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Effect of Water logging on Selected Morphological Characteristics in Maize

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ABSTRACT

A greenhouse experiment was conducted to determine waterlogging tolerance in acidic soils for maize crop improvement in low lying flood prone regions of Western Kenya where waterlogging is a severe problem. Three replicates of nine cultivars, seven tolerant and two susceptible accessions identified after a preliminary screening were subjected to waterlogging to select traits for tolerance to waterlogging using randomized complete block design. 17 day-old seedlings planted in acidic ferralsol soil were exposed to field capacity flooding for 10 days, drained and growth monitored. Waterlogging caused significant reduction in mean number of leaves, leaf area, root collar diameter, seedling height and grain yield. K8 recovered least from water logging. Kan2 and K27 were least affected with regard to leaf tip death and wilting. K8, Br2, K24 and C8 recorded the most significant reduction in leaf area. K3 and Kan2 recorded the least internode length. Plant height recovery was most significant in K27 and K8. Lowest reduction in yield was recorded in Br2 and K3 while the highest grain yield was K3 and Kan2. Reduction on collar root diameter had a significant influence (F value = 2.7) on total grain yield of maize in the affected accessions (y= 1.0183x – 0.5685). There exists a significant genetic variability among Kenyan maize germplasm in terms of response to waterlogging, which can be exploited for crop improvement.

Keywords: Waterlogging, Leaf size, Internode length, Root and Yields.

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INTRODUCTION

In sub-Saharan Africa, maize has the highest yield per hectare compared to all other cereals. Although maize is Africa's most important staple crop, grown by both large and small-scale farmers, total production accounts for only 6% of the total world maize production. The average yield of maize ranges between 1.1-1.8 metric tons per hectare which is less than half the global average of about 4t/ha. Conversely, in the United States, the average yield is about 8t/ha (Jaetzold, 2006; Ngang'a, 2003; Smaling et al., 1992). Maize production is a major occupation for over 3 million Kenyan small holders who are concentrated mainly in Western, Eastern, and Coastal regions and parts of Rift valley. However, the yield has been on a downward trend over the last twenty years characterized with chronic deficits in the production of maize (Ayaga, 2003; Brust and King, 1994). In the flood prone areas of Kenya such as Kano plains, vast parts of Busia district and other areas with black cotton soils such as Kilgoris, Homa bay, parts of Laikipia, Kajiado, Migori and Samburu districts experience significant loss in maize yield estimated at Kshs. 2 billion annually (Oyaya and Ogagul, 1992).

The extent to which waterlogging affect maize yield is determined by several factors including soil characteristics, timing of waterlogging in relation to stage of development, frequency and duration of waterlogging and air-soil temperatures during waterlogging (Lauer, 2001). Maize is frequently subjected to waterlogging, particularly in black cotton soils, which are poorly drained. Although waterlogging triggers physiological and biochemical changes in affected plants, the first major impact of soils completely covered with water is a rapid depletion of oxygen required for plant growth and development (Geigenberger et al., 2000).The changes in nutrient also occur in the status of soil either by leaching or changing their availability to the plant in waterlogged soils. Waterlogged plants undergo significant structural modifications leading to visible changes in cell and organ structure (Imad and Sachs, 1996; Justin and Armstrong, 1987a; Justin and Armstrong, 1987b). Aerenchyma formation is common in the stems and roots of aquatic and flood-tolerant species. Aerenchyma develops by cell separation during development (schizogeny) or by cell death and dissolution (lysogeny). For oxygenation over greater distances, aerenchyma is necessary and effective because it reduces the number of oxygen-consuming cells and lowers the resistance to gas diffusion or convection (Drew, 1997). Development of aerenchyma in waterlogged plants results from cell-wall hydrolysis and eventual cell lysis and is promoted by endogenous ethylene (Imad and Sachs, 1996). It is likely that genes involved in cell-wall hydrolysis under waterlogged conditions are induced in response to ethylene, which tends to accumulate under low oxygen levels. Developing maize accessions tolerant to waterlogging is a very important breeding objective in areas of Kenya prone to waterlogging. Under the International Center for Agricultural Research (ICAR-CIMMYT) collaborative program, large amounts of maize germplasm has been screened for waterlogging tolerance in India (Zaidi et al., 2005). Many promising tolerant lines have been identified and further improved for developing excess moisture tolerant cultivars for waterlogging prone areas of India. Due to fairly high expression of stress-adaptive traits under managed excessive moisture stress conditions, tolerant maize germplasm can be carefully selected and further improved. Various techniques have been used to screen different crops for tolerance to waterlogging.

In wheat, the number of tillers and number of kernels has been used as selection criteria for tolerance to waterlogging (Collaku and Harrison, 2001; Dennis et al., 2000; Li et al., 2008). In barley the percentage chlorosis of leaves has successfully been used as selection criterion for tolerance to waterlogging (Zhou et al., 2004). In soybean, high yield in flooded fields has been used, however other traits such as leaf colour, plant height, root and shoot biomass have been used as markers of flooding tolerance (Tara et al., 1999). Establishing techniques for screening for key aspects of waterlogging tolerance in crops is a prerequisite for the success of any breeding programme. After screening for waterlogging tolerance, the next step would be to produce germplasm to be used for developing more waterlogging tolerant accessions (Collin, 1996). In the absence of direct and reliable selection markers for waterlogging tolerance, a successful breeding program needs to identify physiological and morphological traits that are affected most by waterlogging and the existence of useful genetic variability controlling their expression (Zhou et al., 2004).

It is necessary to identify and evaluate genetic basis of waterlogging tolerance in maize in the flood prone areas of Kenya, so that the traits for tolerance to waterlogging can be combined in improved breeding lines.

Environmental characterization of waterlogging prone areas is very important. This is because interaction with different microelements in different environments often leads to variation in waterlogging tolerance and ranking of germplasm between environments (Collins, 1996). The extent of maize yield reduction due to short periods of waterlogging has not been investigated in Kenya even though maize is the most important staple crop. In South-East Asia where about 15% of total maize growing areas are affected by waterlogging, loss in maize yield is estimated to be about 25 to 30% annually (Zaidi et al., 2005). This study was therefore designed to identify morphological selection criteria that could be useful for identifying tolerant genotypes.

MATERIALS AND METHODS

Experimental Site

The study was conducted at the Chepkoilel Campus (situated in Uasin Gishu district of Rift Valley province) farm located at an altitude of 2180 m above sea level. It is located on longitude 36^o E and latitude 30^o N and at an altitude of 2180 m. The experiment was carried out in the Botany green house of Botany Research Laboratory at temperatures of 18°C ± 2°C and 32°C ± 3°C night/day. The annual rainfall ranges between 900 mm and 1100 mm and is bimodally distributed, with the first peak in April and second peak in August (Jaetzold and Schmidt, 1983). The soils at this site are acidic (pH <5), dark red, friable, rhodic ferralsols (Jaetzold and Schmidt, 1983). The farms around Chepkoilel Campus, which were originally used for commercial large-scale maize and wheat farming, have undergone considerable subdivision and subsistence farming is slowly gaining prominence (Muok, 1997).

Materials

Nine cultivars comprising of tolerant and non-tolerant waterlogging lines were used in the study (Table 1). These cultivars had been selected from an initial population of 71 maize cultivars following a tolerance screening process. The initial maize cultivars were drawn from a worldwide collection of commercial accessions obtained from the Kenya Agricultural Research Institute (KARI) and included accessions from CYMMIT, Brazil, Ecuador, USA, and South Africa and from farmers in Western Kenya.

Sowing and Experimental Design

The experiment was carried out in potted soils. Each pot

Table 1. The source and coding of maize accessions used to test response to waterlogging.

S/No.	Code	Accession/cultivar	Waterlogging characteristics*	Source
1	K24	H625	Highly tolerant	KARI – Kitale / Kenya Seed Company
2	E2	93	Highly susceptible	Ecuador
3	Br2	Brazil Synthetic	Highly tolerant	Brazil
4	Kan2	Accession from Rae (Kano Plains)	Highly tolerant	Kano Plains
5	C8	CIMCali96ASA 3	Highly tolerant	CIMMYT
6	Kat1	DLC1	Highly tolerant	Katumani
7	K3	KTLN70168	Highly tolerant	KARI / Kitale
8	K27	F	Highly tolerant	Kitale
9	K8	KTLN70143	Highly susceptible	KARI / Kitale

*Characteristics following field experimentation. Source: Nyamolo, 2003.

was filled with 2 kg of acidic ferralsol soil of pH 5.5 collected from Chepkoilel farm. A total of 213 pots were sown with three seeds per cultivar/accession in three replications using randomized complete block design. Di-ammonium phosphate (DAP) was applied at the time of sowing at the rate of 247 kg/ha equivalent (Nyle, 2000). The fertilizer was thoroughly mixed with the soil before sowing. Nine accessions (seven tolerant and two susceptible) seedlings were selected for analysis after a preliminary screening process that subjected them to blanket flooding fourteen days after emergence. These accessions were selected after evaluating the number of dead leaves, number of wilted leaves, number of young leaves with dead tips and the general plant health. Three seeds of each accession were planted in 2 kg of soil in pot with application of DAP as above.

The selected accessions were divided into two treatment groups: control (no waterlogging) and waterlogged. Screening for tolerance to waterlogging was done using three replicates in a randomized complete design. Waterlogging was to a depth of 2 cm above soil level fourteen days after emergence and the control was not waterlogged. Waterlogging stress was removed from seedlings by transferring into plastic bags containing twenty kilogram of soil amended with DAP application at the rate of 247 kg/ha equivalent. The plants were top dressed with calcium ammonium nitrate (CAN) at a rate of 185 kg/ha equivalent (Nyle, 2000). The seedlings were allowed to recover for 24 days, and then number of leaves, leaf area, root collar diameter, length of internode and height was measured for both groups. The following parameters were measured before and after waterlogging; Number of leaves, leaf area, root collar diameter and seedling height. In addition, the length of internode and chlorophyll concentrations were also measured for both groups after water had been drained off.

Number of Leaves

The number of leaves of 17-day old seedlings was recorded before waterlogging. The number of leaves was also recorded after ten days of waterlogging and after 24-days of recovery from waterlogging. The data obtained was used to assess if waterlogging leads to early senescence of leaves.

Leaf Area

The leaf length and width at the widest point was measured before and after waterlogging. Individual leaf area was estimated using the relationship, A = L x W x 0.75 (Kemp, 1960). Where A = area; L = length; W = width.

Length of Internode

The lengths of the internodes were measured by taking the distance between the nodes. The length of internode was recorded for twenty seven day old seedlings after ten days of waterlogging. The same was repeated after twenty four days of recovery from waterlogging.

Root Collar Diameter

Root collar diameter was measured by taking the diameter of the emerging seedling at the ground level. This was done for 17-day old seedlings before waterlogging. The same was repeated after ten days of waterlogging and after 24-days of recovery from waterlogging. The relative percentage reduction in root collar diameter yield was computed for each accession and accessions ranked with regard to their ability to withstand waterlogging.

Plant Height

Plant height was measured from the soil level up to the tip of the young shoot. This was done for 17-day old seedlings before waterlogging, after ten days of waterlogging and after 24-days of recovery from waterlogging. The relative percentage reduction in plant height yield was computed for each accession and

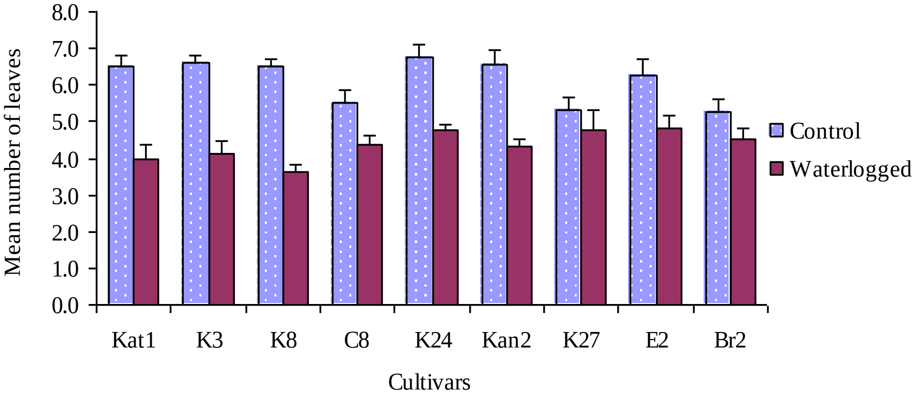

Figure 1. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on number of maize leaves at 17 days after recovery from waterlogging stress.

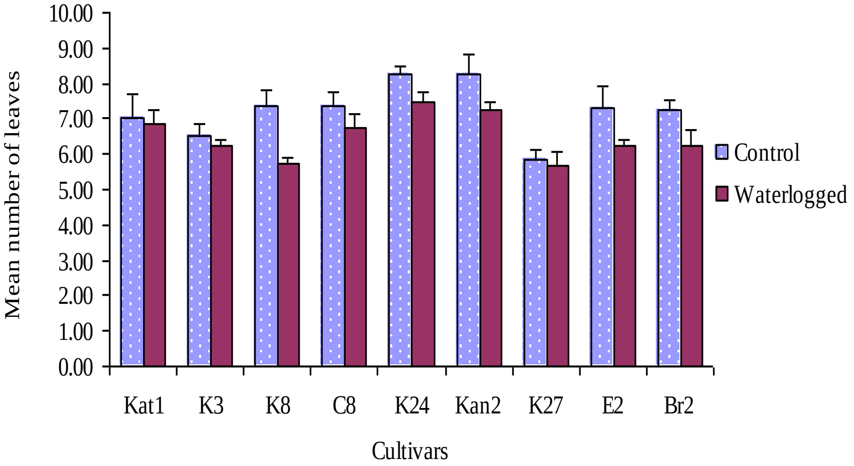

Figure 2. . Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on number of maize leaves at 24 days after recovery from waterlogging stress.

accessions ranked with regard to their ability to withstand waterlogging. Correlation coefficients (R^2) and regression equations detailing the effects of plant height and root collar size on the grain yield were determined at p=0.05.

Determination of Grain Yield

The cobs of established plants that had been allowed to grow to maturity were manually harvested, sun-dried, shelled and the dry weight of grain for every plant determined. The percentage reduction in grain yield was computed for each accession. Accessions were ranked with regard to their ability to withstand waterlogging. Correlation coefficients (R^2) and regression equations detailing the effects of plant height and root collar size on the grain yield were determined at p=0.05.

Data Analysis

All statistical analyses were performed with (SPSS version 11.5) statistical computer packages. Normality of data distribution was checked by means of the skewness and kurtosis (Zar, 2001). Mean differences in the plant parameters among cultivars were analyzed using a one-way Analysis of Variance (One-Way ANOVA). Duncan's Multiples Range test (DMRT) was used to separate means that were significantly different (Michael and Douglas, 2004).

RESULTS

Effect of Waterlogging On Leaf Number and Maize Leaf Area per Plant

Waterlogging caused a significant reduction in the number of leaves as the F-value was 15.10 (p=0.0001) (Figure 1). Waterlogged plants had fewer leaves than the control plant. The most significant ($P < 0.05$) reduction was recorded for K8 followed by Kat1 and K3 while the least reduction was recorded for K27, C8 and Br2. All the controls had more leaf numbers than the waterlogged plants. There was a significant ($P < 0.05$) recovery from waterlogging in terms of the number of leaves (Figure 2). This was recorded for most of the cultivars except K8,

Table 2. Effect of waterlogging for 10 days started at 14 days after emergence on leaves with dead and wilted tips for nine maize cultivars.

Cultivars	Percentage young leaves with dead tips	Percentage young leaves with wilted tips
Kat1	14.9 ± 0.6	4.8 ± 4.2
K3	5.2 ± 3.3	2.3 ± 2.3
K8	15.1 ± 0.5	45.3 ± 1.5
C8	21.2 ± 4.1	2.8 ± 2.8
K24	10.3 ± 5.4	11.9 ± 7.8
Kan2	3.3 ± 3.3	0.0 ± 0.0
K27	0.0 ± 0.0	0.0 ± 0.0
E2	14.2 ± 7.0	3.5 ± 0..2
Br2	12.2 ± 3.9	0.3 ± 0.2

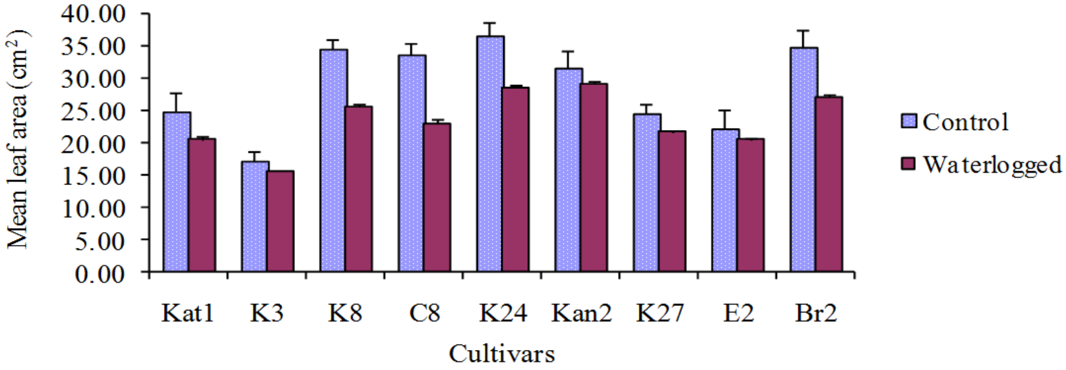

Figure 3. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on leaf area of maize seedling leaves at 10 days after recovery from waterlogging stress.

which showed least recovery and was the most susceptible cultivar (Figure 1). Cultivar K27 which was most tolerant recovered its growth and the leaf number was not significantly different from the control. Thus from this observations, cultivar K27 possessed the best traits for tagging tolerance to waterlogging even though it recorded the least number of leaves. All the control plants had normal leaves as their morphology did not display any distortion (Table 2). Waterlogging caused leaf wilting and death of young leaves at the tip in most plants. Cultivar K27 had the lowest proportion of dead leaf tips followed by Kan2 and were therefore most tolerant. The most significant ($P < 0.05$) differences in dead leaf tips were recorded for cultivars E2, K8, Kat1 and C8. Cultivars Kan2 and K27 unlike K8 and K24 did not succumb to leaf tip wilting and were the most tolerant in this trait.

Waterlogging caused a significant ($F=38.03$; $p=0.0001$) reduction in leaf area for some accessions even though the degree of reduction varied depending on the accession (Figure 3). The most significant reduction in leaf area was recorded in K8, Br2, K24 and C8. The other accessions did not show a significant reduction in leaf area. There was pronounced recovery from waterlogging for all the cultivars although there were no significant ($P>0.05$) differences among the various cultivars (Table 3). However, the seedlings that had been previously waterlogged still had smaller leaf area per plant compared to the control plants 24-days after removal of waterlogging stress.

Waterlogging adversely affected the morphology of the leaves with regard to leaf wilting, leaf number, leaf area, inter-nodal length and plant height and root collar diameter. Generally, waterlogging affected the structural development of maize plants leading to decreases in number of leaves, leaf area, and internode length and plant height. However, cultivars recorded significant variations in the magnitude of leaf and plant morphology upon exposure to waterlogging conditions. Some cultivars therefore displayed desirable tolerance traits that can be exploited for crop improvement. The potential of waterlogging tolerance found in some genotypes is important in identifying cultivars for specific environments and for further use in maize breeding programmes (Singh and Ghildyal, 1980; Qiu et al., 2007; Vantoai et al., 2001; Li et al., 2008).

Generally, most cultivars recorded minimal wilting of young leaf tips in contrast to those that had dead tips. In fact some cultivars did not record the presence of wilting after waterlogging. However, in some of the cultivars the

Table 3. Effect of waterlogging on the leaf area of seedlings of nine maize cultivars on the 24th day of recovery from waterlogging stress.

Maize accessions	Mean leaf area(cm^2)	
	Control (± SE)	Waterlogged (± SE)
Kat1	136.28±7.49	108.05±11.03
K3	91.32±11.06	64.50±3.34
K8	113.98±15.3	85.09±4.64
C8	128.30±13.72	113.11±13.09
K24	148.36±9.69	118.99±8.65
Kan2	130.43±18.88	117.98±12.78
K27	52.29±10.78	55.54±8.96
E2	92.63±13.53	74.67±2.77
Br2	130.74±10.25	101.60±12.12

young leaves were wilted and dying at the tips even though the expectation was that most of the nutrients would be directed to the younger leaves compared to the older ones contrary to Bryan and McKersie (1996) which reported that under normal circumstances the younger leaves would receive more nutrients compared to older ones. Accessions that were tolerant to wilting were similarly observed to have been comparatively tolerant to leaf tip death. The trait is therefore a good measure of waterlogging tolerance. The accessions with presence of wilting and leaf tip dead may have undergone breakdown in the normal nutrient transport within the plant caused by waterlogging. This is particularly so since the control plants did not show death of young leaves at the tips.

Waterlogging may have induced resilient plants to develop survival mechanisms including aerenchyma in response to decreased oxygen levels in the soil. Aerenchyma are large soft cortical tissues with large air spaces that provide low resistance pathway for air diffusion into submerged tissues, and therefore may promote flooding survival under waterlogged conditions (Imad and Sachs,1996). Studies associate the development of aerenchyma in waterlogged plants reveal close association with presence of ethylene and anaerobic conditions which must have prevailed at the time (Yin et al., 2013; Dennis et al., 2000). Waterlogging also caused wilting in leaves. This is a phenomenon that has been reported by other researchers (Bryan and McKersie, 1996). The author further noted that waterlogging increases resistance of roots to water in flow in addition to reduced respiration leading to low ATP synthesis in the roots. On the basis of leaf death some cultivars such as K8 were identified as very susceptible and others such as K27 were classified as tolerant to waterlogging. Waterlogging is reported to cause cell injury or death which, if prolonged, could cause death of the whole plant (Drew, 1997). The results of the present study where waterlogging caused death of leaves starting with the older leaves are in agreement with this observation. The reduction in number and area of leaves results into a reduction in the net light-absorbing surface. This affected photosynthesis leading to a reduction in yield. This shows that the number of dead leaves can be used to identify maize genotypes that are tolerant to waterlogging. Waterlogging also resulted in a decrease in leaf area since the control plants had bigger leaves compared to the waterlogged plants. These reports are similar to those of other studies (Lenore and Graves, 1993; Lauer, 2001; Schwintzer and Lancell, 1983). Waterlogging is known to slow down leaf elongation (Lenore and Graves, 1993).

This observation is in agreement with the results obtained in this study. Leaf elongation is slowed down since waterlogging impedes uptake and transport of nutrients within the plant (Collaku and Harrison, 2001). Observations in tomato shoots indicate that the leaf petioles curve downwards due to cell expansion on the upper surface. This reorients the leaf downwards; the reorientation is an adaptive response to reduce demand for evaporative cooling and transpiration. This epinastic response reduces the intensity and total amount of radiation received by the leaves (Norman et al., 1995). In sunflower waterlogging causes hypertrophic growth that appears as a swelling at the base of the stem or hypocotyls. This growth is due to radial cell division and expansion and is often accompanied by cell collapse and aerenchyma formation (Bryan and McKersie, 1996). This is thus considered to be an adaptive mechanism enabling increased air diffusion from the shoot to the root.

Effect of Waterlogging On Maize Internode Length

Waterlogging caused a significant ($P< 0.05$) reduction in the length of the internode (Figures 4 and 5). Internode lengths were significantly different at 10 day and 24 days after waterlogging (Figures 4 and 5). The most significant reduction was recorded in K8 and K27. The lowest differences were recorded for K3 and Kan2. These two cultivars may therefore be considered for further analysis of tolerance to waterlogging. There was significant ($P < 0.05$) recovery from waterlogging for most of the cultivars (Figures 4 and 5). The greatest recovery was recorded in K3. Other accessions exhibited

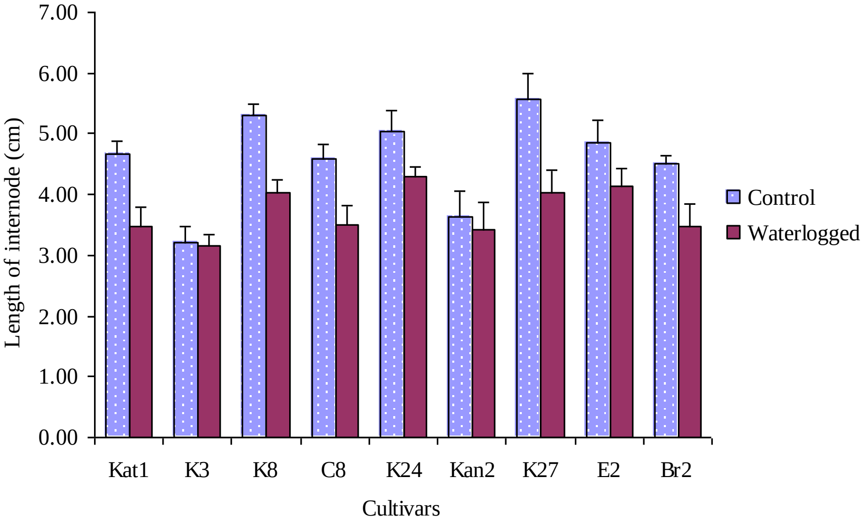

Figure 4. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on the length of internode of maize seedling leaves at 10 days after recovery from waterlogging stress.

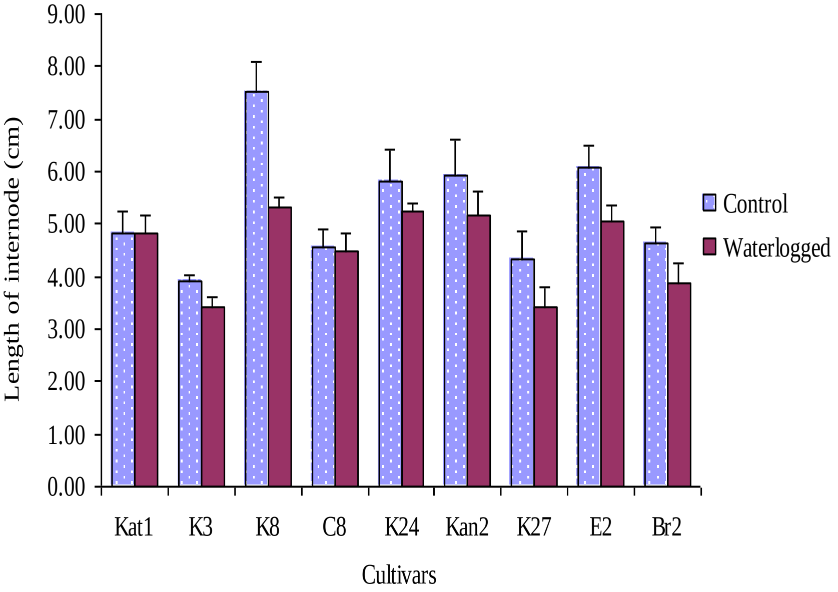

Figure 5. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on the length of internode of maize seedling leaves at 24 days after recovery from waterlogging stress.

significant ($P < 0.05$) differences in internode lengths between the previously waterlogged and control plants. The control plants had longer internodes. Effect of waterlogging on maize height growth: Waterlogging caused significant ($P < 0.05$) reduction in seedling height (Figure 6). The most significant reduction was recorded in K8 and Br2. The rest of the accessions did not show a significant reduction and may be subjected to further analysis of tolerant to waterlogging. There was no significant difference in recovery rate for most of the cultivars although previously waterlogged plants were still shorter than the control plants 24 days after withdrawal of waterlogging stress (Table 4). The most significant recovery was recorded in K27 while K8 recorded least significant recovery.

These results contrast with that of Voesenek et al. (1993) who reported that waterlogging enhanced stem elongation in aquatic, semi-aquatic and terrestrial plants. The differences could be attributable to the fact that maize is non-aquatic plant. Bryan and McKersie (1996) reported that waterlogging caused a rapid elongation of the internodes but Singh and Ghildyal (1980) reported

Table 4. Effect of waterlogging on plant height for 51 day old maize seedlings on the 24th day of recovery from waterlogging stress.

Maize cultivars/accessions	Mean collar diameter ± S.E (cm)		Mean height reduction (cm)	Percentage plant height reduction	Rank
	Control (n = 9)	Waterlogged (n = 9)			
Kat1	71.92±7.49	50.20±11.03	21.72	30.20022	6
K3	57.89±11.06	41.96±3.34	15.93	27.51771	4
K8	83.56±15.3	49.11±4.64	34.45	41.22786	9
C8	63.51±13.72	49.36±3.9	14.15	22.27996	2
K24	81.45±9.69	56.86±8.65	24.59	30.1903	5
Kan2	66.80±18.88	50.05±12.78	16.75	25.07485	3
K27	47.71±10.78	40.48±12.78	7.23	15.15406	1
E2	70.23±13.43	48.26±2.77	21.97	31.28293	7
Br2	71.50±10.25	45.65±12.12	25.85	36.15385	8

Table 5. Effect of waterlogging on root collar diameter for 51 day old maize seedlings on the 24th day of recovery from waterlogging.

Maize cultivars/accessions	Mean collar diameter ± S.E (cm)		Mean root collar reduction (cm)	Percentage root collar reduction	Rank
	Control (n = 9)	Waterlogged (n = 9)			
Kat1	1.0 ± 0.08^{bcde}	0.9 ± 0.11^{abcd}	0.1	10	1
K3	1.0 ± 0.12^{bcde}	0.7 ± 0.06^{a}	0.3	30	6
K8	1.3 ± 0.11^{ef}	0.7 ± 0.13^{ab}	0.6	46.2	8
C8	1.2 ± 0.11^{def}	0.9 ± 0.07^{abc}	0.3	25	3
K24	1.4 ± 0.11^{f}	1.0 ± 0.07^{bcdef}	0.4	28.6	5
Kan2	1.4 ± 0.11^{f}	0.9 ± 0.07^{abcd}	0.5	35.7	7
K27	0.8 ± 0.07^{ab}	0.5 ± 0.07^{a}	0.3	37.5	8
E2	1.2 ± 0.17^{cdef}	0.9 ± 0.08^{abcd}	0.3	25	3
Br2	1.0 ± 0.09^{bcde}	0.8 ± 0.11^{abc}	0.2	20	2

Any two means having the same letter are not significantly different.

that waterlogging resulted into stunted growth of maize. Cultivars K8 and Br2 suffered the greatest reduction in height compared to their controls while K3 and Kat 1 suffered the lowest reduction in height following ten days of waterlogging since they could have closer correlations. Waterlogging also reduced the plant height, which did not discriminate between susceptible and tolerant accessions. However, the present finding is in contrast to the earlier findings of Singh et al. (1980). During their experiment, Singh and Ghildyal (1980) reported that seedling height could be used to screen maize cultivars for tolerance to waterlogging. Again, differences in the results could be due to differences in experimental set up since the latter was a field experiment while this study was conducted in pots in a greenhouse. The stage of growth at which the plants were subjected to waterlogging and duration of waterlogging could also have resulted to the observed differences. Reduction in plant size, leaf area and eventually both the number and size of the fruit or seed results in reduced yield of forage, fruit or seed (Stamp et al., 1996). In cereals, waterlogging reduces leaf elongation (Collaku and Harrison, 2001), and this in turn reduces photosynthesis and therefore grain yield. Increased leaf area index for maximum light interception has a direct, positive effect on the rate of dry matter production (Stamp et al., 1996). The daily net photosynthesis is determined by leaf area, temperature and radiation. Kernel filling in maize is not dependent on previously stored reserves, but is dependent upon current photosynthate transport from the leaves (Evans, 1975).

Effect on Root Collar Diameter

Waterlogging caused a significant reduction in root collar diameter of the maize seedlings in accessions Kat1, Kan2, K27 and Br2 after 27 days after waterlogging (Figure 7). However, the root collar diameter of accessions K3, C8, K24, K8 and E2 were comparatively less affected (Figure 7). Following recovery from flooding, the root collar diameter of all the accessions was affected as they all had a decreased diameter (Table 5).The highest net root diameter reduction was recorded for Kat1, Kan2, BR2 and K27 but the rest of the cultivars showed lowest reduction in root collar diameter (Table 5). Waterlogged seedlings were relatively thinner than the control plants 24 days after withdrawal of the waterlogging stress (Table 5). The most reduction in collar diameter was recorded in cultivars K27, K8, Kan2 and K24. The most tolerant cultivars were Kat1, K3 and Br2.Any two means having a common letter are not

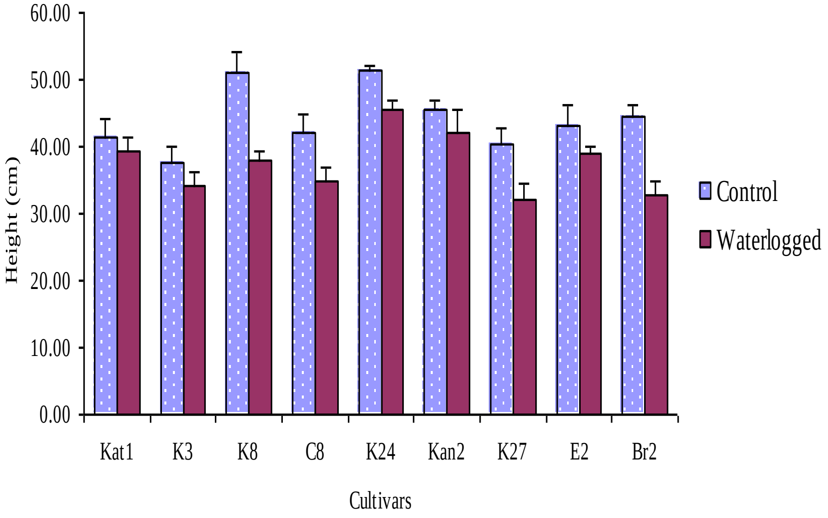

Figure 6. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on the mean maize height of maize seedling leaves at 10 days after recovery from waterlogging stress.

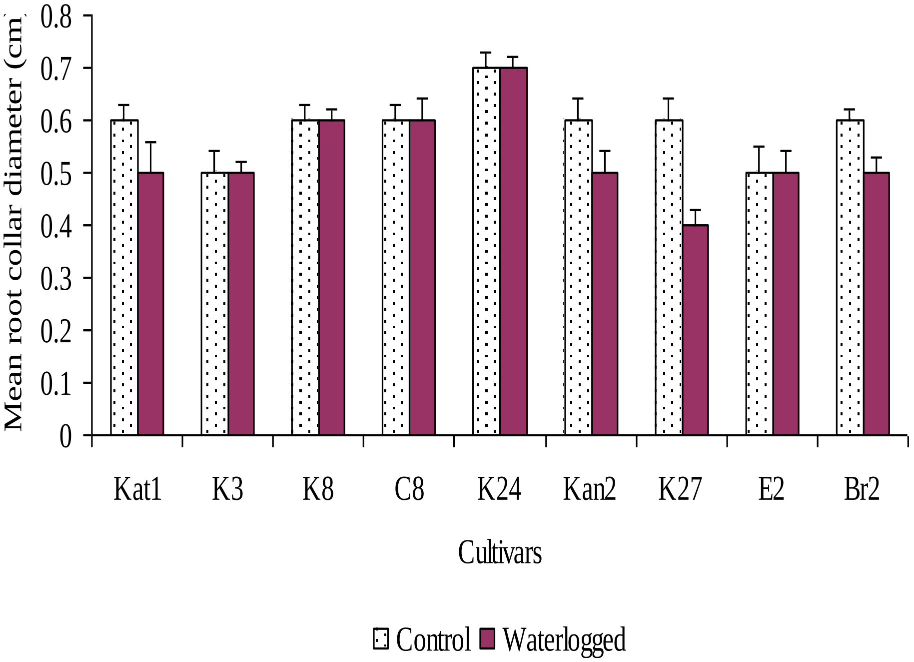

Figure 7. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on the length of internode of maize seedling leaves at 10 days after recovery from waterlogging stress.

significantly different at 5% level of significance. Duncan's Multiples Range test was used to separate means that were significantly different (Michael and Douglas, 2004).

Unlike some cultivars, a few accessions experienced a significant decrease in root collar diameter immediately following flooding. The roots of some accessions were resilient and withstood the flooding period unaffected. This suggests that this trait may be inherited as there was a definite relationship between ability to withstand decrease in root collar diameter and grain yield. As such most affected accessions following recovery from flooding did record the some of the highest grain yield reductions while the least affected accessions that withstood flooding relatively well did have some of the highest decreases in grain yields. There is a high

Table 6.Effect of waterlogging on grain yield and percent yield reduction for maize accessions following recovery after ten days of waterlogging.

Maize accessions	Grain yield (grams)		Grain yield reduction (grams)	percentage reduction in yield	Rank*
	Control (± SE)	Waterlogged(±SE)			
K3	49.6±2.025	41.7±1.088	7.9	15.9	2
K8	47.9±0.828	19.9±0.776	28	58.5	8
C8	49.53±0.927	34.12±0.514	15.41	31.1	5
K24	41.1±1.135	34.6±0.598	6.5	15.8	1
Kan2	53.43±2.054	38.62±1.437	14.81	27.7	4
K27	52.99±2.399	35.44±2.105	17.55	33.1	6
E2	42.59±0.963	22.56±0.805	20.03	47.0	7
Br2	44.1±2.646	35.78±2.081	8.32	18.9	3

probability that the rooting system of some accessions was more resistant to the effects of decreased soil oxygen concentration and increased carbon dioxide and ethylene (Justin and Armstrong, 1987; Justin and Armstrong, 1987b). It is obvious that waterlogging of the soil that occurred during the 10 day induced flooding caused water to enter soil faster than it could drain away under gravity.

Waterlogging leads to poor soil aeration with resultant effects on the growth and function of roots thereby reducing total root growth (Chapman and Carter, 1976). This affected the growth and development of root structure in the soil due to various factors including net loss of oxygen in the soil resulting in increased concentrations of carbon dioxide and ethylene gasses. The duration and severity of flooding is known to be influenced not only by the rate of water input but also by the rate of water flow out from the rooting zone and by the water absorbing capacity of the soil and affecting soil concentrations of oxygen, carbon dioxide and ethylene. In waterlogged soil, diffusion of gases through soil pores is so powerfully subdued by their water content that it fails to match the requirements of developing roots. A decrease of oxygen inflow is the primary cause of injury to roots they support (Boru et al., 2003; Vartapetian and Jackson, 1997). The maximum amount of oxygen dissolved in the floodwater in equilibrium with the air reportedly about 0.03 of that in a similar volume of air itself and often consumed quickly during the early stages of flooding by aerobic micro-organisms and roots (Vartapetian and Jackson, 1997). In addition to causing oxygen shortage, flooding also impedes the diffusive escape and/or oxidative breakdown of gases such as ethylene or carbon dioxide that are produced by roots and soil micro-organisms (Arshad and Frankenberger, 1990; Geigenberger et al., 2000; Jackson and Ricard, 2003; Yin et al., 2013). This leads to accumulations that can influence root growth and function. As previously reported accumulated ethylene can affect plant growth and development by slowing root extension, while carbon dioxide in the soil can severely damage roots of certain species (Arshad and Frankenberger, 1990).

There was a relative decrease in root color diameter upon recovery after flooding with all the controls recording higher root collar diameters in comparison to test plants. This means that the plants that initially displayed resistant to flooding had their root growth affected in the long term, although the effect was at a lower magnitude than the susceptible plants. This implies that for the most resilient accessions, even though waterlogging reduced nutrient uptake and transport, the root collar part of the plant was still able to receive adequate nutrients for normal growth and development. The above results concur with those of Singh and Ghildyal (1980) who reported that waterlogging caused a reduction of root collar diameter. Twenty-four days after the removal of water, all the cultivars except K8 recorded significant recovery. The seedlings were able to recover since the removal of water led to improved oxygenation of the rhizosphere. The plants were now able to take up water and nutrients for photosynthesis leading to growth. The slow recovery of K8 was probably because it might have suffered the greatest root injury during the period of waterlogging. Waterlogging caused a reduction in the elongation of internodes.

Effect on Grain Yield

Waterlogging significantly ($P < 0.05$) reduced maize grain yield per plant as all control plants recorded higher grain yields as compared to test plants (Table 6). Comparatively, accessions K3 and Kan2 recorded the highest grain yields while K8 and E2 the lowest. K8 and E2 in contrast to K24, K3 and Br2 recorded the highest percentage reduction in grain yield when the waterlogged plants were compared to the control plants (Figure 8). The lowest percentage reduction in yield was recorded in Br2 and K3; these two accessions may be considered for further analysis of tolerance to waterlogging. The association between grain yield reduction and the reduction in collar root diameter and plant height was apparent. Generally, there was a significant relationship ($F=2.751811$; $p=0.05$) between a decrease in root collar diameter in recovering plants and grain yield reduction

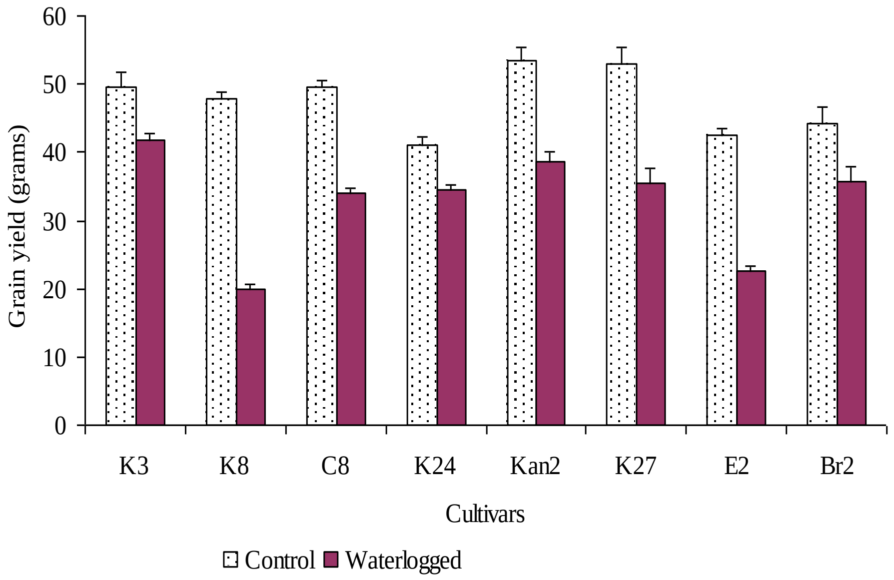

Figure 8. Effect of maize variety and 10 days waterlogging stress started at 14 days after emergence on the mean grain yield of maize seedling leaves after recovery from waterlogging stress.

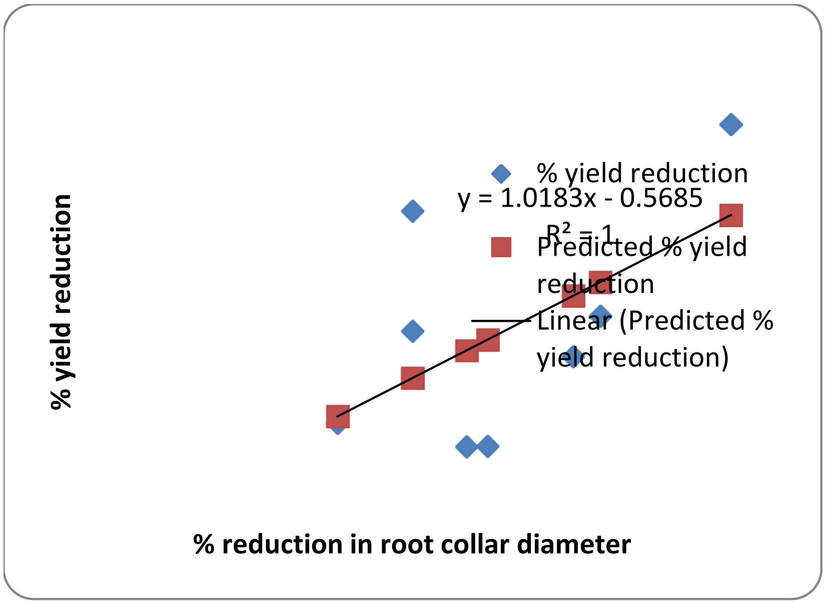

Figure 9. Regression line plot indicating the relationship between the percent reduction root collar diameter and yield reduction following the recovery of maize seedlings from waterlogging stress.

(Figure 9). Reduction on collar root diameter had a significant influence on the total grain yield of maize in the affected accessions as described in the regression equation y= 1.0183x – 0.5685 (where; – 0.5685 was the intercept and 1.018338248 the coefficient of variation). A positive correlation was noted between the percentage grain yield reduction and percentage collar root reduction (R squared=0.314427571; p=0.05) for plants that had prior exposure to waterlogging. Percentage grain yield reduction was computed as a measure of the proportion of yield difference between control and waterlogged plants. *Accessions were ranked with regard to Percentage reduction in yield with the best and worst ranked being the maize accessions with the lowest and the highest percentage yield reduction.

Waterlogging caused a reduction in grain yield for all the cultivars but their respective responses was very different ranging from 14% in K3 to 58% in K8. Mean yield of K3, BR2 and Kan2 were significantly higher than other genotypes under waterlogging treatment. The three cultivars were among those ranked as tolerant under waterlogging stress and could therefore be incorporated into maize breeding for tolerance to waterlogging stress. The results also indicate that early flooding in maize has a long term effect on maize growth and eventual yield. All the cultivars failed to recover completely from waterlogging and registered a drop in yield after waterlogging treatment. Singh and Ghildyal (1980) recorded similar findings. The highest reductions were recorded in K8 and E2. The two had been classified as susceptible hence the results correspond with earlier observations. Grain yield can be used to discriminate between tolerant and susceptible genotypes.

CONCLUSION

There exists appreciable genetic variability among Kenyan maize germplasm in terms of response to waterlogging as findings indicated that different maize germplasm responded differently to waterlogging stress. While 10 days waterlogging stress decreased maize grain yield of some germplasms by more than 30%, it did not affect other germplasms advesely. In conclusioin, cultivars K3, K24 and Br2 are recommended for maize production under temporary waterlogging conditions. Kenyan maize population therefore has useful materials that can be used to improve tolerance of maize to waterlogging.

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