The influence of drought stress on growth, yield and yield components of selected maize genotypes

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SUMMARY

The risk of drought is high in the Sudan savannah zone of West and Central Africa because rainfall in this area is unpredictable in quantity and distribution. Thus, improved maize genotypes tolerant to drought could stabilize maize grain yield in this zone, where recurrent drought threatens grain production. Six maize genotypes, two each of hybrids, open-pollinated varieties (OPVs) and landraces, were evaluated for tolerance to terminal water deficit before flowering. Water deficit significantly reduced growth, grain yield and yield components of the maize genotypes. Significant differences were observed among genotypes for all the traits measured. One hybrid, 9011-30, and two improved OPVs, STR-EV-IWD and IYFD-C0, that showed tolerance to water stress recorded higher grain yield, and accumulated and partitioned more assimilates to the grain than the drought-susceptible genotypes. Also the drought-tolerant genotypes, 9011-30, STR-EV-IWD and IYFD-C0 had more ears/plant and greater numbers of kernels/ear. These genotypes could serve as sources of drought tolerance for the development and improvement of new drought-tolerant maize genotypes.

INTRODUCTION

Drought is one of the major causes of yield losses of maize in the West African savannah. The risk of drought stress is particularly high in the Sudan savannah zone of West Africa because rainfall in this area is unpredictable in quantity and distribution (Fajemisin *et al.* 1985). Annual maize yield loss of about 15% has been attributed to drought in sub-Saharan Africa. However, localized losses may be much higher in the marginal areas where the annual rainfall is below 500 mm, or where the soils are sandy or shallow (Edmeades *et al.* 1995). Drought that co-incides with the flowering period can cause serious yield instability at the farm level, because it allows no opportunities for farmers to replant or otherwise compensate for loss of yield.

Biomass production generally decreases with decreasing water availability (Blackwell *et al.* 1985; Novero *et al.* 1985; Turner *et al.* 1986). Stress experienced by crops during growth has cumulative effects, which are ultimately expressed as a reduction in final biomass production below the unstressed potential.

One of the main causes of barrenness in maize during water-deficit is a reduction in the flush of assimilates to the developing ear below some threshold level necessary to sustain grain formation and growth (Schussler & Westgate 1995). This leads to a large reduction in kernel number (Herrero & Johnson 1981; Westgate & Boyer 1985). Total dry matter production is a good estimator of the degree of adaptation of a genotype to the environment in which it is grown. Kamprath *et al.* (1982) showed that differences in total dry-matter accumulation in maize varieties reflected differences in photosynthetic production after eight cycles of recurrent selection. Drought stress during the grain-filling period primarily affects kernel weight due to a decrease in carbon exchange rates and/or duration of the grain-filling period (Jurgens *et al.* 1978; Jones & Simmons 1983). Bolanos & Edmeades (1996) reported that more than 75% of the variation in grain yields under drought conditions was accounted for by variation in ears and kernels/plant and authors showed that ears and kernels/plant were more important determinants of grain yield than weight/kernel. Individual kernel weight seemed to play a more important role in determining grain yield only in well-watered environments. Improved tolerance to drought is therefore an important breeding

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objective for the International Institute of Tropical Agriculture (IITA), in the effort to stabilize maize production in the dry savannahs of West Africa.

In 1998, IITA maize scientists began screening maize hybrids, improved OPVs, and farmers' local varieties for tolerance to water deficit in an effort to identify superior sources of tolerance to drought for use in the maize breeding programme. The screening was done under controlled conditions. In the water deficit treatment, maize was irrigated only up to 23 days before anthesis. Although significant variations among genotypes were observed for grain yield and other traits under drought stress, the physiological basis for such variation was not studied (Menkir & Akintunde 2001). Also, values for some important secondary traits that show increased genetic variance under drought stress (Bolanos & Edmeades 1996) did not show wide differences between well-watered and water-deficit treatments (Menkir & Akintunde 2001), due to the moderate level of the drought imposed during the study. In order to reveal large genetic differences for important drought-adaptive secondary traits, evaluations should be carried out under severe drought stress. In a series of trials to assess the relative value of drought-adaptive secondary traits in S1 progenies of maize, Bolanos & Edmeades (1996) concluded that intermediate drought stress allowed the manifestation of genetic variability for rates of canopy senescence, weight/kernel, ears/plant and yield while severe drought stress revealed genetic variation for anthesis-silking interval and ears/plant.

The objective of the present study was to determine the effects of drought stress on biomass accumulation and yield components of some maize genotypes with contrasting response to drought-induced stress.

MATERIALS AND METHODS
Sites and experimental design

The study was carried out during the dry seasons of 2001 and 2002 at IITA's experimental farm at Ikenne, southwestern Nigeria ($6°53'$N, $3°42'$E, altitude 60 m a.s.l.). The soil in the experimental station is Eutric nitosol (FAO 1974). The experiment was planted for two consecutive dry seasons in two blocks that received different irrigation treatments. Sprinkler irrigation was used to supply adequate water every week to all blocks from planting to the end of the 4th week. Irrigation was thereafter discontinued in the block with the water-deficit treatments (about 27 days before 50% anthesis) and the crops were allowed to mature on stored moisture. One of the blocks, hereafter referred to as the well-watered treatment, continued to receive adequate water each week until physiological maturity. A randomized complete block design was used to arrange the genotypes in each block. The planting date in both years was 1

Table 1. *Characteristics of genotypes evaluated under water-deficit and well-watered conditions in 2001 and 2002 at Ikenne, Nigeria*

Genotypes	Colour	Type
Hybrids		
9011-30	White	Flint/Dent
9134-14	White	Flint/Dent
OPVs		
STR-EV-IWD	White	Dent
IYFD-C0	Yellow	Flint
Local landraces		
Borno-AccNo10	White	Flint/Dent
Katsina-AccNo1	White	Flint/Dent

December. Plots consisted of six rows, 3 m long, with 0·75 m spacing between rows and 0·25 m between plants. Two seeds were planted per hill and later thinned to one per hill to give a density of 53 333 plants/ha. Nitrogen fertilizer was applied at the rate of 90 kg N/ha in two equal splits, at planting and three weeks after planting. Phosphorus and potassium were basally applied as triple superphosphate and muriate of potash at the rate of 60 kg/ha of each nutrient.

Genotypes

Six genotypes were selected on the basis of their contrasting response to drought stress (A. Menkir, personal communication). The genotypes (Table 1) represented three cultivar types, namely: hybrids, OPVs and local landraces. The two hybrids and the two OPVs were developed at IITA from diverse genetic materials. The landraces were local maize varieties collected by the national maize improvement programmes from farmers' fields in the drier parts of Nigeria. Seeds of these varieties were increased in IITA through bulk pollination for the studies.

Dry matter and yield component assessment

At 50% silking, eight plants from the four central rows of each plot were cut at the soil surface and separated into stems (including leaf sheath, tassel and husks), leaf blades and ears. The plant materials were chopped and oven-dried at 80 °C to constant weight in a forced-air circulation oven. The sampling was repeated during the grain-filling period (milk stage) and at physiological maturity. Grain yield was recorded from five plants of the four central rows of each plot, excluding the end plant of each row. Thus grain yield was recorded from an area of 4 m², containing a total of 20 plants. The total number of plants and ears were counted in each plot at harvest. The number of ears/plant was then calculated as the

Table 2. *Mean monthly temperature and rainfall data at the experimental site, Ikenne, Nigeria, during the cropping period* (*December 2000–March 2001 and December 2001–March 2002*)

| | Temperature (°C) | | | | Rainfall (mm) | |
| | 2000/2001 | | 2001/2002 | | | |
Month	Maximum	Minimum	Maximum	Minimum	2000/2001	2001/2002
December	33·5	22·9	32·7	23·9	0·0	58·6
January	33·5	23·0	33·0	24·0	0·0	0·0
February	35·7	23·3	36·3	24·4	5·2	4·5
March	35·0	24·3	36·0	24·5	115·5	50·2
Mean	34·5	23·4	34·5	24·2	30·2	28·3

total number of ears at harvest divided by the total number of plants harvested. Ears harvested from each plot were shelled and the per cent grain moisture was determined using a Dickey–John moisture tester (Model 14998, Dickey–John Corporation, Auburn, USA). Grain yield adjusted to 12 % moisture was computed from the shelled grain. Four ears were randomly selected from the central row of each plot and dried in an oven at 60 °C for 4 days. After drying, the number of rows in a cob and kernels/ear were counted. Five hundred kernels from each treatment were sampled and weighed to determine a thousand-grain weight.

Data analysis

Statistical analyses were performed using SAS for Windows Release 6.12 (SAS Institute 1997). The SAS procedure used for the ANOVA was GLM (general linear model). Standard errors were used to detect the differences between treatment means.

RESULTS

Environmental conditions

Rainfall during the experiments was low (120·4 mm in 2001 and 113·3 mm in 2002, Table 2). The rain-free period at Ikenne in 2001 and 2002 allowed effective evaluation of the maize genotypes under controlled drought stress. Average temperatures in both years were fairly similar. Mean maximum temperatures were 33·5–35·0 °C in 2001 and 32·7–36·0 °C in 2002. Mean minimum temperatures were 22·9–24·3 °C in 2001 and 23·9–24·5 °C in 2002. These values therefore indicate that the temperature was suitable for the normal growth and development of maize.

Biomass accumulation and distribution

There were highly significant differences in total biomass accumulation and partitioning to stems, leaves and grains at mid-silking, grain-filling and at maturity under both well-watered and water-deficit conditions among maize genotypes (Tables 3 and 4). Also there were significant genotype × water regime interactions across years. In well-watered plots, the accumulation of biomass in leaves, stems and grains did not differ significantly among improved genotypes (hybrids and OPVs) with the exception of 9134-14, which accumulated more biomass in the leaves during mid-silking. The amount of biomass accumulated in all plant parts of the improved genotypes differed significantly from the amount accumulated in landraces for all sampling stages.

Results showed that water deficit reduced total biomass accumulation at 50 % silking by 37 %, at grain-filling period by 34 % and at maturity by 21 % compared with well-watered treatments. The improved genotypes generally had the highest leaf, stem, ear, and total biomass while the landraces had the lowest at all stages of sampling. Of the improved genotypes, the hybrid 9011-30 produced the highest total dry matter at mid-silking period. However, total dry matter was reduced by 14 % while those of the OPVs increased by 30 % at grain-filling period. The drought-susceptible hybrid 9134-14 produced the least total dry matter among the improved genotypes during the grain-filling period. Total leaf dry matter did not differ significantly among all genotypes at mid-silking and grain-filling period. At both sampling stages, leaf dry matter accounted for 30 % of the total biomass production of all maize genotypes. There were significant differences among genotypes for stem and ear dry-matter production at both sampling stages. The hybrid 9011-30 produced the highest stem and ear dry matter during mid-silking and these represented 61 and 11 % of the total biomass production, respectively. Of the landraces, Katsina-AccNo1 produced amounts of stem dry matter similar to that of the improved genotypes during mid-silking except for 9011-30, which produced significantly more stem dry matter than Katsina-AccNo1. During the grain-filling

Table 3. *Biomass production (g/plant) of six maize genotypes at mid-silking and during grain-filling period under optimal moisture and terminal drought conditions*

Genotype	Well-watered				Water-deficit			
	Leaf	Stem	Ear	Total	Leaf	Stem	Ear	Total
Mid-silking								
Hybrid								
9011-30	30·34	70·44	17·42	118·19	26·85	61·95	11·39	102·17
9134-14	34·24	67·26	17·32	118·82	26·69	52·73	6·59	86·15
OPV								
STR-EV-IWD	30·74	69·26	19·24	119·25	26·81	50·43	9·89	87·15
IYFD-C0	31·71	65·24	23·66	120·60	25·70	48·04	10·32	84·03
Landraces								
Katsina-AccNo1	29·13	66·86	8·08	104·07	24·59	47·92	1·26	73·78
Borno-AccNo10	28·62	55·80	4·34	88·75	23·43	40·74	0·18	64·29
Mean	30·80	65·81	15·01	111·61	25·68	50·30	6·61	82·93
S.E.	0·82	2·14	2·98	3·57	0·57	2·85	1·98	3·59
Grain-filling period								
Hybrid								
9011-30	29·89	51·96	59·40	141·24	28·23	41·80	17·87	87·93
9134-14	27·00	54·74	60·77	142·51	26·40	43·60	16·90	86·87
OPV								
STR-EV-IWD	28·30	49·69	59·32	137·30	29·20	46·07	31·10	106·40
IYFD-C0	27·27	41·48	56·52	125·27	29·00	49·30	41·30	119·60
Landraces								
Katsina-AccNo1	25·65	51·39	29·95	106·99	25·30	39·10	11·83	76·17
Borno-AccNo10	30·74	51·89	32·60	115·23	24·13	32·77	6·63	63·53
Mean	28·14	50·19	49·76	128·09	27·04	42·11	20·94	90·08
S.E.	0·78	1·86	5·88	3·84	0·85	2·35	5·26	4·50

Table 4. *Biomass production (g/plant) and HI at physiological maturity of six maize genotypes under well-watered and water-deficit before flowering*

Genotype	Well-watered					Water-deficit				
	Leaf	Stem	Grain	Total	HI	Leaf	Stem	Grain	Total	HI
Hybrid										
9011-30	15·80	69·59	110·84	193·22	0·56	10·53	56·12	46·49	113·14	0·40
9134-14	17·47	70·85	112·33	200·63	0·56	10·91	43·43	31·80	86·21	0·37
OPV										
STR-EV-IWD	20·24	74·16	114·58	208·99	0·55	14·50	46·92	44·31	105·64	0·42
IYFD-C0	17·29	68·68	104·04	190·00	0·55	11·94	47·94	44·28	104·15	0·42
Landraces										
Katsina-AccNo1	12·53	70·26	65·07	147·86	0·44	8·54	49·88	28·56	86·99	0·31
Borno-AccNo10	17·10	64·65	47·53	129·28	0·38	12·70	52·07	4·84	69·70	0·07
Mean	16·74	69·70	92·40	178·83	0·51	11·52	49·39	33·38	94·31	0·33
S.E.	1·03	1·27	11·73	13·20	0·03	0·83	1·79	6·46	6·59	0·05

period, dry-matter accumulation in all plant parts was significantly higher than in the landraces.

During grain-filling, a significant reduction in stem dry-matter accumulation was observed among the genotypes, except for IYFD-C0, compared to the amount at mid-silking. This was accompanied by a significant increase in ear dry-matter accumulation.

At physiological maturity, total dry matter and harvest index (HI) were similar for contrasting improved genotypes but were significantly different for

Table 5. *Yield and yield components of maize genotypes under well-watered and water-deficit conditions*

Genotype	Grain yield (kg/ha)			Ear number (ears/plant)			Kernel number (number/ear)			1000 kernel weight (g)		
	Well-watered	Water-deficit	% reduction	Well-watered	Water-deficit	% reduction	Well-watered	Water-deficit	% reduction	Well-watered	Water-deficit	% Reduction
Hybrids												
9011-30	5912	2511	59	0·96	0·87	9	512	360	30	249	178	29
9134-14	5991	1731	71	0·94	0·83	12	473	302	36	257	170	34
OPV												
STR-EV-IWD	6111	2480	57	0·99	0·83	16	506	345	32	251	176	30
IYFD-C0	5549	2410	58	0·99	0·91	8	459	351	24	247	154	38
Landraces												
Katsina-AccNo1	3471	1768	49	0·85	0·52	39	412	237	42	240	172	28
Borno-AccNo10	2535	265	90	0·77	0·41	47	413	75	82	239	158	34
s.e.	625	350		0·04	0·09		17·8	44·7		2·8	4·0	

the landraces under well-watered conditions (Table 4). The amount of dry matter partitioned to the leaves and stems did not differ significantly among the improved genotypes. The amount of biomass partitioned to the leaves was lower at physiological maturity than at mid-silking or grain-filling. However, a higher amount of biomass was partitioned to the stem. In landraces, the amounts of biomass accumulated in the leaves by Borno-AccNo10 and in the stem by Katsina-AccNo1 were similar to those of the improved genotypes. Under water-deficit, however, there was a 47% reduction in total dry matter across genotypes, compared with the well-watered conditions. This reduction was higher among the landraces than among the improved genotypes, with the exception of the hybrid 9134-14, which had a reduction of 57% in total dry matter. There were also significant differences for HI among the genotypes. HI ranged from 0·07 in Borno-Acc-10 to 0·42 in the OPVs. With the exception of 9134-14, there was no significant difference among the improved genotypes.

Yield and yield components

Moisture deficits affected yield and yield components of all the genotypes (Table 5). Among the genotypes, the hybrids and OPVs performed better than the landraces under both drought conditions and sufficient water supply. Grain yields under well-watered conditions were similar among the improved genotypes and significantly different from the landraces. Grain yield ranged from 2535 kg/ha for Borno-AccNo10 to 6111 kg/ha for STR-EV-IWD. Water deficit significantly reduced the grain yield of all genotypes. There were also significant differences in grain yield among the genotypes. Improved genotypes recorded similar and lower yield reductions than the landraces, except the hybrid 9134-14, which recorded higher yield reductions comparable to the landraces. Among the landraces, Borno-AccNo10 recorded higher yield reductions of over 90%.

Under well-watered conditions, the number of fertile ears/plant in the improved genotypes (hybrids and OPVs) was similar, but higher than the number in the landraces. Water deficit reduced the numbers of ears/plant (Table 5). The two hybrids and the OPV STR-EV-IWD had similar numbers of ears/plant, but lower than that of IYFD-C0. The landraces produced the lowest number of ears/plant under water-deficit conditions. Differences in kernel number/ear among the genotypes under different moisture regimes followed a trend similar to those observed for grain yield (Table 5). Under well-watered conditions, the hybrids and OPVs had similar numbers of kernels/ear, which was 15% greater than those of the landraces. Water deficit reduced the number of kernels/ear by an average of 40% with IYFD-C0, STR-EV-IWD

and 9011-30 showing the smallest decreases in kernel numbers while the landraces had the largest.

There were significant differences among the genotypes for 1000 kernel weight under both well-watered and water-deficit conditions. Under well-watered conditions, 9134-14 produced a significantly higher kernel weight than the other genotypes. Kernel weight among the other improved genotypes did not differ significantly. Kernel weight was similar among the landraces and was significantly lower than those of the improved genotypes. Water-deficit significantly reduced kernel weight in all genotypes. This reduction was more pronounced in IYFD-C0 than in the other genotypes.

DISCUSSION

The maize genotypes included in the present study exhibited significant differences for dry-matter accumulation, grain yield and yield components under moisture deficit conditions. The differences in grain yield and ranking are consistent with the results obtained by Menkir & Akintunde (2001) for the same genotypes. Dry-matter accumulation under water-deficit conditions was higher for improved genotypes than the landraces. The drought-induced reduction in total dry matter supports the findings of Blackwell et al. (1985), Novero et al. (1985), and Turner et al. (1986) who reported that biomass production generally decreases with decreasing water availability. Considerable differences in translocation to the ears or the grains under drought conditions were also found among the genotypes. For example, stem dry matter in 9011-30 was reduced by 33% but this was accompanied by a 57% increase in ear dry-matter accumulation. Similarly, the 9% reduction in stem dry-matter accumulation in STR-EV-IWD was accompanied by a 200% increase in ear dry-matter accumulation. These results corroborate the findings of Edmeades et al. (1993) who observed drought tolerance in advanced selection cycles of the tropical maize population "Tuxpeno Sequia" to be associated with increased ear biomass at anthesis. The present results also reveal a rapid remobilization of assimilates from the stem to the ears, even under severe drought stress. These results indicate that translocation continued to occur in these genotypes even when net accumulation of photosynthates was low. Jurgens et al. (1978) also reported that grain-filling in maize continued under water-deficit conditions and concluded that this occurred because translocation to the grain continued at a modest rate even when there was no net accumulation of photosynthetic material by the desiccated plants. On the contrary, the increase in the ear biomass of IYFD-C0 by 300% was not accompanied by a reduction in stem biomass. This suggested that IYFD-C0 had sufficient assimilates from current photosynthesis for translocation to the ears even under water-deficit conditions. This genotype also had lower stem biomass at grain-filling under well-watered conditions than under water-deficit conditions. Total biomass under well-watered conditions was, however, higher than under water-deficit conditions. The reduction in stem biomass under well-watered conditions was accounted for by a significant increase in the ear biomass above that of the water-deficit conditions. There were also significant differences in HI among the genotypes. The greater differences in HI observed between the improved genotypes and the landraces could be due to differences in the translocation of photosynthates to the grain under stress conditions.

Generally, the yield reduction due to drought stress was smaller in the genotypes that had high yield under well-watered conditions. These results agree with Duvick (1984), Castleberry et al. (1984) and Frederick et al. (1989), who reported that higher yielding hybrids had greater yields than lower yielding hybrids under both optimal and suboptimal soil water availability. However, in the present study, the hybrid 9134-14, which was among the highest yielding genotypes under well-watered conditions, recorded a 70% yield reduction under water-deficit conditions, the largest reduction for the improved maize genotypes. As is the case with the landraces, this was partly due to low biomass production, reduced number of kernels per ear, reduction in individual kernel weight, and reduced translocation of the photosynthate to the grain as indicated by the very low HI. However, numbers of ears/plant were similar to the improved genotypes that produced relatively higher yields under water-deficit conditions. This means that, although high maize yield under water-deficit conditions have been observed to be associated with a high number of fertile ears per plant (Duvick 1984; Russell 1984; Bolanos & Edmeades 1993; Bolanos et al. 1993), only the reduction in other yield-determining traits significantly affected the grain yield of in 9134-14. For the other drought-susceptible genotypes, significant reductions in number of ears/plant contributed to the reduction in grain yield under water-deficit conditions. According to Bolanos & Edmeades (1993), Frederick et al. (1989) and Fischer & Palmer (1984), grain yield is normally more strongly correlated with kernel number/ear than with other yield components. This was confirmed in the present study, with all genotypes that had high numbers of kernels/ear producing higher grain yields than those with lower numbers of kernels/ear. Consequently, genotypes such as 9134-14, Katsina-AccNo1 and Borno-AccNo10 that had significant reductions in the number of kernels per ear under water-deficit conditions recorded higher reductions in yield. Reductions in kernel weight under water-deficit conditions compared with the well-watered conditions ranged from 28 to 34%. These reductions, though prominent among the drought-susceptible genotypes, were smaller than

those of grain yield and number of kernels per ear. This is consistent with results of other studies, which indicate that stress drastically reduces kernel numbers more than the weight of individual kernels (Frey 1981; Kiniry & Ritchie 1985; Grant *et al.* 1989).

CONCLUSIONS

The results of the present study revealed that varietal improvement contributed to significant changes in the amount of dry matter accumulated and partitioned to the ear by the genotypes under both stress and non-stress environments. Genotypes selected for high grain yield under normal growing conditions also had a high level of dry-matter accumulation and partitioned more assimilates to the grain under water-deficit conditions. The improved genotypes produced more numbers of ears/plant and kernels/ear. A major exception was the hybrid 9134-14. This hybrid and the landraces recorded lower biomass production and grain yield under water-deficit conditions. They also partitioned less dry matter to the grain under moisture stress. However, the reduction in individual kernel weight under water-deficit did not significantly affect grain yield. The improved genotypes that performed better under water-deficit conditions could be recommended for release in areas prone to intermittent drought. They could also be used for further varietal improvement for drought tolerance. Secondary traits such as increased ear biomass, number of ears/plant and number of kernels/ear could be useful for rapid selection of maize genotypes for tolerance to drought stress.

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