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Dissecting heat stress tolerance in tropical maize (*Zea mays* L.)

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ABSTRACT

The negative effects of heat stress on maize growth and reproduction is often expressed in terms of significant yield penalty. Germplasm selection based on yield potential along with heat stress adaptive secondary traits, and establishing their interaction under stress helps in identifying suitable heat tolerant genotypes. To dissect intricate nature of heat stress tolerance, two field trials were conducted during spring 2014 and 2015 under natural heat stress conditions. Planting was adjusted to expose reproductive and grain filling period to high temperature regimes during May month in Hyderabad, India. Correlation analysis between grain yield under stress and secondary traits observed in two year experiments indicated that the traits such as - leaf firing (LF) ($r = -0.34^{**}$ and 0.06), tassel blast (TB) ($r = -0.18$ and -0.25), tassel sterility (TS) ($r = -0.08$ and -0.38^{*}), anthesis-silking interval (ASI) ($r = -0.24^{*}$ and -0.02) and senescence (SEN) ($r = -0.27^{**}$ and -0.34^{*}) were negatively correlated, while pollen shedding duration (PSD) ($r = 0.33^{**}$ and 0.4^{*}), seed set percentage (SSP_OP) ($r = 0.76^{**}$ and 0.58^{**}) and chlorophyll content (CHL) ($r = 0.55^{**}$ and 0.41^{*}) were positively associated with grain yield under stress in 2014 and 2015, respectively. An ASI of 2–4 days and PSD of 2–4 days were found advantageous to grain yield under heat stress. Stigma receptivity was less affected under heat stress when compared to pollen viability, yet stigma initiation was delayed under heat stress, which resulted in prolonged ASI. Overall effect of heat stress was expressed in terms of SSP_OP, which explained yield variation by 78.5 and 57.8% for experiment 1 and 2, respectively. Thus, traits that are indicative of reproductive success under heat stress (ASI, TB, TS, pollen viability, stigma receptivity and SSP_OP) and other morpho-physiological traits (LF, SEN and CHL) may be used along with grain yield in index selection of suitable germplasm for heat stress tolerance.

1. Introduction

Impact of climate change on agricultural production will be greatest in the tropics and subtropics, with South Asia projected to be particularly vulnerable from multiple stresses and low adaptive capacity (Rodell et al., 2009; Niyogi et al., 2010). Many climate modeling studies suggested that high day- and night-time temperatures will become more common in the future and may represent a tremendous environmental hurdle to global food production (Lobell et al., 2011b; Cairns et al., 2012). Maize is particularly vulnerable to the reproductive stage heat stress (Cairns et al., 2012). A recent study showed that each degree day spent above 30 °C reduced the final yield of maize by 1% under favorable growing conditions and 1.7% under drought stressed environments (Lobell et al., 2011a). Most of the tropical maize growing areas in South Asia are highly vulnerable to drought and high temperature stress. Spring maize is an important option for intensifying and diversifying cropping systems in South Asia, especially in the upper and middle Indo-Gangetic plains, but is prone to severe heat stress during flowering/early grain filling stages (Prasanna, 2011).

Most of heat stress research has been conducted on temperate maize germplasm for high production, but there is no extensive breeding efforts, especially for heat stress in tropical and

Abbreviations: AD, days to anthesis; ASI, anthesis-silking interval; CHL, chlorophyll content; CIMMYT, international maize and wheat improvement center; GY, grain yield; ICRISAT, International crops research institute for the semi-arid tropics; LF, leaf firing; MTS, membrane thermo-stability; PGM, pollen (morning collected) germination percentage; PSD, pollen shedding duration; SD, days to silking; SEN, senescence; SSP, seed set percentage; SSP_OP, seed set percentage under open pollinated condition; TB, tassel blast; TS, tassel sterility.

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subtropical maize (Cairns et al., 2012). Systematic efforts to develop maize cultivars with high temperature tolerance have only recently been initiated. Initial experiments undertaken by the CIMMYT-Asia team to identify heat stress tolerant tropical maize lines among the elite, drought tolerant (DT) maize germplasm developed in Mexico, Asia and Africa revealed: (a) high vulnerability of most of the tropical maize germplasm, including commercial cultivars in South Asia, to reproductive stage heat stress; and (b) poor correlation between drought and heat tolerance, indicating that physiological mechanisms that contribute to heat stress tolerance in maize may be different from those that contribute to drought tolerance (Zaidi and Cairns, 2011; Cairns et al., 2012).

Among various growth stages, reproductive stages, including flowering and early grain filling, are the most vulnerable stages of maize for heat stress (Schoper et al., 1987a,b; Dass et al., 2010). During tassel initiation to tassel emergence, high temperature causes delay in silking more than Anthesis (Cicchino et al., 2010), damaged tassels, pollen dessication and silk death (Pingali, 2001), which resulted in de-synchronization and reduced fertilization. Poor pollen production ultimately lead to male sterile plants in field. The location of the tassel on top of the plant also provides maximum exposure to extreme temperatures, increasing the probability of pollen damage as a result of heat stress (Cairns et al., 2012). Heat stress not only affects pollen viability after dehiscence, but also during its growth and development before dehiscence (Herrero and Johnson, 1980; Schoper et al., 1987a; Schoper et al., 1987b; Dupuis and Dumas, 1990).

Genetic improvement for any abiotic stress through direct selection for grain yield will be less efficient as its heritability is low under stress condition (Edmeades et al., 1993). Also, the correlation between grain yield under stress and non-stress condition are inconsistent with increase in intensity of stress (Banzigar and Lafitte, 1997; Ribaut et al., 2007). The alternate and effective approach is indirect selection through secondary traits with high heritability and significant association with grain yield under stress (Edmeades et al., 1993; Bänziger et al., 2000; Betrán et al., 2003). With this view the present study is an attempt to understand the key reproductive and other secondary traits associated with heat stress tolerance in tropical maize that could be used for effective selection in heat stress breeding program.

2. Material and methods

2.1. Germplasm

Seventy-five diverse tropical maize inbred lines from CIMMYT -Asia maize program were evaluated under natural heat stress during summer season of 2014 (Experiment 1). In 2015 (Experiment 2), based on pollen viability and stigma receptivity of 75 entries in experiment 1, a sub-set of 15 entries: 8 entries with high or moderated pollen viability, stigma receptivity and 7 entries with either low in pollen viability and/or stigma receptivity were selected for evaluation. Details of inbred lines used in the study is given in Supplementary Table S1.

2.2. Experimental site, cultural practices and stress management

Experiments were conducted at the Asia Maize Program, CIMMYT located in the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) campus, Hyderabad, India (17.3850°N, 78.4867°E, 545 masl). Soil of the experimental station is characterized as vertisol, 1.3–1.8 m in depth with a pH of 7.6. The 2014 trial was laid-out in α-lattice design with two replications. Each plot had two rows with a row length of 3.0 m. Row-to-row and plant-to-plant spacing were 75.0 cm and 20.0 cm, respectively. Two elite maize hybrids (designated as, Hybrid-1 and Hybrids-2) with similar flowering time to test entries were planted in glass-house under optimal conditions throughout growing period. Planting of both elite hybrids in glass-house and test-entries in field was done on same day, so that both reaches to flowering stage at almost same time. Planting of hybrids was done in pots placed outside the glass house and shifted in-side about two weeks before tassel emergence, so that their whole reproductive phase is maintained under optimal temperature and other growing conditions. Number of plants for both hybrids in green-house was five times to the number of test entry plots in field for heat stress phenotyping. Before flowering five plants in each hybrid were labeled as female (silk under optimal condition) for each test entry in the field. These labeled plants were pollinated with pollen exposed to heat stress under field condition from their respective test entries. Out of two rows plot of test entry in field, one row was maintained as open pollinated and other row was used as heat stressed silk source to receive the pollen from hybrids in glass house under optimal condition. Pollen collected from both the hybrids were separately transferred to the field and were used to pollinate the test entry plants at proper silk emergence stage. Manual pollination was carried out with care to prevent any contamination, and after the pollination, silks were covered with paper bag to insure that no silk is exposed for pollination. Similarly, heat stressed pollens from individual test entries in field were used to pollinate five plants each in the two hybrids grown in glass-house under optimal conditions. Pollination in both the conditions was done during high temperature time of the day (between 11.00a.m. to 1.00p.m.).

In summer 2015, trial of the selected 15 entries from previous year was laid-out in α-lattice design with three replications. Each plot was planted in single 4.0 m long row with plant-to-plant and row-to-row spacing 75.0 cm and 20.0 cm, respectively. The trial was kept for open pollination

In both the years planting of the experiment was taken-up during 3rd week of March (15th and 17th March, respectively) so that whole reproductive stage (from tassel emergence to early grain-filling stage) is fully exposed to high temperature regime during last week of April to mid-May (Supplementary Fig. S3). All the entries in field experiment were over-sown and thinned to one plant per hill at V_2 growth stage. Before planting 60 kg nitrogen (N) ha^{-1} in the form of urea, 60 kg phosphorous ha^{-1} as single super phosphate, 40 kg potassium ha^{-1} as muriate of potash and 10 kg zinc as zinc sulfate were applied as a basal dressing. Second and third doses of N (each 30 kg N ha^{-1}) were side-dressed at knee-high and tassel emergence stages. Nutrient application in pot culture was done at the same rate and applied on soil weight basis. Pre-emergence application of pendimethalin and atrazine (both at 0.75 kg ha^{-1} a.i., tank mixed) were used for weed management in the experimental plots. The summer season at the experimental site was largely rain-free with few light showers in the month of March and April, however, most part of May month was largely dry (Supplementary Fig. S3). Experiments were maintained at optimal moisture by scheduling weekly irrigation in order to avoid any drought stress. Experiments were kept free from insect, weeds and diseases using recommended post-emergence chemical measures, and managed under optimal agronomic practices.

2.3. Observations

Data on various morpho-physiological traits were recorded using standard protocol for heat stress phenotyping (Zaidi et al., 2016). Days from planting to anthesis (AD) or silking (SD), was recorded when 50% plants had extruded anther or produced silks, by daily visual observations during the flowering period. ASI was calculated as difference between number of days to 50% silking and 50% anthesis. Once days to 50% anthesis in a plot are noted,