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Heat stress in temperate and tropical maize hybrids: Kernel growth, water relations and assimilate availability for grain filling

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ABSTRACT

Several studies have indicated that maize (*Zea mays* L.) kernel weight is severely affected by heat stress, but this response was never evaluated under field conditions. Our objective was to assess the effect of brief episodes of above-optimum temperatures on the dynamics of biomass and water accumulation in kernels of maize hybrids with contrasting tolerance to heat stress. Heat effect on assimilate supply from the plant (i.e., current biomass production and water-soluble carbohydrates in stem) to developing grains was also analyzed. Field experiments included a factorial combination of (i) three hybrids (Te: temperate; Tr: tropical; TeTr: Te × Tr), (ii) two temperature regimes, control and heated during daytime hours (ca. 33–40°C at ear level), and (ii) three 15-d periods (GS1: immediately before anthesis; GS2: from silking onwards; GS3: early phase of active grain filling). Heat effects on final kernel weight were larger (i) when they occurred during the first half of effective grain filling (−23.1% for GS3) than around flowering (−4.8% for GS1, −6.3% for GS2), and (ii) for the Te hybrid (−20.4%) than for the TeTr (−8.6%) and the Tr (−6.8%) hybrids. Heating around flowering (i) enhanced the assimilate availability per kernel during the effective grain-filling period, (ii) increased carbohydrates reserves in stem at physiological maturity, (iii) and had no significant effect on the dynamics of biomass and water accumulation in kernels. The opposite trend was detected among plots heated during GS3, which mostly exhibited the interruption of grain filling. Robust associations were established between (i) carbohydrate reserves in stem at physiological maturity and assimilate availability per kernel during effective grain filling ($r^2 = 0.49$; $P < 0.001$), and (ii) the rate of water loss from kernels and the duration of effective grain filling ($r^2 = 0.71$; $P < 0.001$). These responses underlay the enhanced sensitivity to heat stress of the hybrid with full temperate genetic background.

1. Introduction

Heat stress reduces maize (*Zea mays* L.) grain yield due to its negative effect on plant growth (Cicchino et al., 2010b) and development (Cicchino et al., 2010a). The magnitude of yield responses to above-optimum temperatures depends upon a complex function of intensity, duration, and rate of increase in temperature (Wahid et al., 2007). Further, plants sensitivity varies along the crop cycle and differs among genotypes according to their thermotolerance level (Rattalino Edreira and Otegui, 2012). Few studies have examined the effect of heat stress on maize grain yield under field conditions. Most of them focused on the physiological determinants of grain yield (Cicchino et al., 2010b; Rattalino Edreira and Otegui, 2012) and kernel number (Rattalino Edreira et al., 2011; Rattalino Edreira and Otegui, 2013), but not on those of kernel growth. The effects of above-optimum temperatures on maize kernel growth have been studied using *in vitro* cultures of grains (Commuri and Jones, 1999; Commuri and Jones, 2001; Cheikh and Jones, 1994; Jones et al., 1984; Singletary et al., 1994), isolated plant grown in controlled-environments (Badu-Apraku et al., 1983; Wilhelm et al., 1999), or ears subject to temperature manipulations (Commuri and Jones, 2001). These studies provided information about the effect of heating on kernel ultrastructure and on metabolic processes involved in endosperm cell division and starch deposition. However, results cannot be directly extrapolated to field conditions

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Abbreviations: D_{EGF}, duration of effective grain filling; Exp_n, experiment n; GS_n, growth stage n; H, hybrid; KGR_{EGF}, kernel growth rate during effective grain filling; SSR_{CP}, source-sink ratio during the critical period for kernel set; SSR_{EGF}, source-sink ratio during effective grain filling; T_C, non-heated control plot; Te, temperate hybrid; TeTr, temperate × tropical hybrid; T_H, heated plot; Tr, tropical hybrid; TR, temperature regime; WSC, water-soluble carbohydrates.

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for two main reasons. First, most heating treatments did not reproduce the daily variations in air temperature, as they usually consisted of periodic exposures to constant temperatures of variable duration. Second, the above-mentioned studies evaluated kernel growth without considering the possible effects of heating on assimilate supply from the plant to developing grains (i.e., heat effects on the source as well as on the sink).

Under non-limiting water and nutritional conditions, kernel weight is more strongly associated with the rate of kernel growth than with the duration of grain filling (Borrás and Otegui, 2001), and kernel growth rate is positively correlated with the establishment of kernel sink capacity (i.e., number of endosperm cells and amyloplasts) during the first stages of kernel growth known as *lag* phase (Capitanio et al., 1983; Reddy and Daynard, 1983). This capacity is recognized as the potential kernel weight and depends upon assimilate availability per kernel (i.e., source-sink ratio) during this phase (Lemcoff and Loomis, 1994). Plant growth rate per kernel during the critical period for kernel set (ca. 30 d around silking; Fischer and Palmer, 1984; Grant et al., 1989; Kiniry and Ritchie, 1985) has been considered a good estimator of such source-sink ratio, which is highly correlated with both kernel growth rate and potential kernel weight (Gambín et al., 2006). This conceptual framework allow us to speculate that the occurrence of a heat stress event around flowering that promotes a larger decrease in kernel set than in plant growth rate (i.e., increased source-sink ratio) may enhance the potential kernel weight. However, negative effects of heating on endosperm cell division and amyloplast biogenesis (Commuri and Jones, 1999; Denyer et al., 1994; Engelen-Eigles et al., 2001; Jones et al., 1985; Singletary et al., 1994) may limit the determination of potential kernel weight independently of assimilate availability. This suggests the existence of a trade-off between indirect and direct effects of the stress (i.e., mediated or not by assimilate availability, respectively).

Final kernel weight is also affected by growing conditions during the effective grain-filling period (Borrás and Otegui, 2001; Cirilo and Andrade, 1996). Under non-limiting conditions, the source of assimilates is usually abundant enough to cope with kernel demand, and final kernel weight do not increase much in response to enhanced assimilate availability per kernel (Borrás et al., 2004; Gambín et al., 2008). By contrast, kernel growth is highly susceptible to source limitations during this phase (Borrás et al., 2004), which reduce kernel weight by shortening of grain filling (Badu-Apraku et al., 1983; Echarte et al., 2006; NeSmith and Ritchie, 1992; Ouattar et al., 1987a; Westgate, 1994). In this situation, grain filling can be partially sustained by carbohydrate reserves in the stem (Andrade and Ferreiro, 1996; Jones and Simmons, 1983; Uhart and Andrade, 1995), which are recognized as one of the most important traits conferring tolerance to abiotic stresses (Blum, 1998; Slewinski, 2012), including heat stress (Blum et al., 1994; Tahir and Nakata, 2005; Yang et al., 2002). The contribution of this source of carbon to maize grain filling has been evaluated in a recent study on heat stress in temperate and tropical hybrids (Rattalino Edreira and Otegui, 2012). In that research, the temperate hybrid was the most sensitive to heating during effective grain filling, and its low tolerance to heating was not related to a reduced use of reserves. However, this trait was estimated as the difference between grain yield and crop biomass increase during effective grain filling, which might not reflect the actual contribution of carbohydrate reserves to biomass accumulation in the grain during the crop cycle.

The study of kernel water relations is an alternative way for assessing kernel growth dynamics. In maize, for example, some associations have been reported between (i) maximum kernel water content and kernel growth rate during effective grain filling (Borrás et al., 2003), (ii) rate of water loss from the kernel after reaching its maximum water content and duration of grain filling (Gambín et al., 2007), and (iii) kernel moisture concentration and the onset of physiological maturity, which commonly ranges between 300 and 350 mg H_2O g fw^{-1} (Westgate and Boyer, 1986). These relationships have been established for a wide range of genotypes (Gambín et al., 2007) and environmental conditions (Borrás et al., 2003; Sala et al., 2007b), which indicates that dry matter accumulation and water content in kernels are closely coordinated during grain filling (Schnyder and Baum, 1992). Nevertheless, source reductions during effective grain filling cause the arrest of biomass allocation to kernels and a premature decline in their water status, a condition that uncouples water from dry matter dynamics in kernels (Sala et al., 2007b). Similar responses may be expected for maize subjected to heat stress during effective grain filling due to its severe effect on plant growth (Rattalino Edreira and Otegui, 2012), but the actual impact is unknown.

The aim of the current paper was to assess the effect of brief episodes of above-optimum temperatures (e.g., less than 4 h of temperatures above 35 °C per day) during the critical period for kernel set or the first half of effective grain filling on the dynamics of biomass and water accumulation in kernels of three maize hybrids of different genetic background (temperate, tropical and temperate × tropical) grown under field conditions.

2. Materials and methods

2.1. Crop husbandry and treatments description

Field experiments were conducted during 2008–2009 (Exp_1) and 2009–2010 (Exp_2) at the experimental field of the University of Buenos Aires, Argentina (34°25'S, 58°25'W) on a silty clay loam soil (Vertic Argiudoll; USDA soil survey system). Treatments included a factorial combination of (i) three F1 hybrids (H) of contrasting genetic background (Te: temperate, Tr: tropical, and TeTr: temperate × tropical), (ii) two temperature regimes (TR) applied during daytime hours (T_C: control with no heating, T_H: heated ca. 33–40 °C at ear level), and (iii) three different growth stages (GS). Hybrids were 2M545HX (Te), 2B710HX (Tr), and 2A120HX (TeTr), all currently produced by Dow Agrosciences Argentina for different regions of this country (Rattalino Edreira et al., 2011). The relative maturities of tested hybrids were 124 for Te, 136 for Tr, and 128 for TeTr hybrids. In both experiments, a single stand density of nine plants m^{-2} was used. Crops were fertilized with urea at a rate of 200 kg N ha^{-1} at V_6 (Ritchie and Hanway, 1982). Water availability of the uppermost 1 m of the soil profile was kept near field capacity throughout the growing season by means of drip irrigation. Weeds, diseases and insects were adequately controlled. More details about crop husbandry can be found in Rattalino Edreira et al. (2011).

Treatments were distributed in a split split-plot design, with growth stages, hybrids and temperature regimes in the main plot, subplot and sub-subplot (hereafter termed plots), respectively. Three replicates were always used. Main plots were 10 m length, with six rows separated at 0.5 m between rows. Temperature regime shelters covered an area of 6 m^2 of the four central rows of main plots. These treatment areas were enclosed with transparent polyethylene film (100 μm thickness) mounted on 3.6-m high wood structures (Cicchino et al., 2010a). For T_C shelters, the lateral films were opened up to 1.4 m above soil surface. This was done to avoid differences in incident radiation due to the polyethylene film. For T_H shelters, the film reached the soil surface on all sides, except one side that had a 10 cm opening at the bottom. Additionally, roofs of all shelters were pierced (hole size: 0.3 cm^2; holes density: 50 holes m^{-2}) to avoid excessive heating in the upper part of the canopy and to allow gas exchange. Heating depended mainly on temperature rise promoted by the greenhouse effect of the polyethylene enclosure (Cicchino