Temporal dynamics of kernel set of tropical sweet maize (*Zea mays* L.) as influenced by genotype and mild drought

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Abstract

Maize grain yield is often affected by drought stress at flowering. Fast and synchronous emergence of silks probably is the key to high kernel set but non-destructive methods to follow the temporal grain set were missing. We solved this problem by marking flint kernels on the ears of sweet maize to reflect daily kernel set, as modern sweet maize is quite similar in vigor to field maize in Thailand. The effects of mild pre-anthesis drought stress and of the genotype were examined in two experiments (over two years both). The highest number of kernels resulted from pollination on the first or second day of silking. More than 90% of the kernels per ear were usually set by day four or five. Mild drought stress reduced the number of kernel-bearing positions along the ear as well as the number of kernels per position on each day of pollination in 2007 but there was no significant deviation in the principal grain set curve. As a consequence of mild drought stress, the differences in daily kernel set between the two water regimes were rather small compared to the differences among genotypes, for which genotype-specific deviations from the general pattern of daily kernel set were observed. Most important, a new tool exists now to reliably study variable stress situations, using normal grains on sweet maize ears or yellow grains on white grain ears as visual marker systems.

Keywords: sweet maize, flowering dynamics, kernel set, visual markers, drought stress

Introduction

There is a strong correlation between the number of exserted silks and the number of kernels (Bassetti et al, 1993a), provided that the supply of viable pollen does not limit kernel set and that the developing kernels do not abort. The percentage of exposed silks during the first eight days of silking (i.e. the period of silk emergence) was similar at all flower positions along the ears of two maize genotypes and the rate of silk elongation was always highest when the silks appeared from the husks and gradually decreased thereafter; However, the rate of silk elongation on the first three days of silking varied substantially between genotypes (Bassetti et al, 1993b). According to Cárcova et al (2003) the rate of silk elongation of a long-eared hybrid was delayed compared to a short-eared one. Genotypic differences in silk elongation are positively associated with the growth rates of the plant and the ear (Borrás et al, 2007; Pagano et al, 2007). Such relationships suggest that high rates of silk elongation and silk extrusion favor the rate of kernel set and therefore high grain yield.

Progress in potential grain yield is fastest under favorable conditions with less interaction between genotypes and environments than under stress. However, the growing conditions for maize in practical agriculture are rarely optimal. But breeding progress has to be accelerated for drought-prone rainfed production systems as well (Sivakumar, 2005). Drought stress decreases yields particularly when it occurs at flowering (Salter et al, 1967; Saini et al, 2000), because of decreased growth rates of ears and silks and delayed emergence of silks. Reduced water potential of the silks may affect their receptivity for pollen (Schoper et al, 1986). Furthermore, successfully pollinated ovaries, which develop into kernels, may abort due to the reduced availability of photosynthetic assimilates under drought stress (Hall, 2001). According to Rupitak et al (2010) the largest proportion of kernels per ear in sweet maize was set on the first two days of silking.

A visual marker system was used to determine whether (i) drought stress at flowering affected kernel set, (ii) temporal dynamics of kernel set differed among genotypes with ears of unequal size and shape, and (iii) such differences were stable across years. The specific questions were: Does drought stress induce proportional reductions in daily kernel set on individual days during silking? Do the reductions in kernel number per ear result mainly from a shorter kernel-bearing segment

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along the ear (i.e. fewer kernel positions) or from a lower number of kernels per position?

Materials and Methods

Plant materials

The following sweet maize hybrids were used: Hibrix10 (Pacific Seeds Ltd) and Sugar73 (Novartis Seeds Ltd) in 2004 and 2005, Insee2 (Kasetsart University, KU) in 2007 and 2008. Hibrix10 produces long ears (~20 cm) compared to Insee2 and Sugar73 (~18 cm). The conventional hybrids SW3851 and SW4452 were used as the dominant pollen donors to mark grain set on specific days by normal hard grains, well distinguishable from dry shrunken grains of sweet maize.

Experimental site and experimental design

The experiments were conducted in the dry season (November to April) between 2004 and 2008 at Suwan Farm in Thailand (14.5°N, 101°E, 360 m above sea level). The climate is tropical (Gerpacio et al, 2007). The distribution of rainfall is bimodal with a minor peak in May and a major peak in September. The total annual precipitation is about 1,000 to 1,200 mm. The soil is a Rhodic Kandiustox Oxisol (USDA taxonomy) (Land Development Department, 2009).

Prior to sowing, 25 kg N and 30 kg P per hectare were incorporated; 115 kg N per hectare were applied one month after sowing. Herbicides and insecticides were used as required, according to local practices. One experimental plot always consisted of six rows, 6 m long and 0.75 m apart, with 21 plants per row. Three seeds were sown manually in each mound at 6 cm depth; redundant plants were removed at the 4-leaf stage. The distance between adjacent plants in a row was 0.3 m, resulting in a population density of 4.44 plants m^{-2}. The experiments were arranged as split-plots; the main factor was irrigation. The water treatments were well-watered (WW) and drought stress (DS). To establish the crop stands all treatments alike were sprinkler-irrigated four times during the first three weeks after sowing. Thereafter, plots were furrow-irrigated once a week (~30 mm); in DS treatments water was withheld from three weeks before flowering until the end of flowering. Within each repeated irrigation block, hybrids were randomly arranged (in 2004 and 2005). The total number of repetitions for each treatment combination was six.

Environmental data

Air temperature, precipitation, relative air humidity, the speed and direction of the wind, and water evaporation were measured every three hours at Suwan Farm. The soil water potential was measured by placing Watermark® soil moisture sensors at three soil depths: 30, 60 and 90 cm at one position in the WW treatment and at one (2007) or three (2008) position in the DS treatment. The daily soil water potential was recorded from one week before the last irrigation until one week after flowering. During the same period, the leaf water potential of the youngest fully expanded leaf of 10 randomly selected plants in three plots per treatment was measured once a day before daybreak in 2008 using a Scholander pressure bomb (Boyer, 1995).

Determination of kernel set

In 2007 and 2008, 28 homogeneous plants, chosen randomly from the four middle rows of each plot, had their ear primordia covered with glassine bags. The ears of 7 (2004 and 2005) or 14 (2007 and 2008) plants per plot were pollinated with pollen of well-watered plants on seven consecutive days. In the latter two years a second batch of 14 plants per plot was pollinated with pollen of drought-stressed donor plants, but as there was no significant effect of stressed pollen on grain set, those data are not shown explicitly but are integrated in the statistical analysis as repetitions. The ears received pollen of sweet maize on six days and pollen of flint maize on one day. Each of the seven plants taken as one unique batch per plot was pollinated by pollen of flint maize once on a specific day (day 1 to 7). Air-dried mature ears were divided into kernel-wide segments, and the shriveled and hard kernels in each segment were counted. Thus, the total kernel number and the number of shriveled and hard kernels as well as the number of kernel rows and the number of kernel-bearing positions per ear were automatically recorded. The hard kernels represent the daily kernel set, according to the day, on which the ears had been

Table 1 - Average daily minimum and maximum temperatures (Temp) and relative air humidity (RH), average daily water evaporation from the soil surface (Evap), wind speed (Wind), number of days with wind speed above 5 m/s (Windy days), and total rainfall (Rain) during the flowering period (Period) in four field experiments at Suwan Farm from 2004 to 2008 (Year).

Year	Period	Temp		RH		Evap	Wind	Windy days	Rain
		Max	Min	Max	Min				
	d	°C	°C	%	%	mm	m/s	d	mm
2004	14	31.7	17.5	83.2	32.3	7.0	2.8	3	0.0
2005	12	32.9	21.8	90.3	61.6	6.7	2.0	0	21.8
2007	11	27.7	16.8	69.5	35.8	8.3	4.5	7	0.0
2008	15	30.1	19.9	88.3	51.5	4.6	2.3	2	17.9

pollinated by pollen of flint maize.

Flowering time and silk elongation

In 2007 and 2008 the average time from sowing to male and female flowering was recorded as the number of days from sowing to the day, on which 50% of the plants in the middle two rows had started to shed pollen and to exsert silks, respectively. In 2008, the ear primordia of 120 representative uniform plants (five plants per plot, 60 plants per water regime) were covered with glassine bags before silking. During the first week of silking, the length of the exserting silks was recorded daily, and the silks were cut back to the tip of the husk leaves.

Statistical analysis

The following traits were determined from the number and distribution of the shriveled and hard kernels per ear: (i) total number of kernels per ear, (ii) daily kernel set (i.e. number of kernels set per ear on the day that pollen of flint maize was supplied), (iii) number of kernels per position (i.e. distribution of kernels along the ear), and (iv) distribution of daily kernel set along the ear (i.e. number of kernels per position that were set on the day of pollination by flint maize). Some ears with unusual and sometimes incomplete grain set were removed before the analysis, i.e. about 9 % (2004), 11 % (2005), 20 % (2007), and 4 % (2008) of the ears.

All the data were analyzed by means of the package np (nonparametric kernel smoothing methods for mixed data types; Hayfield et al, 2008) in R (R Development Core Team, 2009), as described by Rupitak et al (2010) but with different regression models. The regression models for the data of 2004 and 2005 included the following variables: (i) "genotype" (total number of kernels per ear), (ii) "day" and "genotype" (daily kernel set), (iii) "genotype" and "position along the ear" (distribution of kernels along the ear), and (iv) "day", "genotype" and "position along the ear" (distribution of daily kernel set along the ear).

The regression models for the data of 2007 and 2008 included the following variables: (i) "irrigation" (total number of kernels per ear), (ii) "day" and "irrigation" (daily kernel set), (iii) "irrigation" and "position along the ear" (distribution of kernels along the ear), and (iv) "day", "irrigation" and "position along the ear" (distribution of daily kernel set along the ear).

The resulting data for daily kernel set and distribution along the ear are referred to as "absolute" data. The absolute daily number of kernels was divided by the sum of the seven respective values and multiplied by the average number of total kernels per ear. The resulting data are referred to as the "predicted" data of daily kernel set and enabled a meaningful comparison of daily kernel set with respect to the entire data set (for details see Rupitak et al, 2010). Furthermore, to account for differences in kernel set between the WW and DS treatments in 2007 and 2008, the absolute number of daily kernels in the DS treatments was adjusted to the total number of kernels per ear in the WW treatment of the same experiment.

The explanatory variables in the npreg() regression model for silk length were "irrigation" and "day".

Results

Meteorological data

Table 1 gives the meteorological data for all experiments. In 2004 and 2007, there was no precipitation, and the temperature and relative air humidity were lower than in 2005 and 2008. At the same time there were more windy days. The soil water potential decreased over time in the DS treatments (data not shown) and was lowest at the end of the stress period: -100 and -193 kPa (at 30 cm), -91 and -108 kPa (at 60 cm), and -33 and -38 kPa (at 90 cm) in 2007 and 2008, respectively. The pre-dawn leaf water potential in 2008 during the stress period just differed at the end of the stress period when the average value in the DS treatment (-63 ± 4 kPa, mean ± standard error) was lower than in the WW treatment (-32 ± 2 kPa).

Flowering and silk elongation

The average time from sowing to male flowering was about 66 days in the WW treatment in 2007 and 2008. In DS male flowering was just delayed by one day but the anthesis-to-silking interval was increased up to three days. The average cumulative length of the silks per ear was 29.9 cm (WW) and 28.0 cm (DS). In WW silk elongation was maximal on the first and second days of silking (5.3 cm d^{-1}) and decreased

Table 2 - Average number of kernels per ear ± standard error (KNO) in four field experiments (Year) with different sweet maize hybrids (Genotype) under well-watered conditions (WW) or with drought stress at flowering (DS). Ears: the number of evaluated ears; KR: percentage of ears with 12, 14, or 16 kernel rows.

Year	Genotype	Regime	KNO	Ears	12 KR (%)	14 KR (%)	16 KR (%)
2004	Hibrix10	WW	548.8 ± 10.3	37	13.5	67.6	16.2
	Sugar73	WW	557.7 ± 10.0	37	5.4	70.3	24.3
2005	Hibrix10	WW	593.2 ± 11.9	38	7.9	47.4	42.1
	Sugar73	WW	593.0 ± 11.9	37	2.7	27.0	67.6
2007	Insee2	WW	451.8 ± 4.6	271	46.9	48.3	4.8
	Insee2	DS	397.3 ± 4.7	260	44.6	49.2	5.8
2008	Insee2	WW	423.1 ± 4.1	320	43.8	45.9	10.3
	Insee2	DS	423.1 ± 4.1	326	46.3	48.5	5.2

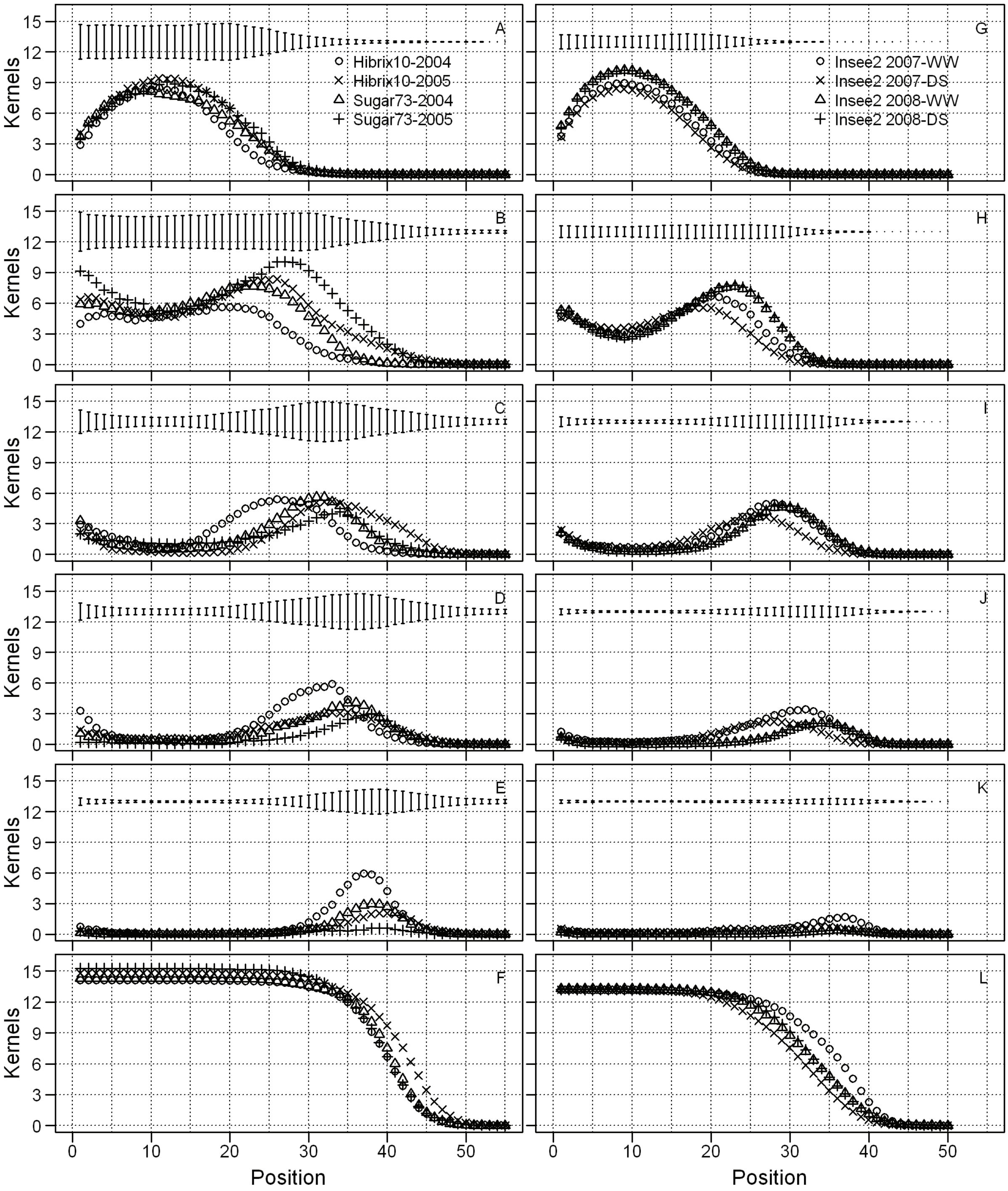

Figure 1 - Curves of average predicted daily kernel set per position along the ear on days 1 to 5 of silking (A-E and G-K) and total number of kernels per position along the ear (F and L). A-F: data for two sweet maize hybrids (Hibrix10 and Sugar73) in 2004 and 2005, G-L: data for one sweet maize hybrid (Insee2) in 2007 and 2008 in the well-watered (WW) or the drought stress (DS) treatment. Vertical segments above the curves represent average standard error of the corresponding absolute number of kernels per position.

thereafter (from 5.1 cm d^{-1} on day 3 to 2.4 cm d^{-1} on day 7). Silk elongation was significantly shorter in the DS treatment on days 2 to 4.

Kernel set in general

The total number of kernels (KNO) per ear was slightly lower in 2004 than in 2005 for both hybrids (Table 2). There were significant differences between years with regard to the ratio of ears with 12, 14, and 16 kernel rows of both hybrids (χ^2 = 7.1, P-value = 0.05 for Hibrix10 and χ^2 = 14.9, P-value < 0.001 for

Table 3 - Number of kernels representing absolute daily kernel set (ADK) and corresponding percentages in relation to the sum of seven values of daily kernel set (%ADK) or in relation to total number of kernels per ear (%KNO) (see Table 2) of two sweet maize hybrids (Genotype) in 2005.

		Day							
Genotype	Traits	1	2	3	4	5	6	7	Total
Hibrix10	ADK	140.7	167.1	101.7	67.6	36.6	16.8	10.4	540.9
	%ADK	26.0	30.9	18.8	12.5	6.8	3.1	1.9	100.0
	%KNO	23.7	28.2	17.1	11.4	6.2	2.8	1.8	91.2
Sugar73	ADK	110.1	139.1	67.7	38.7	15.3	6.7	3.2	380.8
	%ADK	28.9	36.5	17.8	10.2	4.0	1.8	0.8	100.0
	%KNO	18.6	23.4	11.4	6.5	2.6	1.1	0.5	64.1

Sugar73). Correspondingly, Hibrix10 and Sugar73 produced on average about 14 kernel rows per ear in 2004 and about 15 kernel rows in 2005 (Figure 1F). Hibrix10 had significantly more kernels than Sugar73 toward the tip of the ear (i.e. between positions 37 and 48) in 2005. Thus, kernel set at the bottom of the ears of both genotypes responded to year-specific environmental conditions to about the same extent. At the tip of the ears, however, this was not the case.

Irrespective of the year and the water regime, Insee2 produced ears with a lower average number of kernel rows, fewer kernel-bearing positions, and fewer kernels per position towards the tip of the ear than Hibrix10 and Sugar73 (Figure 1F, L). Even though a direct comparison is impossible, because Insee2 was not evaluated in the same years as the other two genotypes, these results suggest that Insee2 had a lower potential yield.

Effects of DS on kernel number per ear of Insee2 were observed only in 2007. The reduction by 12%, compared to WW (Table 2), resulted mainly from reductions in the number of kernels per position towards the tip of the ear (Figure 1L).

Daily kernel set in general

For all genotypes, more than 90% of the kernels usually came from pollinations on the first five days of silking. Hibrix10 and Sugar73 always produced the largest number of kernels on day 2 (Table 3), Insee2 on day 1 (ADK in Table 4). In 2004 the sum of the ADK values corresponded well to the total kernel number per ear (KNO) of both genotypes, whereas in 2005, the sum of the ADK values underestimated KNO; in 2007 and 2008 (Insee2) corresponding values were somewhat overestimated (data for KNO not shown). Only in 2005, the %ADK of Hibrix10 was lower than that of Sugar73 on days 1 and 2 but higher on days 3 to 7, because the percentage of kernels set on ears of Sugar73 decreased rapidly after day 2 (Table 3). Data for 2004 are not shown as both hybrids were never significantly different according to the predictions by the non-parametric model. There were differences in the percentage of daily kernel set between WW (%ADK) and DS (%KNOww) in 2007, with the largest differences at the beginning of silking (Table 4) whereas data from 2008 did not differ at all, same as in 2004.

Daily kernel set along the ear

Kernel set along the ear generally progressed faster in 2005 than in 2004 (Figure 1A-E), especially on days 2 and 3 (Figure 1B, C), as indicated by the higher ADK toward the tip of the ear. The silks apparently grew faster in 2005 than in 2004 on the first three days of silking. Kernel set of Hibrix10 lagged behind that of Sugar73 on day 2 in both years as well as on day 3 in 2004 (Figure 1B, C). The segment along the ears of Hibrix10 where at least four kernels were initiated on day 2 stretched from position 1 to 25 in 2004; it was 6 positions shorter than that along the ears of Sugar73. In 2005, the respective segment was considerably longer for both genotypes but still shorter for Hibrix10 (positions 1 to 32) than for Sugar73 (positions 1 to 36). Thus, kernel set of Sugar73 progressed very fast during the first two days of silking. Already by day 3, up to 15 kernels were initiated between positions 5 and 19, which corresponded to almost 100% of the final kernel number at these positions (data not shown). On later days, however, Hibrix10 produced more kernels than Sugar73 (Figure 1D, E), with the result that the differences in the cumulative values of predicted daily kernel set between the genotypes vanished by days 4 and 5. Hibrix10 produced even more kernels than Sugar73 at the tip of the ear in 2005, but at the cost of a slightly lower kernel number at lower positions (Figure 1F).

Figure 1 G-L shows the progress of daily kernel set along the ears of Insee2 in 2007 and 2008. Corresponding to the results presented in Table 4, drought stress had significant effects on daily kernel set along the ear in 2007 only. Drought stress reduced the number of kernel-bearing positions and the number of kernels per position on each day of pollination. The segment along the ear where at least four kernels were set on day 1 was shorter in the DS treatment (between positions 2 and 18) than in the WW treatment (between positions 2 and 19). From day 2 onwards, the progress of kernel set was slower under DS than under WW conditions. The largest drought-induced reductions in the number of kernels per position were observed on day 2 at around position 24.

Table 4 - Number of kernels representing absolute daily kernel set (ADK) and corresponding percentages in relation to the sum of the seven values of daily kernel set (%ADK), the total number of kernels per ear (%KNO) (see Table 2) in the corresponding water regime, or the total number of kernels per ear in the WW treatment (%KNOww) of the hybrid Insee2 in 2007.

		Day							
Water regime	Traits	1	2	3	4	5	6	7	Total
WW	ADK	158.8	140.0	86.0	53.8	25.2	22.5	16.3	502.6
	%ADK	31.6	27.8	17.1	10.7	5.0	4.5	3.2	100.0
	%KNO	35.1	31.0	19.0	11.9	5.6	5.0	3.6	111.2
DS	%KNO	40.0	35.2	21.6	13.6	6.4	5.7	4.1	126.6
	%KNOww	27.8	24.4	15.0	9.4	4.4	4.0	2.8	87.8

Discussion

There is a general pattern of daily kernel set

The general pattern of kernel set along the ear was quite stable, starting on the lower part of the ear on the first day of silking. The largest number of kernels resulted from pollination on days 1 and 2 of silking, irrespective of the genotypes or water management; most of these kernels were located on the lower half of the ear. These results generalize the findings by Rupitak et al (2010) for a broader set of genotypes and environments. Indeed, the largest number of kernels were set on the first two days of silking and that the distribution of daily kernel set along the ear followed a bell-shaped curve on day 1 of silking and a double bell-shaped curve on subsequent days.

There are genotype-specific deviations from the general pattern of daily kernel set

Despite the apparent general pattern, the progress of kernel set differed between years and genotypes. The data of 2005 proved that the environmental conditions (in a given year) accelerated the average exsertion of silks of both genotypes compared to 2004. Moreover, Hibrix10, the hybrid with longer ears, produced more kernels at the tip of the ear than Sugar73, whereas the latter produced slightly more kernels per position (“thicker” ears) between positions 1 and 30 (Figure 1F). The %ADK in 2005 proved that it took Hibrix10 longer to complete kernel set than Sugar73. Assuming that the data on daily kernel set give an approximation of the number of exserted silks that were receptive on the respective day of silking, as reported by Bassetti et al (1993b), then the exsertion of the silks of Hibrix10 was slower than that the exsertion of the silks of Sugar73. Cárcova et al (2003) also found that the growth of the silks of a long-eared hybrid (with a high number of spikelets per ear) was slower than that of a short-eared hybrid. Furthermore, the genotype-specific differences in the temporal dynamics of kernel set along the ear corresponded to the findings of Bassetti et al (1993a) that the duration of silk development is specific to a hybrid. Anderson et al (2004) also found differences among hybrids in the length of the pollination period, required to maximize kernel set, as well as in the rate of silk elongation and the decline in silk receptivity over time.

The percentage of daily kernels differed among the hybrids; the genotype-specific differences remained relatively constant across years, especially with respect to the day, on which most kernels were initiated. The genotypic differences in the percentage of daily kernel set remained relatively constant across years. Nevertheless, the largest number of kernels was always set on the first or second day of silking, as reported generally in literature (Sadras et al, 1985; Bassetti et al, 1993a; Anderson et al, 2004; Rupitak et al, 2010).

Mild drought stress reduced silk elongation to a greater extent than the number of kernels per position

Drought stress usually shortens the duration of silking (Hall et al, 1982; Bassetti et al, 1993C), but this was not the case here; instead it caused relatively small albeit significant reductions in the elongation of the silks and the average number of kernels per ear in 2007. Silk elongation was also slower in DS of 2008, whereas kernel number was not affected. Seemingly silk elongation is more sensitive to drought stress than kernel set. This is in agreement with Bassetti et al (1993c), who observed that silk elongation was inhibited when the water potential of the silks decreased below -0.8 MPa without affecting kernel set above -1.0 MPa (Bassetti et al, 1993c).

It was possible to model some of the effects of mild drought stress on daily kernel set and the distribution of kernels along the ear in 2007. Drought stress affected the daily number of kernels by reducing the number of kernel-bearing positions along the ear and by reducing the number of kernels per position. Nevertheless, the number of kernel rows per ear of Insee2 was quite stable under DS compared to WW conditions, as the heritability of this trait seems to be usually high (Daniel, 1963). All in all, the reduction in the number of kernel-bearing positions along the ear was the result of cumulated reductions on all seven days of pollination.

Conclusions

Targeted pollination of ears of sweet maize with pollen of flint maize provided a reliable visual marker, an aid to answering questions about maize grain set when sweet maize genotypes are similar in vigor to field maize. The dynamics of kernel set are influenced by year-specific environmental conditions during the flowering period. Although two modern sweet maize varieties (Hibrix10 and Sugar73) had a similar final number of kernels per ear, daily kernel set and the distribution of daily kernel set along the ear differed between both genotypes, reflecting different rates of elongation and emergence of the silks and proving a genetic impact on the progress of daily kernel set along the ear.

The reductions in the number of kernels per ear, induced by drought stress, resulted from a reduction in kernel number per position, which finally led to a reduction in the number of kernel-bearing positions towards the tip of the ear. Compared to the differences between the genotypes, differences in daily kernel set were smaller between the water regimes. Still, the genotypic effects on the dynamics of flowering are probably more stable across years than the effects of mild drought stress.

A new tool exists now to reliably study variable stress situations, especially the impact of severe stress on grain set dynamics. For this purpose normal grains on sweet maize ears or yellow grains on white grain ears can be used as visual marker systems.

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