Kasetsart J. (Nat. Sci.) 48 : 837 - 850 (2014)

Anthesis and Silking Dynamics of Maize under Contrasting Nitrogen and Water Levels

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ABSTRACT

Anthesis-silking and kernel setting may vary with the plant growth rate and environment. Two field experiments were conducted in December 2010 and January 2012 focusing on the short pre-anthesis and the prolonged bracketing-flowering stage drought (PBD), respectively, at the National Corn and Sorghum Research Center, Thailand. A split plot design with factorial randomized complete blocks was established with three replications, where two water regimes (well-watered and water-stressed) formed the main plots and two maize hybrids (Pioneer 30B80 and Suwan 4452) and three nitrogen levels (0, 160 (optimal) and 320 (supra-optimal) $kg.ha^{-1}$ of N) collectively formed subplots. Under all conditions, relatively more biomass partitioning to the roots during the early vegetative stage might have lowered aerial growth and subsequently caused a slight delay in anthesis and silking in Pioneer 30B80. Albeit the plant and silk growth rates during the bracketing-flowering stage were higher in Pioneer 30B80 (even under combined stresses, which shortened the anthesis-silking period and interval (ASI) that caused more kernel setting than Suwan 4452), Pioneer 30B80 failed to complete 100% silking under PBD. Silking was more affected than anthesis by both stresses especially under PBD. Across the varieties, optimal nitrogen and water accelerated plant and silk growth, which also subsequently influenced timely flowering and shortened the ASI followed by more kernel setting.

Keywords: anthesis, maize, pre-anthesis drought, silking, supra-optimal nitrogen

INTRODUCTION

Maize (*Zea mays* L.) is a monoecious plant (Irish and Nelson, 1989). Its yield under water stress depends on multitudinous factors, including the plant developmental stage, intensity and duration of water limitations, hybrid susceptibility, and vulnerability to soil drought and nitrogen (Bruce *et al*., 2002). In maize, the critical yield period centered around flowering, with one initial ovule setting during ear development and another final kernel setting during pollination (Edwards, 2009). A diminished number of kernels per ear is an immutable component of yield reduction under drought stress (Sadras *et al.*, 1985; Undersander, 1987). Nevertheless, with below-optimal environmental conditions, the kernel number may be limited by asynchrony (Johnson and Herrero, 1981) or a reduction in silk receptivity (Bassetti and Westgate, 1993). Anderson *et al.* (2004) reported that under controlled environmental conditions, the silk

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Received date : 02/10/13 Accepted date : 22/08/14

growth rate reduced after pollination and finally stopped after fertilization. However, different varieties may have different silk growth patterns and under open field conditions these may respond differently to water and nitrogen levels. Stresses such as drought, high density, low fertility and long photoperiods may impact the silk growth rate and health. Silk water potential is important for silk elongation (Anderson, 1996) but it has very limited or no capacity for osmotic adjustment (Westgate and Boyer, 1985). Therefore, continuous uptaking of water is important where a strong root system may be able to play an important role under stress conditions and the effect of nitrogen on root growth should be verified as well. A strong root system may also influence the crop growth rate and subsequently anthesis and silking dynamics under stress conditions. Different studies have shown that the crop growth rate during critical yield periods is very important for maize kernel yield (Early *et al.*, 1966; Tollenaar *et al.*, 1992; Andrade *et al.*, 1999) but none of these showed an interaction with nitrogen or water stress. Environmental conditions that alter plant growth during this period may affect the temporal separation of male (anthesis) and female (silking) floral maturity and may change the anthesis-silking interval, which is very important for successful pollination (Castiano, 2014). Different studies have demonstrated a negative relationship between the final grain yield and the anthesis-silking interval (ASI) but a positive relationship between the grain yield and kernel number (Edmeades and Daynard, 1979; Hall *et al.*, 1982); thus, more kernel setting is desirable to ensure a sufficient final yield. However, the relationship of the crop growth rate at bracketing flowering with anthesis or silking, and the ASI with kernel setting have yet to be determined under contrasting water and nitrogen levels.

Therefore, the objective of this research was to determine the effect of pre or bracketing flowering stage drought and contrasting nitrogen levels on the anthesis and silking dynamics and their subsequent effects on the kernel setting of two maize hybrids.

MATERIALS AND METHODS

The two field studies were carried out at the National Corn and Sorghum Research Center, Thailand during the dry seasons of 2010–11 and 2012 (hereafter referred to as experiments 2011 and 2012, respectively) using a split plot design with factorial randomized complete block (RCB) arrangements of the treatments in three replications. Two water regimes (W_1 = well-watered and W_2 = water-stressed) were imposed on the main plots and the subplots consisted of a combination of two varieties (V_1 = Pioneer 30B80 and V_2 = Suwan 4452) and three N levels (N_1 = 0, N_2 = 160 (optimal) and N_3 = 320 (supra optimal) kg.ha^{-1} of N). The soil in the experimental field was a clay type with low N content. Seeds were planted on 3 December 2010 and 14 January 2012 at a spacing of 75 × 25cm, maintaining one plant per hill. Treatment wise, half of the urea (N = 46%) as a source of nitrogen was applied basally and the remaining half was applied as a side dressing at 34 days after planting (DAP) at about the 8-leaf stage followed by irrigation. Sprinkler irrigation was provided every week from seed planting to 5 wk after planting (WAP) and thereafter, furrow irrigation was provided weekly up to physiological maturity. Plant stages were considered as per the control (well-watered and optimal nitrogen) plants. Two tensiometers per replication were used to monitor the soil water tension and field capacity. Irrigation in the water-stressed (WS) block was suspended during 35 DAP to 64 DAP in 2011 defined as the short pre-anthesis drought (SPD) and during 35 DAP to 76 DAP in 2012 defined as the prolonged bracketing flowering stage drought (PBD) and then irrigation was resumed up to physiological maturity, as with the well-watered (WW) block.There was no rainfall during the water stress period in 2011 and only very little rainfall occurred twice in 2012 during the water stress period (2 mm and 3 mm at 12 and 21 d after water withholding, respectively). The average daily temperature was relatively higher during the crop growing season (January to April) in 2012 than in 2011. Weeds were removed manually during the crop growing season and there were no remarkable disease or insect outbreaks.

All parameters were measured in both years except the silk water content, which was considered only in 2012 when the water stress period occurred. The dry matter of different plant parts was determined by the oven dry method (Hart, 1967) and dried to achieve constant weight. To determine the root dry matter (RDM), roots were collected from 0 to 40 cm soil depth from five plants randomly taken from each subplot just before (RDM_{bs}) and after (RDM_{as}) the water stress period. To calculate the aerial crop growth rate (CGR), five aboveground plants were randomly collected from each subplot at 6 and 8 WAP to determine the vegetative crop growth rate (CGR_v) whereas 10 and 13 WAP sampling was used for the bracketing flowering (CGR_f) period; the dry matter was determined for all samples. The CGR was calculated by adopting the formula of Watson (1967) expressed in grams per square meter per day (Equation 1):

$$CGR = (W_2-W_1) / (t_2-t_1) \quad (1)$$

where W_1 is the dry weight at time t_1, W_2 is the dry weight at time t_2, both in grams per square meter and t_2-t_1 is the time interval in days.

The dates of anthesis (that is, at least one extruded anther visible at the tassel) and silking of the primary ear (that is, at least one silk visibly extruding from the husks) were recorded from 100 pre-selected plants in the four central non-destructive rows avoiding border effects. The anthesis and silking percentages were calculated as the number of plants attaining those stages every day interval following Ge *et al.* (2012). The anthesis silking interval (ASI) was calculated as the difference between the days to 50% silking and the days to 50% anthesis. The silk growth rate (SGR) was determined in centimeters per day by measuring the length of the pre-selected outer side silk of the husk from the primary ear of five pre-selected plants per subplot daily at 0700 0900 hours. The measurements commenced from first silk emergence that is, 0 days after silking (DAS) and continued until no effective extension could be detected because of silk senescence. Care was taken to minimize tissue handling and to determine the silk length consistently. The silk water content (SWC) was determined gravimetrically at 0 DAS from three primary ears of three plants per subplot. Destructive primary ear sampling occurred randomly from the destructive rows of each subplot in the morning and samples were kept in an ice box covered with a plastic bag to avoid moisture loss and the fresh weight of the separated silks was measured as soon as possible and then the oven-dried weight was determined. Missing kernels and filled kernels were counted from five mature, primary ears collected randomly from each subplot avoiding any border effect to calculate the filled kernel percentage, which is mentioned hereafter as kernel setting.

Different data were subjected to analysis of variance appropriate for a split plot design with factorial RCB arrangements. Separate analysis of variance was performed for each measurement. A linear relationship was determined between the different parameters. Mean separations were tested for significance using Fisher's protected least significance difference (LSD) procedure at the $P = 0.05$ level.

RESULTS AND DISCUSSION

Root dry matter

The results from both years showed that the RDM was significantly reduced due to water stress and a zero N level (both before and after the water stress period) for both varieties (Table 1). The RDM might have been reduced under water stress due to considerably increased soil mechanical resistance against root growth (Whitmore and Whalley, 2009). N stress might have resulted in less root branching (Eghball and Maranville, 1993) in the maize through less cell differentiation (Burkholder and McVeigh, 1940), which successively caused less RDM. Supra-optimal N also decreased RDM (corroborated by Oikeh *et al.*,1999) and this might have been due to the toxic effects of excess N (Wang *et al.*, 2008) or penetration of excess NH_4^+ through the roots that might replace K^+, accompanied by an increase in chloride (Britto and Kronzucker, 2002), which could impede photosynthesis.

Increased N application might cause decreased P availability in the plant (Ashraf *et al.*, 2001; Saneoka *et al.*, 2004), which might be a barrier for proper root growth (Olczyk *et al.*, 2003) and corroborates the outcome of the current experiment. Pioneer 30B80 produced more RDM than Suwan 4452 at all interactions. However, it was relatively more sensitive to supra-optimal N (reduced 12.07 and 1.94% more than Suwan 4452 over the control during 2011 and 2012, respectively after the WS period) as shown by Table2. On the other hand, Suwan 4452 was more susceptible to water stress (reduced 4.56 and 12.02% more than Pioneer 30B80 over the control during 2011 and 2012, respectively after the WS period) as shown by Table 3. The RDM after a water stress period in 2012 was much higher than that of 2011, because in 2012 the plants had a longer time (2 wk more) for root growth due to the late finish of the water stress period (Table 3). Well-watered and optimal N simultaneously influenced RDM production (Table 4). The lowest RDM was obtained from Suwan 4452 under combined stress (Table 2). Continuous and relatively smooth root growth in Pioneer 30B80 might have been influenced by the early establishment of roots in the soil and the subsequent continuous uptake of water and nutrients from a greater soil area even under water stress conditions, which might have helped

Table 1 Main effect of water regime, variety and N level on physiological traits of maize grown at the National Corn and Sorghum Research Center, Thailand in 2011 and 2012.

Treatment	RDM_{bs} (g per plant)		RDM_{as} (g per plant)		CGR_v ($g.m^{-2}.d^{-1}$)		CGR_f ($g.m^{-2}.d^{-1}$)		SWC (%)	KS (%)	
	2011	2012	2011	2012	2011	2012	2011	2012	2012	2011	2012
Water regime											
W_1	1.27	1.75	17.15^a	39.24^a	17.80^a	18.70^a	20.87^a	21.58^a	90.65^a	93.69^a	92.28^a
W_2	1.24	1.73	8.48^b	26.23$_b$	10.81^b	11.44^b	14.60^b	10.12^b	89.18^b	82.23^b	72.37^b
F–test (W)	NS	NS	**	**	**	**	**	**	*	**	**
Variety											
V_1	1.48^a	1.99^a	16.04^a	43.09^a	12.62^b	13.72^b	18.93^a	16.48^a	90.04	90.28^a	84.76^a
V_2	1.03^b	1.48^b	9.59^b	22.38^b	15.99^a	16.43^a	16.53^b	15.23^b	89.79	85.63^b	79.88^b
F–test (V)	**	**	**	**	**	**	**	**	NS	**	**
N level											
N_1	0.94^c	1.35^c	7.41^c	21.36^c	9.59^c	10.12^c	13.56^c	11.27^c	89.72	84.45^c	77.27^c
N_2	1.67^a	2.11^a	18.14^a	46.28^a	17.57^a	18.37^a	22.77^a	20.42^a	90.05	91.07^a	85.96^a
N_3	1.17^b	1.75^b	12.90^b	30.56^b	15.75^b	16.73^b	16.86^b	15.86^b	89.97	88.34^b	83.73^b
F–test (N)	**	**	**	**	**	**	**	**	NS	**	**

W_1 = Well-watered; W_2 = Water-stressed; V_1 = Pioneer 30B80; V_2 = Suwan 4452; N_1, N_2 and N_3 = 0, 160 and 320 kg.ha-1 of N, respectively; RDMbs = Root dry matter before water stress; RDMas = Root dry matter after water stress; CGRv = Crop growth rate during vegetative stage; CGRf = Crop growth rate during bracketing flowering period; SWC = Silk water content; KS = Kernel setting.

Means within a column with the same or no letters are not significant at $P < 0.05$ based on the least significant difference test; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$; NS = Not significant.

photosynthesis and the partitioning of photo-assimilates to the roots. A higher RDM might have made Pioneer 30B80 relatively less susceptible to water stress and this result was also supported by Farooq *et al.* (2009) and Liu *et al.* (2011).

Crop growth rate

The CGR was significantly reduced due to water stress (Ge *et al.*, 2012), and zero (Uhart and Andrade, 1995) and supra-optimal N application during both vegetative and flowering periods in both years (Table 1). The CGR_f decreased more due to water stress in 2012 (53.10%) than in 2011 (30.04%) over the control, because the prolonged water stress period continued up to the flowering period in 2012 but finished before flowering and before the plant could recover in 2011. These results were partially supported by Ge *et al.* (2012). The CGR_v was lower (21.08 and 16.49% in 2011 and 2012, respectively) in Pioneer 30B80 than Suwan 4452 and this might have been due to more dry matter partitioning to roots (30.41 and 25.63% in 2011 and 2012, respectively) in Pioneer 30B80 in that period. Contrariwise, the CGR_f was higher (12.68 and 7.58% in 2011 and 2012, respectively) in Pioneer 30B80 than Suwan 4452 (Table 1) even under water stress conditions when it was 18.81 and 7.14% higher in 2011 and 2012, respectively (Table 2) and it might have been accelerated by taking up more water and nutrients through the early establishment of more roots in the soil. Optimal N also enhanced CGR under all conditions in both years (Tables 1, 2, 3, 4 and 5). The suppression of CGR by supra-optimal and zero N levels in both years might have resulted from the reduced supply of essential nutrients through the reduced amount of roots (Table 1) and less transfer of photo-assimilates from the reduced leaf area (data not shown). However, at all stages, the CGRs of Pioneer 30B80 and Suwan 4452 were more reduced due to supra-optimal and zero N application, respectively, (Table 3).

Under all conditions, the CGR was relatively higher during 2012 than 2011 which might have been due to the rapid and early growth, which might have been boosted by the relatively higher temperature during the growing period in 2012 (data not shown) except during the water stress conditions of CGR_f during 2012, when the plants suffered prolonged stress compared to 2011. A positive, linear and significant relationship was observed in both years between RDM_{as} and CGR_f (Figure 5a).

Table 2 Effects of variety × nitrogen interaction on physiological traits of maize grown at the National Corn and Sorghum Research Center, Thailand in 2011 and 2012.

Treatment	RDM_{bs} (g per plant)		RDM_{as} (g per plant)		CGR_v ($g.m^{-2}.d^{-1}$)		CGR_f ($g.m^{-2}.d^{-1}$)		SWC (%)	KS (%)	
	2011	2012	2011	2012	2011	2012	2011	2012	2012	2011	2012
$V_1 \times N_1$	1.11^c	1.68^d	9.79^c	28.83$_d$	9.45^e	10.47^d	15.14^e	12.33^d	89.94	88.00^{bc}	80.80^d
$V_1 \times N_2$	2.00^a	2.31^a	23.00^a	60.74^a	15.47^c	16.80^b	24.26^a	21.06^a	90.13	93.43^a	88.42^a
$V_1 \times N_3$	1.33^b	1.99^b	15.34^b	39.70^b	12.93^d	13.90^c	17.39^c	16.04^c	90.04	89.43^b	85.06^b
$V_2 \times N_1$	0.76^e	1.03^f	5.04^d	13.89^f	9.73^e	9.77^d	11.99^f	10.21^e	89.50	80.91^d	73.74^e
$V_2 \times N_2$	1.33^b	1.91^c	13.28^b	31.83^c	19.67^a	19.95^a	21.28^b	19.77^b	89.97	88.72^{bc}	83.51^{bc}
$V_2 \times N_3$	1.01^d	1.51^e	10.46^c	21.42^e	18.56^b	19.56^a	16.32^d	15.69^c	89.90	87.26^c	82.40^{cd}
F–test	**	**	**	**	**	**	*	*	NS	**	*

V_1 = Pioneer 30B80; V_2 = Suwan 4452; N_1, N_2 and N_3 = 0, 160 and 320 kg.ha-1 of N, respectively; RDMbs = Root dry matter before water stress; RDMas = Root dry matter after water stress; CGRv = Crop growth rate during vegetative stage; CGRf = Crop growth rate during bracketing flowering period; SWC = Silk water content; KS = Kernel setting.

Means within a column with the same or no letters are not significant at $P < 0.05$ based on the least significant difference test; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$; NS = Not significant.

Anthesis and silking dynamics

It was found that the starting, 50% and finishing of anthesis and silking of the two maize varieties were significantly delayed due to both water (supported by Ge *et al.*, 2012) and N stress in both years (Figures 1 and 2). Both anthesis and silking started about 1 wk earlier in 2012 than in 2011 perhaps due to the overall faster plant growth in 2012 (Table 1), which might have resulted from the relatively higher growing season temperature in 2012. Silking was more affected by either water or N stress than anthesis and the total silking period was longer under water-stressed conditions than well-watered conditions (Figures 1c and 1d). The starting of anthesis and silking were slightly delayed in Pioneer 30B80 compared to Suwan 4452 (Figures 1 and 2) except for silking in 2012 (Figures 1d and 2d); this may have been caused by the slower crop growth rate during the vegetative stage (Table 1). Contrariwise, Pioneer 30B80 attained 50% even though it finished its anthesis and silking earlier than Suwan 4452, that is, the total anthesis-silking period in this variety was shorter than for Suwan 4452.

Table 3 Effects of water regime × variety interaction on physiological traits of maize grown at the National Corn and Sorghum Research Center, Thailand in 2011 and 2012.

Treatment	RDM_{bs} (g per plant)		RDM_{as} (g per plant)		CGR_v ($g.m^{-2}.d^{-1}$)		CGR_f ($g.m^{-2}.d^{-1}$)		SWC (%)	KS (%)	
	2011	2012	2011	2012	2011	2012	2011	2012	2012	2011	2012
$W_1 \times V_1$	1.50	2.00	21.22^a	50.35^a	15.37^b	16.92^b	21.75^a	22.45	90.67	94.72^a	93.36^a
$W_1 \times V_2$	1.04	1.49	13.08^b	28.13^c	20.23^a	20.49^a	19.99^b	20.70	90.63	92.65^b	91.19^b
$W_2 \times V_1$	1.46	1.99	10.86^c	35.82^b	9.86^d	10.52^d	16.11^c	10.50	89.41	85.84^c	76.15^c
$W_2 \times V_2$	1.02	1.47	6.10^d	16.63^d	11.75^c	12.36^c	13.08^d	9.75	88.95	78.61^d	68.58^d
F–test	NS	NS	**	**	**	*	*	NS	NS	**	**

W_1 = Well-watered; W_2 = Water-stressed; V_1 = Pioneer 30B80; V_2 = Suwan 4452; RDMbs = Root dry matter before water stress; RDMas = Root dry matter after water stress; CGRv = Crop growth rate during vegetative stage; CGRf = Crop growth rate during bracketing flowering period; SWC = Silk water content; KS = Kernel setting.
Means within a column with the same or no letters are not significant at $P < 0.05$ based on the least significant difference test; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$; NS = Not significant.

Table 4 Effects of water regime × nitrogen interaction on physiological traits of maize the National Corn and Sorghum Research Center, Thailand in 2011 and 2012.

Treatment	RDM_{bs} (g per plant)		RDM_{as} (g per plant)		CGR_v ($g.m^{-2}.d^{-1}$)		CGR_f ($g.m^{-2}.d^{-1}$)		SWC (%)	KS (%)	
	2011	2012	2011	2012	2011	2012	2011	2012	2012	2011	2012
$W_1 \times N_1$	0.92^e	1.33^d	7.92^d	25.72^c	12.19^d	13.00^c	16.65^{cd}	16.47^c	90.55	90.93^b	89.77^b
$W_1 \times N_2$	1.75^a	2.13^a	25.83^a	53.77^a	21.91^a	22.96^a	28.01^a	28.23^a	90.73	95.62^a	94.05^a
$W_1 \times N_3$	1.14^d	1.78^b	17.71^b	38.24^b	19.29^b	20.16^b	17.94^b	20.04^b	90.68	94.50^a	93.00^a
$W_2 \times N_1$	0.95^e	1.37^d	6.91^d	17.00^e	6.99^e	7.24^d	10.48^e	6.07^f	88.90	77.98^e	64.77^e
$W_2 \times N_2$	1.58^b	2.10^a	10.45^c	38.80^b	13.22^c	13.79^c	17.53^{bc}	12.61^d	89.38	86.52^c	77.87^c
$W_2 \times N_3$	1.19^c	1.72^c	8.08^d	22.88^d	12.20^d	13.29^c	15.77^d	11.69^e	89.27	82.19^d	74.46^d
F–test	**	**	**	**	**	**	**	**	NS	**	**

W_1 = Well-watered; W_2 = Water-stressed; N_1, N_2 and N_3 = 0, 160 and 320 kg.ha-1 of N, respectively; RDMbs = Root dry matter before water stress; RDMas = Root dry matter after water stress; CGRv = Crop growth rate during vegetative stage; CGRf = Crop growth rate during bracketing flowering period; SWC = Silk water content; KS = Kernel setting.
Means within a column with the same or no letters are not significant at $P < 0.05$ based on the least significant difference test; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$; NS = Not significant.

Due to water stress, the starting, 50% and finishing of anthesis or silking was delayed by about 2, 2 and 1 d or 4, 4 and 4 d, respectively, during 2011 and 1, 2 and 2 d or 3, 4 and 6 d, respectively, during 2012 in Pioneer 30B80 whereas for Suwan 4452 it was 2, 2 and 1 d or 4, 5 and 5 d, respectively, during 2011 and 2, 2 and 3 d or 5, 7 and 8 d, respectively, during 2012 (Figures 1a, 1b, 1c and 1d). The 50% silking was delayed even more (about 2 d) in Suwan 4452 than in Pioneer 30B80 over the control due to the prolonged drought during 2012 (Figure 1d). On the other hand, due to the zero N stress, the starting, 50% and finishing of anthesis or silking were delayed by about 1, 3 and 2 d or 3, 4 and 4 d, respectively, during 2011 and 2, 2 and 3 d or 2, 3 and 5 d, respectively during 2012 in Pioneer 30B80 whereas for Suwan 4452, it was 2, 4 and 3 d or 5, 6 and 5 d, respectively, during 2011 and 2, 3 and 3 d or 2, 5 and 4 d, respectively, during 2012 (Figures 2a, 2b, 2c and 2d).

It was found that all plants could not reach silking irrespective of the prolonged drought (Ge *et al.*, 2012) or N stress during 2012 in Suwan 4452 (Figures 1d and 2d). Both anthesis and silking were more delayed due to water and N stress compared to the control in Suwan 4452 than in Pioneer 30B80. This might have been due to the very poor osmotic adjustment capacity of the silk whereas Pioneer 30B80 could continue to supply relatively more water and also nutrients through its greater root volume. The total silking period and days to 50% silking were also broader in Suwan 4452 due to water stress especially under prolonged drought, which caused higher ASI. This might have been due to less water and nutrient uptake during the water stress period through the poor root system in Suwan 4452. Optimal N and water always accelerated anthesis and silking. Fast silking might have offered some

Table 5 Effects of water regime × variety × nitrogen interaction on physiological traits of maize grown at the National Corn and Sorghum Research Center, Thailand in 2011and 2012.

Treatment	RDM$_{bs}$ (g per plant)		RDM$_{as}$ (g per plant)		CGR$_{v}$ ($g.m^{-2}.d^{-1}$)		CGR$_{f}$ ($g.m^{-2}.d^{-1}$)		SWC (%)	KS (%)	
	2011	2012	2011	2012	2011	2012	2011	2012	2012	2011	2012
$W_1 \times V_1 \times N_1$	1.17^{d}	1.67	10.33^{d}	34.21	12.46^{de}	13.87^{de}	17.65^{cd}	17.96	90.60	92.88^{b}	91.41
$W_1 \times V_1 \times N_2$	2.00^{a}	2.33	32.67^{a}	68.33	19.18^{b}	20.94^{b}	28.65^{a}	29.05	90.73	96.09^{a}	94.79
$W_1 \times V_1 \times N_3$	1.33^{c}	2.00	20.67^{b}	48.52	14.48^{c}	15.94^{c}	18.94^{bc}	20.34	90.67	95.20^{ab}	93.88
$W_1 \times V_2 \times N_1$	0.67^{h}	1.00	5.50^{ef}	17.22	11.92^{ef}	12.12^{ef}	15.65^{f}	14.97	90.49	88.98^{c}	88.13
$W_1 \times V_2 \times N_2$	1.50^{b}	1.92	18.99^{b}	39.21	24.65^{a}	24.98^{a}	27.37^{a}	27.41	90.72	95.15^{ab}	93.31
$W_1 \times V_2 \times N_3$	0.95^{f}	1.56	14.75^{c}	27.95	24.11^{a}	24.38^{a}	16.94^{de}	19.73	90.69	93.80^{ab}	92.12
$W_2 \times V_1 \times N_1$	1.06^{e}	1.69	9.24^{d}	23.45	6.45^{h}	7.06^{g}	12.62^{g}	6.69	89.28	83.12^{de}	70.19
$W_2 \times V_1 \times N_2$	2.00^{a}	2.29	13.33^{c}	53.14	11.76^{ef}	12.65^{ef}	19.87^{b}	13.08	89.53	90.76^{bc}	82.04
$W_2 \times V_1 \times N_3$	1.33^{c}	1.98	10.00^{d}	30.87	11.39^{f}	11.86^{f}	15.84^{ef}	11.74	89.42	83.66^{de}	76.23
$W_2 \times V_2 \times N_1$	0.85^{g}	1.05	4.57^{f}	10.55	7.54^{g}	7.42^{g}	8.33^{h}	5.46	88.51	72.84^{f}	59.35
$W_2 \times V_2 \times N_2$	1.17^{d}	1.90	7.57^{de}	24.45	14.69^{c}	14.93^{cd}	15.20^{f}	12.14	89.22	82.28^{de}	73.71
$W_2 \times V_2 \times N_3$	1.06^{e}	1.45	6.16^{ef}	14.89	13.01^{d}	14.73^{cd}	15.71^{f}	11.65	89.11	80.72^{e}	72.68
F–test	**	NS	*	NS	**	**	**	NS	NS	*	NS

W_1 = Well-watered; W_2 = Water-stressed; V_1 = Pioneer 30B80; V_2 = Suwan 4452; N_1, N_2 and N_3 = 0, 160 and 320 kg.ha-1 of N, respectively; RDMbs = Root dry matter before water stress; RDMas = Root dry matter after water stress; CGRv = Crop growth rate during vegetative stage; CGRf = Crop growth rate during bracketing flowering period; SWC = Silk water content; KS = Kernel setting.

Means within a column with the same or no letters are not significant at $P < 0.05$ based on the least significant difference test; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$; NS = Not significant.

advantages by increasing the silk exposure to shedding pollen, and this could enhance kernel setting under protandry conditions (Anderson *et al.*, 2004). On the other hand, Borras *et al.* (2007) also agreed that under conditions that inhibit plant growth, female flower development is delayed relative to that of the male flowers resulting in an increase in the ASI. However, it was evident that both anthesis and silking were accelerated by CGR and the relationship between CGR_f and the days to 50% anthesis or silking was negative and highly significant (Figures 4a and 4b).

Silk water content

The silk water content is very important for emergence from the ear husk but emergence occurred during the water stress period in 2012. As a result, the SWC was significantly decreased (1.62%) due to water stress averaged across variety and nitrogen levels (Table 1). This might have been caused by a loss of silk receptivity (Bassetti and Westgate, 1993). Though variety, nitrogen levels and all other interactions were not significant on SWC, N stress under water-stressed conditions reduced the SWC noticeably (Table 4). Silk is very sensitive to the water content among the plant parts of maize and it contains a higher ratio of water than any other part (Abendroth, 2005) especially during the silk emergence period (90.65%).

Silk growth rate

The initial SGR was always higher in Pioneer 30B80 than in Suwan 4452 during 2011 and 2012 (Figures 3a, 3b, 3c and 3d) and this might have been due to the greater water and nutrient uptake through more roots as well as the

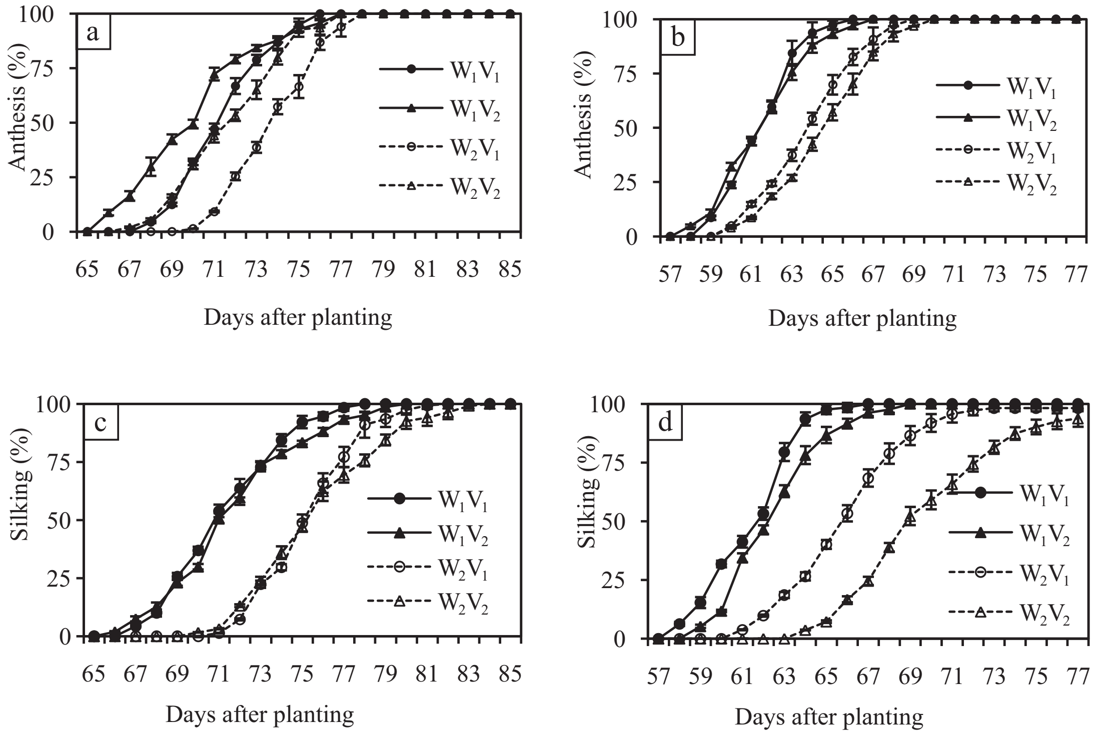

Figure 1 Dynamics of Pioneer 30B80 (V_1) and Suwan 4452 (V_2) maize varieties under well-watered (W_1) and water-stressed (W_2) conditions under short pre-anthesis drought (SPD) 2011 and prolonged bracketing-flowering stage drought (PBD) 2012 for: (a)Anthesis, SPD, 2011; (b) Anthesis, PBD 2012; (c)Silking, SPD, 2011; (d) Silking, PBD, 2012. (Vertical error bars = ± SD.)

varietal characters. In general, maximum SGR was observed 1 d after first silking (DAFS), then it decreased gradually at 2 DAFS and sharply at 3 DAFS (in accord with Kapu and Cosgrove, 2010), and thereafter the SGR was negligible (in accord with Anderson *et al.*, 2004) except under the water stress conditions during 2012 (Figure 3b).

Initially and up to 2 DAFS, the SGR was higher in Pioneer 30B80 under well-watered conditions than in Suwan 4452, and at 3 DAFS it was almost the same (Figures 3a and 3b). Nonetheless, the SGR was higher after 1 DAFS in both varieties and thereafter it decreased under water stress conditions during 2011 whereas a decreasing trend was observed from 1 DAFS onward during 2012 (Figures 3a and 3b). In fact, this was due to the recovery of plants after the pre-anthesis water stress period during 2011 while the plants had been suffering from continuous water stress under prolonged drought during 2012. The SGR was lower in Suwan 4452 especially, under prolonged drought (in accord with Westgate and Boyer, 1986) during 2012 (Figures 3a and 3b). Overall, the silk growth rate became slower chronologically after 2 or 3 DAFS and its sudden drop might have been after pollination (Carcova *et al.*, 2003) (Figure 3). Here, it was also found that water stressed plant silk still continued its growth (Westgate and Boyer, 1986) as shown in Figures 3a and 3b, especially for Suwan 4452 even after 6 DAFS (Figure 3b). It seemed that there might have been poor pollination due to the greater difference between anthesis and silking (Westgate and Boyer, 1985). The SGR almost ceased after seven DAFS in all treatments, perhaps due to ovary fertilization or silk senescence. In the case of high

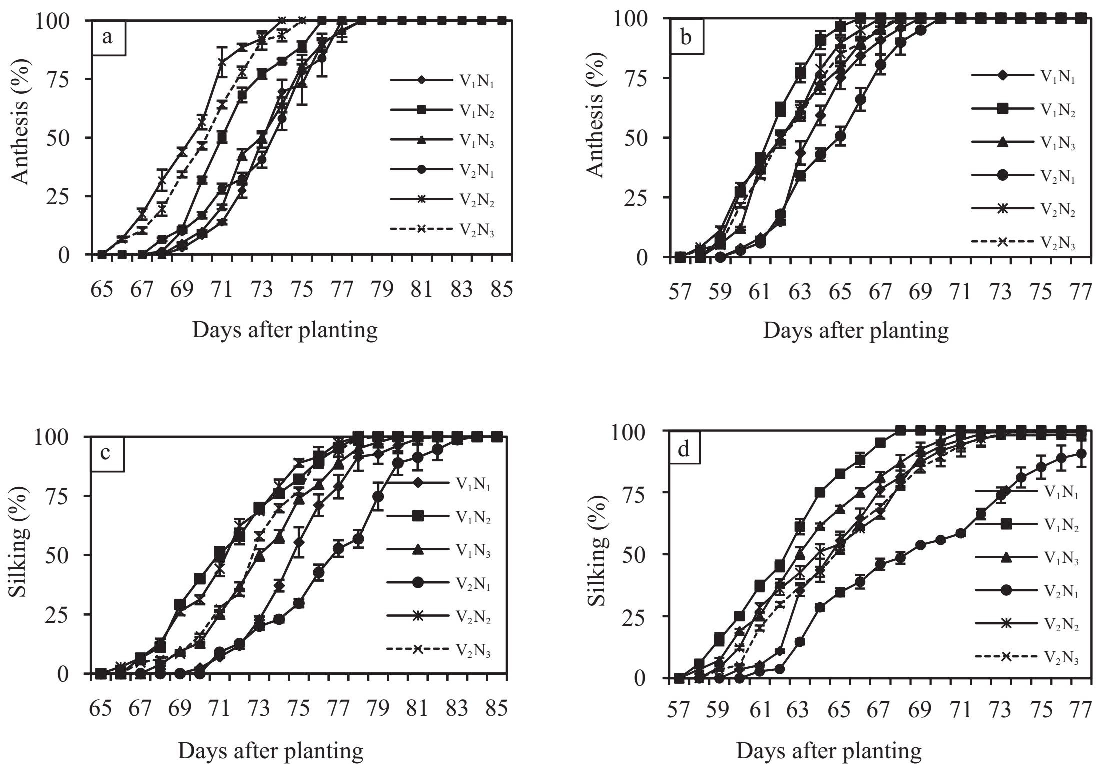

Figure 2 Dynamics of Pioneer 30B80 (V_1) and Suwan 4452 (V_2) maize varieties under 0 (N_1), 160 (N_2) and 320 (N_3) kg.ha^{-1} of N, respectively, during 2011 and 2012 for (a) Anthesis, short pre-anthesis drought (SPD), 2011; (b) Anthesis, prolonged bracketing-flowering stage drought (PBD) 2012; (c)Silking, SPD, 2011; (d) Silking, PBD, 2012. (Vertical error bars = ± SD.).

ASI, the pollen source for pollination might have been the plants of the same treatments, which had a later anthesis stage. Silk elongated very slowly before ceasing growth; this could have been due to slow pollen tube formation or slow movement of the pollen towards the ovary or a failure to fertilize. The highest initial SGR was found in Pioneer 30B80 with optimal N during both years whereas Suwan 4452 with zero N produced the lowest (Figures 3c and 3d). Both the varieties performed better under optimal N conditions than under the supra-optimal or zero N levels. Optimal N enhanced PGR (Table 1) which might also have accelerated SGR. The zero N condition delayed silking, which might have caused a broad ASI and less pollination, and as a result it was found that silk growth continued for longer than with other N levels, especially in Suwan 4452 (Figure 3d). Silk growth depends on cell elongation and cell differentiation, which is accelerated by proper nitrogen nutrition (Burkholder and McVeigh, 1940). A positive turgor, which depends on water availability, is a requisite for cell extension and growth under water stress conditions (Cosgrove, 1981) and it was found that the silk of the Pioneer 30B80 variety could retain relatively more water. For the above reasons, the silk growth rate might have been higher in Pioneer 30B80, especially under optimal N and water conditions.

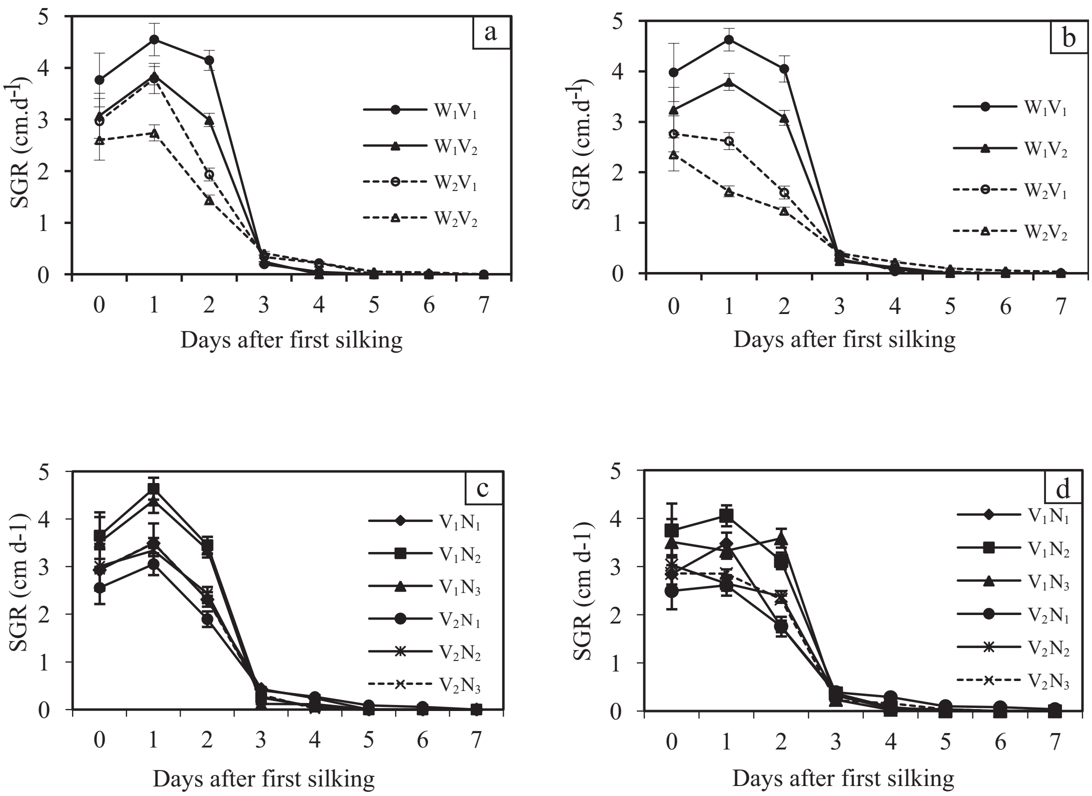

Figure 3 Silk growth rate (SGR) of Pioneer 30B80 (V_1) and Suwan 4452 (V_2) maize varieties under well-watered (W_1) and water-stressed (W_2) conditions across nitrogen levels: (a) Short pre-anthesis drought (SPD) 2011; (b) Prolonged bracketing-flowering stage drought (PBD) 2012; and under 0 (N_1), 160 (N_2) and 320 (N_3) kg. ha^{-1} of N across the water levels: (c) SPD 2011; (d) PBD 2012. (Vertical error bars = ± SD.)

Kernel setting

The highest and significant kernel setting was observed in Pioneer 30B80 with the interactions of water and N levels in both years (Tables 1, 2, 3 and 4). Optimal N and well-watered conditions enhanced kernel setting in both varieties (Table 4) and this might have had a subsequent effect on the synchronization of anthesis and silking (Banziger *et al.*, 2002), which was accelerated by a greater CGR_f (Uhart and Andrade, 1995) as shown in Figure 4. Kernel setting was reduced 9.35% more due to PBD in 2012 than by SPD in 2011 (Table 1) where Suwan 4452 reduced 5.78 and 6.36% more under SPD and PBD, respectively, than Pioneer 30B80 compared with the control (Table 2). The N level also significantly affected KS (Table 1) as also noted by Uhart and Andrade (1995) and the two maize varieties responded differently to N application (Table 3). Pioneer 30B80 reduced its KS by 5.81 and 4.28% in 2011 and by 8.62 and 3.80% in 2012 due to zero and supra-optimal N whereas Suwan 4452 reduced by 8.80 and 1.65% in 2011 and by 11.70 and 1.33% in 2012 due to zero and supra-optimal N compared to optimal N. Thus, it was found that likewise for RDM and CGR_f, Suwan 4452 was more susceptible to zero N and Pioneer 30B80 was more sensitive to supra-optimal N regarding KS. The KS was severely reduced in Suwan 4452 due to the combined stress of water and N (Table 5), while the ASI was more than 6 d. The reduction of KS might have been due to the greater ASI or the lower SWC (Westgate and Boyer, 1986). Kernel setting depends on the initial ovule setting and finally on successful pollination and fertilization of the ovary. The higher ovule setting in Pioneer 30B80 with the optimal N might have been due to the higher CGR_f (Uhart and Andrade, 1995). Bassetti and Westgate (1993) reported that successful fertilization depends on several conditions, such as, the pollen availability, ASI, silk receptivity, silk water content, capability of pollen tube formation, distance to the ovary, speed of the pollen toward the ovary and sufficient assimilate supply to the kernel just after fertilization (Westgate and Boyer, 1986). The above characteristics were mostly favored by optimal N and water, which resulted in greater kernel setting in both the varieties where Pioneer 30B80 showed better performance which perhaps could be due also to its higher RDM, CGR_f,SWC and short ASI. However, a negative and significant linear relationship was found between KS and ASI during 2011 and 2012 (Figure 5b).

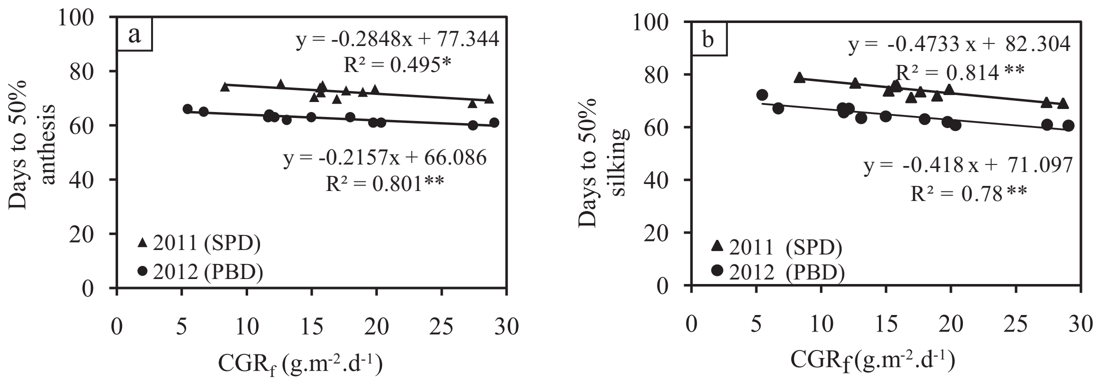

Figure 4 Linear regressions of: (a) Days to 50% anthesis; (b) Silking on crop growth rate at bracketing flowering (CGR_f) during 2011 and 2012 (SPD = short pre-anthesis drought; PBD = prolonged bracketing-flowering stage drought; R^2 = Correlation coefficient; ** = Significant at P = 0.01.).

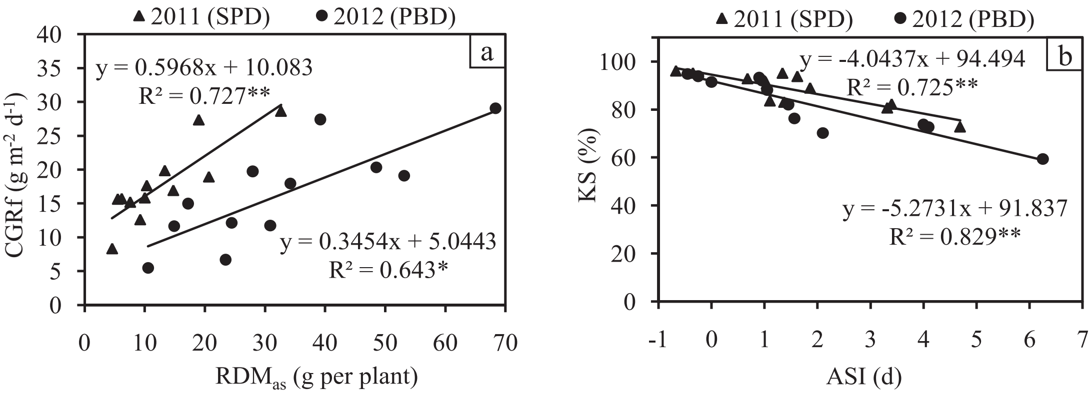

Figure 5 Linear regressions during 2011 and 2012 of: (a) Crop growth rate during bracketing flowering period (CGR_f) on root dry matter after water stress (RDM_{as}); (b) Kernel setting (KS) on anthesis-silking interval (ASI). (SPD = short pre-anthesis drought; PBD = prolonged bracketing-flowering stage drought; R^2 = Correlation coefficient; * = Significant at $P = 0.05$; ** = Significant at $P = 0.01$.)

CONCLUSION

The anthesis and silking dynamics of maize were affected by the crop growth pattern with environmental and genotypic differences. The results of this study also demonstrated the interactions of water, N and variety on the growth, development, flowering and kernel setting of maize. Water and N inputs must be closely matched, so that efficient utilization of each input can be achieved. For a maize crop to benefit from soil N, there must be sufficient water available. Low and supra-optimal N and also water stress significantly reduced plant performance. Prolonged water stress exhibited increased detrimental effects on all growth and kernel setting parameters in different developmental stages. The results suggest that proper root establishment in the soil during the early vegetative stage before the onset of drought is an important characteristic of a variety to overcome the stress period and optimal N application could accelerate root growth. Besides the environmental pollution, supra optimal nitrogen is detrimental for root production and subsequently for plant growth and kernel setting. Proper plant and silk growth during the bracketing flowering stage, sufficient silk water content and synchronization of anthesis and silking could enhance the kernel setting, which is a major determinant of grain yield. Therefore, breeders can use the above mentioned traits for further development of improved maize variety to increase production under environmental stress.

ACKNOWLEDGEMENTS

This work was supported by the National Agricultural Technology Project (NATP), Phase-1, Bangladesh Agricultural Research Council (BARC) and was conducted in the National Corn and Sorghum Research Center (NCSRC), Thailand with the collaboration of the Faculty of Agriculture, Kasetsart University, Bangkok, Thailand.

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