceptible varieties (SV). They included varieties such as NASE 1, Rugogoma and Mercury. The other grouping included varieties that lost all their leaves immediately after onset of stress only to recover immediately with increase in relative humidity or early recovering varieties (ERV). They included NASE 16, NASE 19 and Bukalasa (Plate 2). Some varieties had both mechanisms but were not very pronounced in each case.

Cumulative changes in leaf properties over the growth period

For determination of the differences in the rate of growth and development among the cassava varieties used in this study, cumulative changes in leaf properties were determined and the results obtained are presented in Table 2. Significant differences were observed for petiole length among variety groups at 4 months after planting where the early recovering varieties had the highest cumulative petiole length growth observed. Stay green varieties had low cumulative petiole growth even at 4 months after planting. Negative cumulative increase in petiole length at 8 months after planting coincided with onset of stress. Highest reductions were observed for susceptible varieties (-22.4%) and the lowest for stay green varieties (-13.4%) at the end of the critical stress period. At 9 months after planting, the early recovering varieties had lost almost all leaves only to recover them a month later (Table 2). At twelve months after planting, (one month post recovery), early recovering varieties had gained more new leaves hence positive cumulative percentage differences (231.4%) observed. However, the cumulative change was low in susceptible varieties (18.3%) while it was negative (-13.4%) for stay green varieties at twelve months after planting.

Significant variations ($P<0.05$) were observed in leaf lobe numbers at four months after planting with the early recovering varieties having the highest cumulative leaf lobe numbers (25.3%) compared to stay green varieties (4.2%) and susceptible varieties (14.7%). The pattern changed with onset of stress (eight months after planting) where severe reductions were observed for susceptible varieties (-48.6%) while low cumulative reductions were observed for stay green varieties (-14.3%) and early recovering varieties (-25.1). Differences occurred in the rate of reduction with stay green varieties having the highest cumulative reductions rate over the growth period. However, the early recovering varieties lost all the leaves as the stress period progressed making it difficult to follow the changes that occurred. Unlike petiole length, there were significant differences in the rate of reduction of leaf lobes between stay green varieties and early recovering varieties throughout the whole growth period. At twelve months after planting, stay green varieties had negative changes (-34.6%) while early recovering varieties had positive cumulative changes (234%) in leaf lobe numbers having regained a significant number of new leaves.

Changes in leaf lobe sizes were measured as leaf lobe width and length and decreased with growth time across

Table 2. Cumulative changes in leaf properties among different phenotypic groups for the 12 month growth period.

Time (months)	Leaf number	Petiole length	Leaf lobe No.	Leaf lobe width	Leaf lobe length
SGV4	238.9	6.22	4.15	29.33	4.32
ERV4	318.7	22.21	25.34	15.72	22.79
SV4	227.6	14.69	14.69	20	25.05
SGV6	115.6	-21.6	-17.4	-28.63	-24.98
ERV6	83.7	-35.61	-34.6	-27.85	-32.2
SV6	129	-35.26	-15.07	-32.91	-33.37
SGV8	131.4	-13.4	-14.3	-11.08	-26.47
ERV8	-59.8	-15.02	-25.09	-28.69	-38.69
SV8	66.2	-22.37	-48.61	-8.54	-20.04
SGV10	-59	-31.77	-5.24	-10.71	-14.25
ERV10	-67.9	-40.49	-49.63	-6.14	-21.15
SV10	-69.3	-23.73	26.88	-26.65	-17.99
SGV12	-58.3	-14.31	-1.89	-13.54	-13.35
ERV12	264	231.36	547.76	17.31	56.54
SV12	-47.3	18.3	61.69	21.08	1.54
CRC10 SGV	426.9	-60.58	-32.79	-21.09	-61.38
CRC10 ERV	274.72	-68.92	-83.99	-46.96	-69.25
CRC10 SV	353.52	-66.68	-22.11	-48.1	-46.35
CRC12 SGV	294.88	-59.88	-34.68	-34.63	-71.73
CRC12 ERV	430.96	129.96	463.78	-29.65	-12.71
CRC12 SV	244.96	-38.68	39.58	-27.02	-44.81

SGV = Stay green varieties, ERV = Early recovering varieties, SV = Susceptible varieties, 4, 6, 8, 10, 12 = months after planting (MAP), CRC10 = Total cumulative change 10 MAP (after peak stress), CRC12 = Total cumulative change 12MAP (at harvest).

the different varieties. At maximum vegetative growth between four and six months after planting, leaves were characterized into four broad categories including the short broad leaved (length between 14 and 17 cm and width between 6.5 and 7.5 cm), long broad leaved (length between 21 and 24 cm and width between 6.0 and 7.5 cm), short narrow leaved (length between 15 and 17 cm and width between 5.0 and 6.0 cm) and long narrow leaved (length between 21 and 23 cm and width between 4.5 and 6.0 cm). Most of the stay green varieties had short broad leaves and high cumulative increase in leaf lobe width and low cumulative increase in leaf lobe length (Figure 1). The early recovering varieties had intermediate characteristics with most of them having high cumulative leaf lobe length. On the other hand, the susceptible varieties had broad and long leaves. At onset of stress (eight months after planting), high cumulative reductions in leaf lobe length and width were observed for early recovering varieties (-38.7%) compared to stay green varieties (-26.5%) and susceptible varieties (-20.1%). Cumulative reductions were also observed to occur for both leaf length and leaf width at ten months after planting although major reductions were observed for leaf width.

Typically over 60% reductions for leaf lobe width compared to 35 to 45% reduction in leaf lobe length were observed (Figure 1). There were no significant ($P>0.05$) differences for cumulative leaf lobe width between stay green and susceptible varieties much as considerable changes were observed for leaf lobe length between the two. After the plants had recovered from the stress and at twelve months after planting, positive cumulative differences for leaf lobe length (more than 55% gain in leaf lobe length) compared to leaf lobe width (17% gain in leaf lobe width) were recorded for early recovering varieties. However, negative cumulative differences were observed for stay green varieties (an average of -13.5% for both leaf lobe width and length) (Table 2). For leaf lobe length, positive cumulative differences were observed for early recovering varieties (56.5%) while the susceptible varieties had low positive changes (1.5%) implying that on recovery, susceptible varieties produced broad but shorter leaves, a general change in leaf morphology. Still negative differences were observed for stay green varieties in this instance (-13.5%) (Table 2).

Changes in leaf numbers, leaf lobe numbers and leaf sizes were related to plant biomass accumulation and development. Leaf lobe numbers for stay green varieties remained fairly constant over the growth period and were slightly affected after critical hydrothermal stress at ten months after planting. They ranged from 6.5 to 7.2 leaf lobes on average (Plate 3). Among the early recovering varieties, leaf lobe numbers peaked at four months after planting with some varieties having up to an average

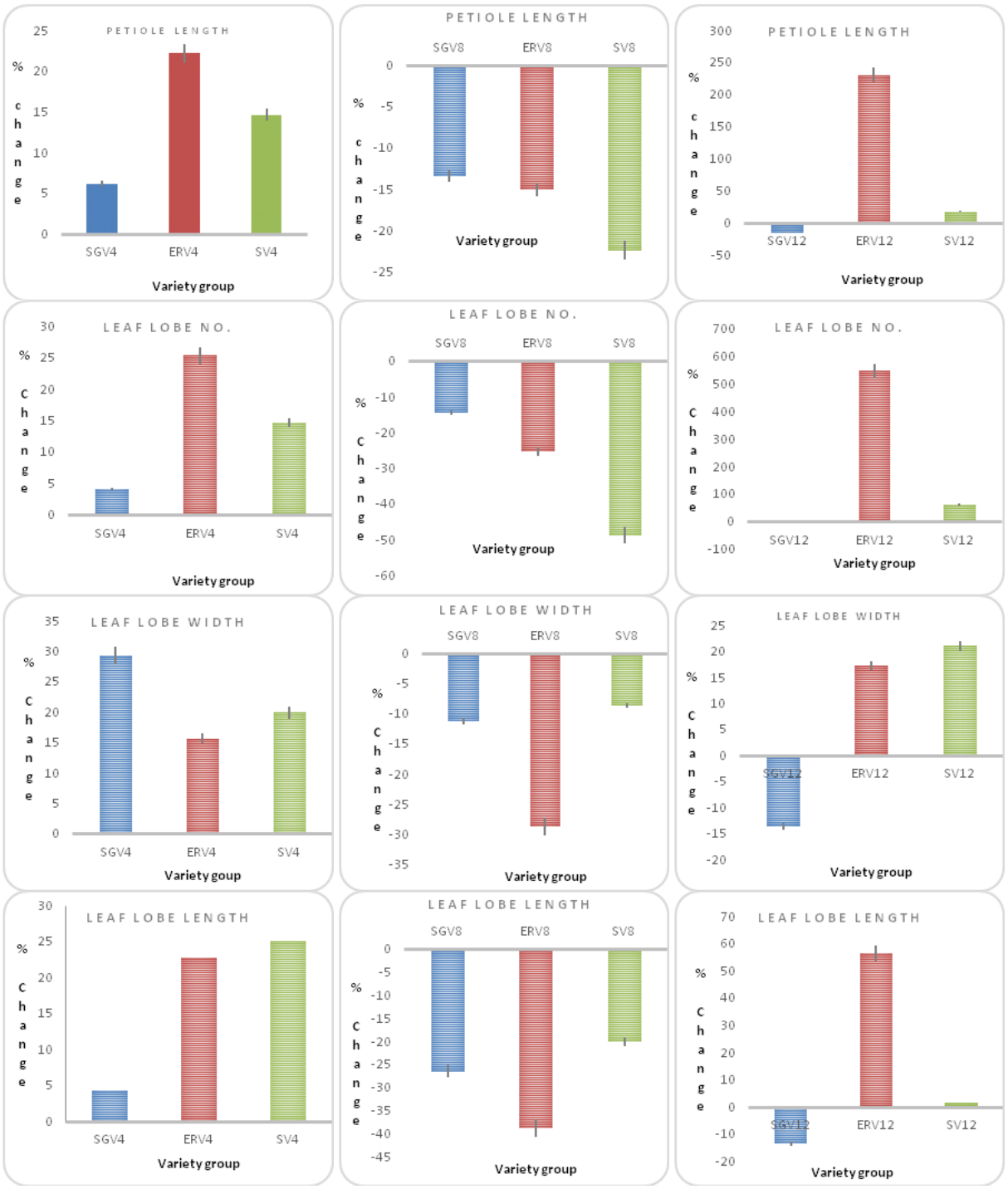

Figure 1. Percentage changes in different leaf properties at different times of crop growth and development compared to the preceding period.

of 9 leaf lobes. However, a drop was observed by six months after planting and with the onset of stress the plants shed off most of the leaves and leaf lobe numbers dropped significantly to no leaves or just one leaf lobe. On recovery, the average number of 7.4 leaf lobes was reinstated (Figure 2A) for these varieties. Susceptible varieties did not lose all the leaves during the stress period and had averages of about 3 dechlorophyllated leaf lobes with little or no capacity to carry out photosynthetic metabolism.

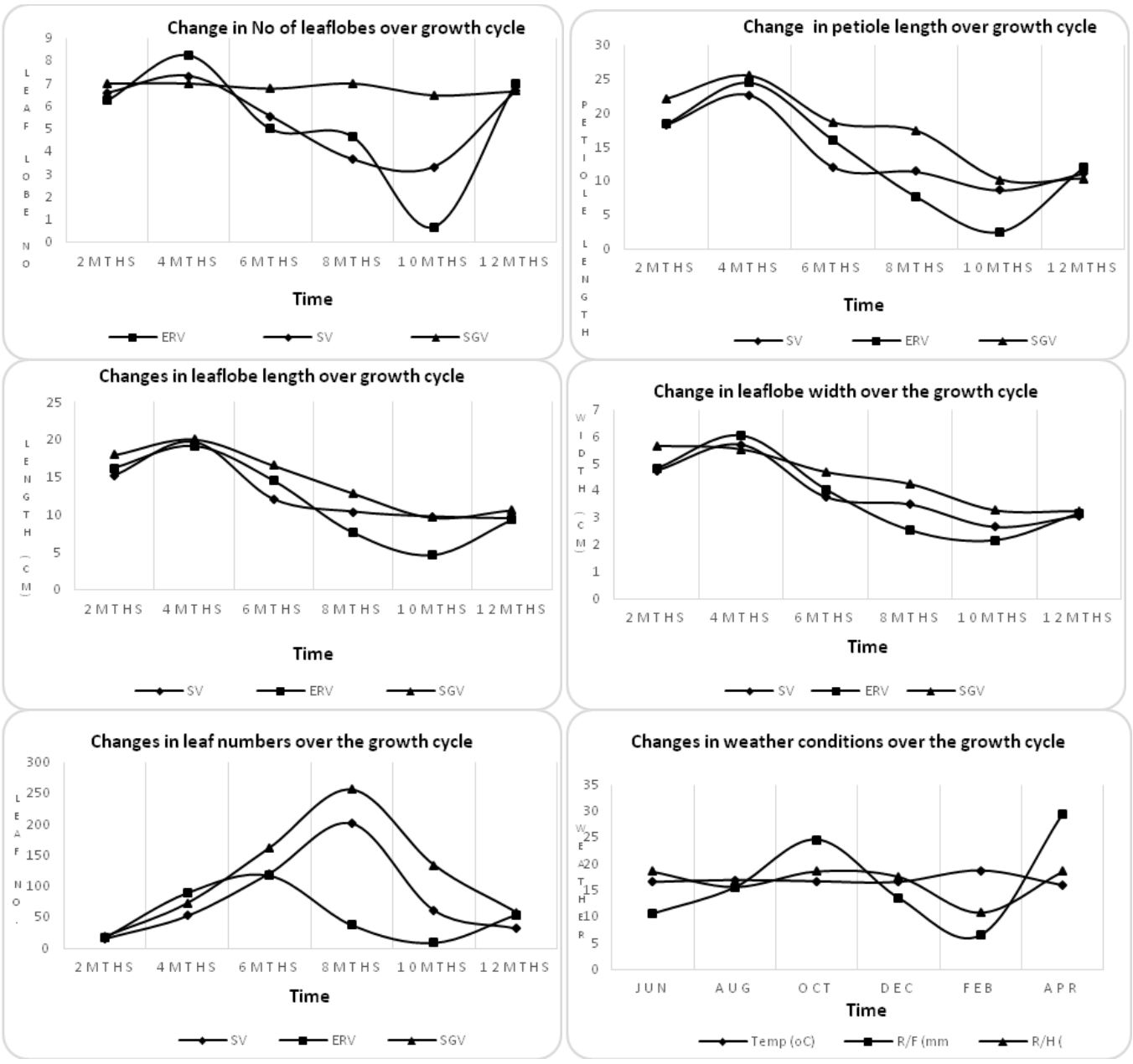

Figure 2. Comparisons for changes in leaf properties among the three broad variety groups tested from two to twelve months.

At two months after planting, petiole length ranged between 15.4 and 23.2 cm and the highest was recorded for the stay green varieties (Figure 2). The length of petioles increased significantly and by four months after planting, it ranged from 22.1 to 25.4 cm. Reductions in petiole growth were observed for all the varieties studied at six months after planting where petiole length ranged from 14.3 to 19.2 cm. In particular, the stay green varieties posted higher petiole lengths at all times compared to early recovering varieties and susceptible varieties. Reductions in moisture and increments temperature between six to eight months after planting resulted into significant reductions in petiole length among the susceptible and stay green varieties. In stay green varieties, petiole length reduced from an average17.2 cm on onset of hydrothermal stress to about 11.0 cm by the end of this stress period. No significant ($P>0.05$) increments in petiole length were observed after stress in these varieties with an average of 11.2 cm registered at 12 months after planting (Figure 2B). Among the susceptible varieties, petiole length dropped significantly from 13.7 cm at onset of hydrothermal stress

Plate 3. Photographic representation of changes in leaf numbers from 6 to 9 leaf lobes before the onset of stress to 3 to 4 leaf lobes on mild stress, to 1 leaf lobe or no leaves at maximum stress.

to about 2.3 cm by end of peak stress, a 70% reduction. The early recovering varieties had a recovery mechanism where the petiole increased in size as new leaves were produced when hydrothermal stress was relieved (Figure 2B). By two months after planting, leaf lobes lengths ranging between 15 and 18 cm were registered which increased up to 21.5 cm on average by four months after planting. However after that, a drop in size was observed ranging from 13 to 17 cm by six months after planting and 7 to 14 cm by eight months after planting just like other plant morphological properties. Onset of hydrothermal stress resulted into a more significant negative effects in leaf size growth with lengths ranging from 4 to 9 cm by the end of the stress period although increments were observed after recovery with up to about 11.5 cm registered. Differences occurred among varieties in terms of reduction in leaf size with more significant drops observed for stay green varieties (40% reduction) compared to susceptible varieties (10% reduction) and early recovering varieties (24%) (Figure 2C).

The leaf lobe width followed the same pattern as length (Figure 2D).

Changes in total leaf numbers over the growth period

Accumulation of biomass in plants is as a result of leaf production which form the biggest part of the above ground biomass and are important in photosynthesis. However, plant leaf numbers vary due to genetic differences but most importantly due to changes in the environment. Thus, the variations in leaf numbers were determined and the results are presented in Figure 2E and Table 3. At two months after planting, most plants had average leaf numbers between 12 and 24 leaves which increased up to 40 to 94 leaves by 4 MAP.

Table 3. Progressive change in leaf numbers (LN) in comparison with percentage change (Δ %) over the growth cycle.

Accession	LN2	4Δ%	LN4	6Δ%	LN6	8Δ%	LN8	10Δ%	LN10	12Δ%	LN12	%CC10	%CC12	%TCC
Bao	16.42	236	55.17	164.2	145.8	35.487	197.5	-76.456	46.5	-39.1	28.33	359.2	320	-39
Nase 12	19.83	282.9	75.92	94.06	147.3	0.1154	147.5	-62.597	55.17	-60.7	21.67	314.4	254	-61
Nase 1	14.67	306.1	59.58	149.7	148.8	35.657	201.8	-87.698	24.83	-35.6	16	403.8	368	-36
72-TME-14	19.91	215.6	62.83	136.1	148.3	-51.743	71.58	-59.486	29	25.9	36.5	240.4	266	26
Nyaraboke	16.08	227.6	52.67	129.5	120.9	66.167	200.8	-69.292	61.67	-47.3	32.5	353.9	307	-47
Kwatamumpale	18.17	189.4	52.58	160.6	137	-7.1752	127.2	-43.383	72	-11.1	64	299.4	288	-11
Mpologoma	13.75	197.6	40.92	195.7	121	123.97	271	-86.041	37.83	-52.9	17.83	431.2	378	-53
Magana	21.58	326.7	92.08	143.3	224	9.4866	245.3	-68.33	77.67	-67.6	25.17	411.1	344	-68
Bukalasa	19.08	174.3	52.33	180.3	146.7	48.463	217.8	-90.664	20.33	32	26.83	312.3	344	32
Nase 2	16.08	284.5	61.83	73.23	107.1	288.46	416.1	-61.866	158.7	-85.3	23.33	584.3	499	-85
Rugogoma	19.08	245.9	66	69.03	111.6	156.14	285.8	-66.639	95.33	-85.5	13.83	404.4	319	-85
TME 204	18	227.8	59	170.2	159.4	14.806	183	-50	91.5	-79	19.17	362.7	284	-79
266Bam	17.17	421.8	89.58	31.23	117.6	-67.889	37.75	-76.159	9	348	40.33	309	657	348
Gwalanda	19.75	243.9	67.92	159.9	176.6	5.7774	186.8	-73.403	49.67	-30.9	34.33	336.2	305	-31
Nase 3	15.1	192.5	44.17	212.4	138	214.49	434	-73.541	114.8	-77.1	26.33	545.9	469	-77
MM96/4271	20.75	283.5	79.58	91.71	152.6	-8.613	139.4	-87.211	17.83	85.1	33	279.4	364	85
Mercury	17.33	225	56.33	125.4	127	31.207	166.6	-76.486	39.17	-33.2	26.17	305.1	272	-33
MM97/2961	20.91	214.1	65.67	128.6	150.1	-15.116	127.4	-81.69	23.33	77.9	41.5	245.8	324	78
O686	18.33	294.6	72.33	124.1	162.1	58.022	256.2	-47.625	134.2	-56.9	57.83	429.1	372	-57
I/92/0067	18.33	251	64.33	149.6	160.6	47.805	237.3	-67.417	77.33	-32.5	52.17	381	348	-33

Emphasis is on plant reaction 8MAP at the onset of peak stress up to 12MAP at harvest time. LN=Leaf numbers at different bimonthly periods. Δ%=change in leaf numbers as a percentage of the original number two months before.

Progressive increments were observed with time to an average of 107 to 177 leaves by six months after planting and 120 to 417 at eight months after planting representing a broad range of leaf numbers across different varieties. After this, leaf numbers fell significantly to as low as only 9 leaves per plant in early recovering varieties and 158 leaves in some of the stay green varieties at ten months after planting during the critical stress period. However, after critical hydrothermal stress, continued growth resulted into more leaves depending on the mechanism of tolerance to stress displayed.

The number of leaves increased significantly reaching the peak at 6 MAP for early recovering varieties (125 leaves on average) and at 8 MAP for susceptible varieties (200 leaves on average) and stay green varieties (250 leaves on average) per plant. In early recovering varieties, there were losses in the number of leaves at onset of critical hydrothermal stress at eight months after planting. Such losses continued throughout the stress period reaching a minimum of an average of two leaves per plant by peak stress at 10 MAP representing an average loss of 80% in the total leaf numbers (Table 3). However on recovery, early recovering plants regained most of the leaves per plant at the end of the growth period representing an average gain of over 95% and an overall net gain of 15% of the leaves compared to the period before critical hydrothermal stress period. For the stay green varieties, drops in leaf numbers started later in the critical hydrothermal stress period at about 9 MAP. Significant ($p<0.05$) losses in leaves were observed from about 250 leaves registered at 8 MAP to a loss of about 48%

of all the leaves by 10 MAP. With no recovery mechanism presented in these varieties, continued leaf loss was observed up to about 78 leaves per plant by the end of the growth cycle representing an average net loss of about 98% of the total leaves compared to the period before critical hydrothermal stress. The same pattern was observed for susceptible varieties although more losses (70%) were registered by 10 MAP and with up to 34 leaves per plant at the end of the growth period representing about 100% loss in leaves compared to the leaf number before the stress period (Figure 2E). While the early recovering variety plants shed off their leaves, the stay green and susceptible varieties maintained their leaves, significantly reducing the leaf size and slowly reducing leaf numbers through normal leaf senescence. However, on recovery, the ERV easily and spontaneously gained photosynthesizing leaves and by harvest time had the same leaf numbers as stay green varieties. Variations in leaf numbers among the different variety groups were significant ($p<0.05$) between six and ten months after planting but specifically at eight months after planting. This coincides with the period of peak stress and the variations were more pronounced between the stay green varieties and the early recovering varieties. While stay green varieties like Magana, NASE 3, NASE 2, I/92/0067 and MH96/0686 maintained high leaf numbers even during the stress period with the highest average leaf number being 416 leaves at eight months after planting, varieties like NASE 16 NASE 19, and Bukalasa lost most of the leaves with more than 76.2% reductions immediately after onset of critical hydrothermal stress (Table 3). Percentage total cumulative changes (%TCC) in leaf number at ten months after planting was high among the stay green varieties (350 to 580%) and low for the early recovering varieties (200 to 310%) showing that the stay green varieties maintained leaves over a long period of time during stress compared to other varieties. Percentage total cumulative change at twelve months after planting was almost equal for both stay green and early recovering varieties but low for the susceptible varieties (Table 3). Total cumulative percentage change for the entire growth period was high and positive for the early recovering varieties (260 to 348%) and low and negative for susceptible varieties and stay green varieties (-80%). Based on this, the stay green varieties maintained some of the leaves although a negative cumulative percentage was observed after critical hydrothermal stress. Some of the test varieties recovered increasing the leaf numbers by eleven and twelve months after planting. Such an increment defines recovery of the plant after stress.

Thus, depending on the number of leaves on the plant, selections for drought tolerant varieties can be made easily where high leaf numbers before stress depicts a characteristic stay green variety and low leaf numbers lost immediately at onset of stress depict an early recovering variety. Among the varieties that showed a recovery mechanism, the time of recovery varied hence differences in the ability to recover during stress. The value of the total cumulative change (%TCC) at harvest can also be an important selection indicator for tolerance to stress especially if plant yield components are taken into consideration. For selection of the stay green phenotype, varieties which showed a high positive percentage between 100 and 290% eight months after planting can be important

Changes in plant height as a determinant of growth rate

Above ground biomass increments are related to the height of the plant and hence there was need to assess the variations in plant height to supplement the selection methods of hydrothermal stress tolerant varieties. Results for changes in plant height as a factor of plant growth rate are presented in Table 4. High growth rates were observed for all varieties between two and four months after planting where some varieties achieved more than 350% plant height changes compared to the height after germination. In particular high progressive changes in the growth rate were observed in NASE 16(397%), NASE 2(345%) and Mpologoma (323.7%). At six months after planting, reduced growth rates were observed with limited growth increments ranging between 30 and 80% except for the stay green variety NASE 3 with up to 135.2% growth increments. By eight months after planting, exceedingly low growth rates were observed with some varieties exhibiting negative growth rates such as NASE 16(-1.49%) due to loss of leaves and shoots at the onset of critical hydrothermal stress. At ten months after planting, a few varieties posted positive growth changes especially the stay green varieties such as I/92/0067 and Magana and some early recovering varieties such as Bukalasa. Most of the other varieties had negative growth increments due to the effect of stress on the growth and development of shoots during the stress period. Severe growth retardation was observed in varieties such as Rugogoma, Mercury, NASE 1 and Mpologoma, susceptible varieties which had most of their shoot drying up during the critical stress period and hence reductions in growth. On a cumulative basis and up to ten months after planting, high growth rates were observed for mainly stay green varieties such as Magana, MH96/0686, NASE 3, NASE 2 and the early recovering variety NASE 16 while at twelve months after planting, high cumulative growth was observed for NASE 2, NASE 16 and MH96/0686. Over all high growth rates for the whole growth period were observed for Magana, NASE 16, and MH96/0686 while low growth rates were observed for Nyaraboke, NASE 1 and NASE 3. Varieties with overall high growth rates and yield after recovery such as NASE 16 and Magana can be selected and deployed as moisture and temperature stress tolerant varieties.

Table 4. Progressive change in plant height (PH) in comparison with percentage change (Δ%) over the growth cycle on a bimonthly basis.

Accession	PH2	PH4	4Δ%	PH6	6Δ%	PH8	8Δ%	PH10	10Δ%	PH12	12Δ%	CR10 mths	CR12mths	FCAR
Bao	37.42	133.8	257.64	203.6	52.11	228.33	12.17	234	2.48	225	-3.8	324	321	-3.85
Nase 12	30.73	91.25	196.94	162.9	78.51	180.5	10.81	179.17	-0.7	155	-13	286	272	-13.4
Nase 1	32.36	104.4	222.68	179.7	72.06	217.42	21.01	209.33	-3.7	167	-20	312	292	-20.1
72-TME-14	34.32	99.75	190.64	186.6	87.03	241.08	29.22	245.33	1.76	198	-19	309	289	-19.2
Nyaraboke	*32.32*	*121.3*	*275.15*	*187.7*	*54.77*	*210.67*	*12.26*	*219.16*	*4.03*	*148*	*-33*	*346*	*314*	*-32.7*
Kwatamumpale	41.41	127.8	208.5	225.4	76.47	245.17	8.75	252.5	2.99	234	-7.2	297	290	-7.2
Mpologoma	29.99	127.1	323.74	215.9	69.88	266.17	23.29	282.67	6.2	232	-18	423	405	-17.9
Magana	38.05	136.7	259.18	224.1	63.97	256.25	14.34	273.67	6.8	279	1.83	344	346	1.83
Bukalasa	46.56	153	228.61	219	43.14	252.67	15.37	270.67	7.12	264	-2.6	294	292	-2.59
Nase 2	24.08	107.2	345.06	169.4	58.1	218.5	28.95	231.67	6.03	164	-29	438	409	-29.4
Rugogoma	40.06	145	261.95	214.1	47.66	252.42	17.89	251.67	-0.3	224	-11	327	316	-11.1
TME 204	45.75	157.3	243.89	230.6	46.55	263.92	14.47	274	3.82	261	-4.7	309	304	-4.68
266Bam	32.23	160.3	397.47	234.4	46.22	231.17	-1.39	243	5.12	252	3.57	447	451	3.57
Gwalanda	52.73	147.8	180.21	227	53.63	267.42	17.81	274	2.46	236	-14	254	240	-13.9
Nase 3	23.83	70.58	196.18	166	135.2	211.5	27.41	188	-11	133	-29	348	318	-29.3
MM96/4271	37.02	128	245.76	215	67.96	237.67	10.54	226.67	-4.6	182	-20	320	300	-19.6
Mercury	41.48	159.1	283.63	183.3	15.21	214.25	16.87	217.67	1.6	186	-15	317	303	-14.7
MM97/2961	42.67	150.6	252.89	208.8	38.65	250.17	19.82	246.67	1.4	200	-19	313	294	-19.1
O686	33.83	130.6	285.98	230.8	76.73	276.25	19.7	266.67	3.47	285	6.75	386	393	6.75
I/92/0067	38.23	134.6	252.02	203.6	51.25	254.83	25.19	283.67	11.3	255	-10	340	330	-10.1

FCAR = Final change after recovery, PH = Plant height, CR10 = Cumulative percentage change at peak stress (10 months), CR12 = Cumulative percentage change after recovery (12months). Bolded = Varieties showing recovery mechanisms/stay green mechanisms. Bolded/italicized = susceptible variety, Nyaraboke.

Harvest index related parameters

The ratio of the below ground biomass (cassava yield components) to the above ground biomass was estimated and compared to root related properties such as Dry matter yield, cortex thickness and root number. Variations among genotypes were observed in morphological parameters such as root cortex thickness, and the branching level and number of branches. The cortex thickness was positively correlated to root number (r = 0.84), root weight (r = 0.62) and stem weight (r = 0.51). The early recovering varieties had a smaller cortex thickness (0.2 to 0.3 cm) compared to stay green varieties which had cortex thickness of 0.35 to 0.55 cm and the susceptible varieties which had cortex thickness of between 0.3 and 0.4 cm. A bigger cortex was thus related to high levels of resilience to stress as earlier observed by (Okogbenin et al., 2013). Plant height in the different genotypes was positively correlated to the stem diameter (r = 0.33) and root weight (r = 0.28). The harvest index varied significantly within the different genotypes and was negatively correlated to plant height (r = -0.19) and stem weight (-0.42). High harvest index was recorded for early recovering varieties while low harvest index was recorded for the stay green varieties. The number of roots varied significantly in different cassava varieties although no significant differences were observed for root weight ($p > 0.05$). Generally stem related properties were not significantly ($p>0.05$) different among different cassava varieties although shoot weight was positively correlated to root number (r = 0.53) and root weight (r = 0.69). Likewise stem

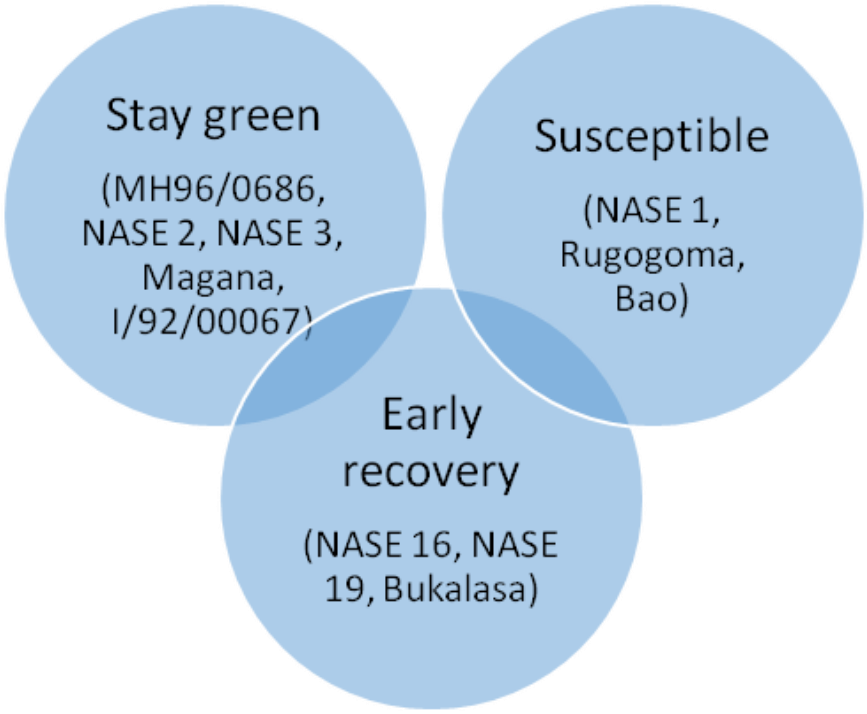

Figure 3. Varieties selected under the stay green and early recovering in relation to the susceptible varieties.

diameter was positively correlated to root weight (r = 0.57) and root number (r = 0.68). Since no differences were observed for stem related parameters, the yield components that varied significantly between different varieties are the main determinants of stress resilience in plants.

Selection of hydrothermal stress tolerant and avoidant varieties

This study was mainly conducted to understand the phenotypic mechanisms for tolerance to hydrothermal stress in cassava varieties and from the results above, a number of plant properties were identified that were key in the selection of tolerant varieties. These selections and their mechanisms are presented in Figure 3. Selections for the stay green mechanism were mainly based on the ability of the plant to accumulate biomass during the vegetative stage of growth from two to six months after planting. Plants which accumulated a lot of biomass at this time maintained substantively higher biomass contents during stress, had higher rate of leaf retention and higher growth rates. In addition, they had lower harvest indices and they were identified as stay green varieties. However, cassava plants displaying the stay green mechanism did not necessary maintain high leaf lobe numbers but instead reduced the number of leaf lobes at a lower rate compared to other varieties as the critical hydrothermal stress period progressed (Figure 2). On the other hand, selection for the early recovering mechanism were based on the loss of leaves immediately at onset of critical hydrothermal stress, the ability to produce new shoots immediately on removal of hydrothermal stress, leaf re-growth and maintenance immediately after hydrothermal stress and higher harvest indices (Figure 2). Like in the stay green mechanism, the early recovering mechanism was mainly based on leaf lobe number maintenance after hydrothermal stress but not maintenance of individual leaves. Plants which displayed no mechanism and easily succumbed to stress were described as susceptible plants.

DISCUSSION

Changes in biomass allocation and accumulation during the cassava plant growth cycle are expected. These changes describe the inherent plant characteristics which are mediated by both the genetic component of the plant and its interaction with the environment. Such changes determine the yield potential of the plant in period of normal growth where as in stress conditions; the environment plays a big role in influencing the rate of growth and ultimately affecting the yield potential of the cassava plant as earlier observed by Osorio et al. (1993). In this study, the effects of stress resulted into significant changes in plant morphology resulting into altered yield

Table 5. Variations observed for different parameters at harvest.

Source of variation	d.f.	s.s.	m.s.	v.r.	F pr.	CV	LSD
Cortex Thickness 19	19	0.347	0.021	6.52	<.001	21.3	0.121
Branch length	19	1034	5174.	4.74	<.001	1.30	77.16
Harvest Index	19	1.658	0.083	3.14	0.001	25.9	0.379
Plant Height 19	19	55909.	2795.	2.57	0.006	11.7	77.07
Root Number 19	19	210.09	10.504	2.24	0.015	23.8	5.057
Root Weight	19	57.55	2.878	0.69	0.812	41.3	4.77
Stem diameter	19	12.52	0.6260	1.16	0.334	19.4	1.714
Stem weight	19	411.	20.55	1.01	0.468	52.9	10.51

compared to the control conditions. The stress conditions also resulted into reduced growth rates and the plants ability to attain a particular growth height or leaf area index as observed (Tables 2 and 3). The results also showed that low moisture and elevated temperature stress had significant effects on dry matter accumulation, root numbers and size, plant height and also leaf lobe length and leaf width. Such significant differences in shoot based biomass affected the plants ability to effectively increase its root based biomass resulting into reductions in yield and yield components.

Reductions in leaf size and leaf expansion were observed as the main factors that cause loss in biomass during stress. Shoot and leaf biomass in most plants accumulates in a curve-linear fashion increasing to maximum by the time the plant gets into the reproductive stage (Ranawake et al., 2011). This was observed in cassava between two to six months after planting as the plants increased their biomass content linearly though variety based differences were observed showing that some of these traits are partly under genetic control (Figure 1 and Table 3). Differences observed in petiole length and leaf size (drought related traits) among variety groups at the onset of hydrothermal stress show that tolerance mechanisms are related to plant genetic makeup. Such variations result into differences in accumulation of biomass in different varieties describing a stress tolerance criterion for a particular variety. Negative changes in leaf size properties and the petiole length at eight months after planting shows the negative influence of hydrothermal stress on cassava plants. This had an impact on the harvest index as observed later on in the growth cycle of the plant and even the harvest parameters as shown in Table 5. High rates of biomass accumulation observed earlier in the plants growth cycle may be a preparatory measure for carbon sequestration preparing for periods of low carbon uptake. Hydrothermal stress increases the imbalance between carbon supply and demand resulting into reduced biomass and loss of reproductive organs (Blum, 2005). Cassava plants which have mechanisms of increasing above ground biomass for purposes of increased photosynthetic and growth metabolism may be more prepared to counteract effects of stress compared to the others which slowly accumulate biomass as has been observed in other plants by Ranawake et al. (2011). Specific increments in biomass earlier before stress was observed in the early recovering and stay green varieties which by six months after planting had significant biomass in the above ground parts hence were prepared for onset of stress later in the growth cycle

Correlation between the above ground biomass especially the stem characteristics with root biomass points to the influence of the above ground biomass on the sink (root) organs. It also points to the importance of the root cortex as one of the sink organs in stress tolerance as observed by Cohen et al. (2005) and Okogbenin et al. (2013). This also explains the correlation between harvest index and biomass parameters such as leaf size and plant height (Table 5). Higher values for cortex thickness in stay green varieties also point to the use of the storage reserves in times of stress. Thus, breeding for stress tolerance requires a full understanding of the relationships between biomass and root mass for selection of plants that effectively accumulate photosynthetic biomass and offset the effects of stress. The differences observed before onset of stress among the different variety groups but especially for the stay green and early recovering varieties point to the fact that stress tolerance or avoidance mechanism are a function of plants genetic framework as was earlier confirmed by Thornley (1972).

The positive cumulative increments in leaf sizes observed post stress in early recovering varieties were due to production of new vigorous leaves compared to the stay green varieties which maintained old non vigorous leaves. This implies that avoidance mechanisms are desired to allow the plant to attain a certain level of metabolic activity after stress which helps the plant to grow faster and revive the photosynthetic processes necessary for increasing plant biomass (Peroni et al., 2012). Observed changes in leaf morphology after stress for leaf size had an implication on the form and type of metabolism carried out by these leaves as suggested by Aguirreza'bal (2006). Leaves produced due to heterotrophic metabolism by using the plants own

resources have less biomass and hence low photosynthetic capacity as observed by Hedayati et al. (2013) in other species of Euphorbiaceae. However, such leaves were able to regain normal metabolism and normal morphology although in the stay green varieties the morphological state of the leaves did not change a lot, an indicator of compromised photosynthetic metabolism. The efforts put forward by the plants to regain normal leaf morphology after recovery was observed for early recovering varieties suggesting that leaf and plant morphology need to be reinstated for optimal functioning of the cassava plants metabolic apparatus. This may also be related to particular genetic mechanisms meant to help the plant attain the former metabolic state as observed by Blum (2005).

The maintenance of a fairly constant leaf area index by stay green varieties during growth period and even in the stress period describes a tolerance mechanism by cassava plants as suggested by Asadi et al. (2012) and Turyagyenda et al. (2013). Such a mechanism may allow plants to minimally photosynthesize and maintain basic growth and physiological activities throughout the growth period. However, it comes with basic changes in rate, type and direction of translocated material in such plants. This explains the variations in root parameters among different varieties (Table 5) which also point to the importance of stored material in the root in allowing plants to cope with stress.

The differences observed at harvest in the different cassava varieties for root properties are an indicator of differences in yield in addition to the use of stored material as reserve metabolites to help the plant counteract stress as suggested by Zotz et al. (2002). Plant growth rate was probably dependent on increased rates of metabolism that increase the available plant resources meant for growth and development and hence helping the plant to achieve relevant metabolites that usher it into the reproductive phase as was observed by Blum (2005). This is due to increase in the rates of both respiratory and photosynthetic metabolism (Thornly, 1972). Interference in any of these forms of metabolism by either biotic or abiotic stress results into reduced growth hence reduction in plant growth properties as the critical hydrothermal stress conditions are maintained. The significant differences between the varieties tested for plant height, shoot dry weight and root based properties showed that some varieties were more sensitive while others were more tolerant. This has been reported in cereals such as wheat (Pauk et al., 2010) and *Jatropha curcas* (Hedayati et al., 2013) where plant height also decreased with increasing levels of water stress conditions.

Understanding how biomass reductions are photosynthetically driven is very important in determining their effect on the partitioning of photo assimilates to the significant parts of the plant at different growth times (Seyed et al., 2012). Since biomass accumulation during stress is mainly heterotrophic and is dependent on carbon resources in the root for growth support (Holzapfel et al., 2010), there is a significant effect of stress on harvest index as was observed in different cassava varieties (reducing in susceptible and stay green varieties due to use of stored resources to maintain basic metabolic processes) in effect reducing crop yield. Thus, selection of tolerant plants should account for the impact of hydrothermal stress on storage organs of cassava as a food resource. Loss in root weight and hence yield reduces the food and industrial value of cassava.

Apart from the leaves, the branching ability (determinant of shoot biomass) of the plant also has roles to play as far as stress tolerance/resistance is concerned. An increase in root to shoot ratio (or root to total dry matter ratio), as proposed by Steinberg et al. (1990) and attributable mainly to a reduction in shoot growth, was observed when water was limiting. This was a main mechanism for the stress avoidant plants of the early recovering varieties which maintained a low LAI. The size-dependent changes in biomass partitioning from direct changes in the carbon allocation process observed for these cassava plants reveal that water deficits probably act on biomass allometry by slowing down growth and adjusting plant size to the reduced amounts of carbon assimilated. This may be as a result of stomatal closure and decreased leaf area (Osorio et al., 1993). Employment of such mechanisms by cassava plants during abiotic stresses in different ways (hence the different phenotypes observed during stress) shows that cassava varieties differ in their ability to utilize the critically reduced amount of water available to the plant during drought incidence. If biomass production in the different varieties and the trend of water use efficiency are taken into account, it follows that when water is available to the plant, transpiration is unimpeded by stomata and lesser changes in biomass allocation and plant morphology may be expected as suggested by Bergantine et al. (2004).

Based on the results and observations from the field, it was realized that biomass based selection is important in the selection of hydrothermal stress tolerant plants. However, in earlier studies, (Okogbenin et al., 2013; Turyagyenda et al., 2013), selections were based on biomass properties such as high leaf retention during stress, high biomass retention during stress, high growth rates and high harvest indices. Such a selection mechanism based on leaf retention is not exhaustive since in this case even plants with mixed reactions will be selected even if the leaf morphology is severely compromised. In addition, selections only based on growth rate during stress will not easily identify drought avoidant plants that display a recovery mechanism after stress since these plants will be in a state of dormancy during this time. Thus, the author propose that selections for hydrothermal stress tolerant and avoidant plants be taken into account by considering phenotypic parameters

such as leaf lobe retention during stress, cumulative leaf lobe retention during the growth cycle of the plant, and cumulative rate of growth during the plant growth cycle coupled to high harvest indices (Table 5). This will allow for selection of hydrothermal stress tolerant and avoidant plants falling under two broad stress tolerance mechanisms identified as stay green and early recovering mechanisms. It will also allow for possible understanding of plants that have mixed mechanisms and fall under the intersection between stress tolerant and avoidant plants in addition to identifying the stress susceptible plants as shown in Figure 3.

Conclusions

Results from this work showed that hydrothermal stress reduced biomass due to changes in the plants' morphological properties. The reductions were mainly in leaf based biomass and leaf related properties compared to the whole plant. Since leaves are the most sensitive organs to drought stress and respond quickly to low water availability, such a study is imperative in understanding the responses of cassava plants to water deficit and increased temperature, factors that mainly contribute to drought. Modification of plant morphological properties in response to stress does not only have an effect in controlling water loss but also provides an energy saving mechanism including saving stored resources in the plant. In cases where this is not possible, the plant either utilizes its resources to tolerate the stress or completely succumbs to the effects of stress and is hence susceptible. Identifying this in cassava is possible by studies on cassava plant phenotypic properties. And thus in this study, hydrothermal stress tolerant and avoidant plants were selected based on leaf lobe retention, biomass accumulation based selection during the vegetative stage of growth, leaf and leaf lobe recovery immediately after elimination of hydrothermal stress, selection based on number of fibrous roots/root cortex and selection based on harvest index after stress. However, relating these phenotypic properties to their genetic controls may provide a much more reliable basis for selection of tolerant varieties of cassava.

Conflict of Interests

This work was carried out by NARO scientists in collaboration with partners and funders. None of the parties have raised any concerns regarding this work and there is no conflict of interest in regard to the material contained in this study.

ACKNOWLEDGEMENTS

This work was supported by the Bio-Innovate project, a subsidiary of SIDA grant under National Agriculture Research Organization (NARO).

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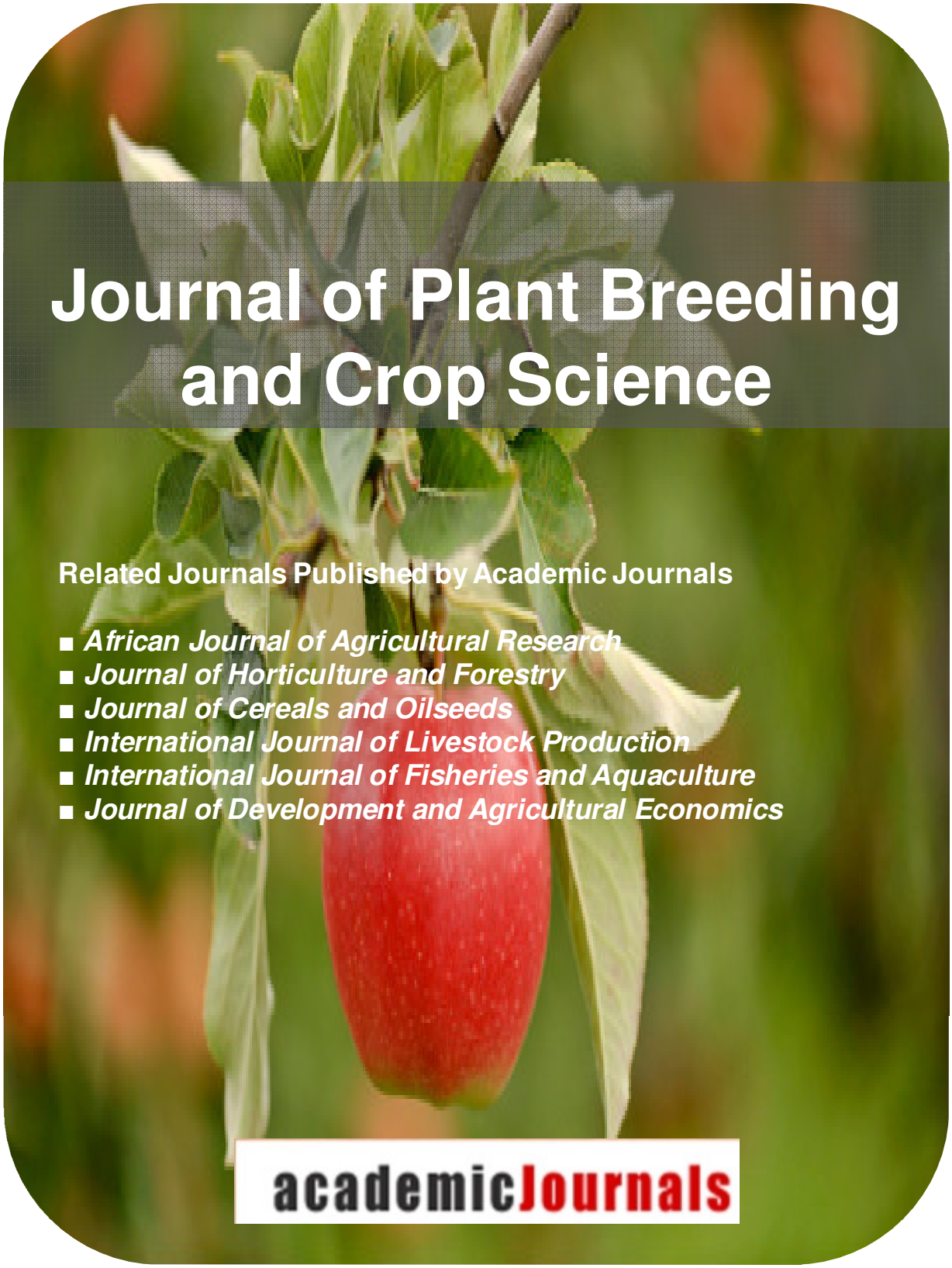

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