



Yield response to heat stress as affected by nitrogen availability in maize



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ABSTRACT

Maize yield has to be increased in the next decades in order to satisfy world demand. This increase has to be achieved in a scenario of climate change particularly characterised by heat stress. Several agronomic and genetic strategies for increased tolerance to high temperatures will be necessary. Some results in other crops showed interactions between high temperature stress and nitrogen (N) availability. To the best of our knowledge, this interaction has not been tested in maize. Therefore, the aim of this study was to explore, under field conditions, whether the magnitude of yield penalty imposed by elevated canopy air temperature around flowering or during early grain filling is affected by N availability. In particular we aimed to (i) quantify the magnitude of yield losses by heat stress around flowering and during early grain filling, (ii) determine whether N fertilisation affects these magnitudes, and (iii) identify whether the effects are indirect (through affecting growth) or directly on the grain set and/or grain growth capacity. Four field experiments were carried out during four consecutive years in NE Spain. The treatments consisted in a factorial combination of one or two hybrids, two or three levels of N fertilisation and three temperature conditions. The temperature treatments consisted of a control (plots grown under natural temperature throughout the growing season) and two treatments in which the temperatures of the canopy were increased in the field for relatively short periods. All experiments were well watered to avoid water stress.

The elevated canopy air temperature treatment only increased the maximum temperature in a relatively small magnitude (mean daily temperature was increased at the ears height by c. 1 °C each day of treatment). However, yield penalty imposed by heat stress was in general very noticeable and dramatic when the treatment included the critical period for grain number determination, around silking. The damage was much stronger in the long- than in the short-cycle hybrid. Exposing the plants to elevated canopy air temperature during the critical period reduced harvest index, from values of around 46% in unheated conditions to 20% under elevated canopy air temperature, being the reduction higher under N200 than under N0 fertilisation treatments.

As far as we are aware, we showed for the first time in maize grown in field conditions, that the losses in yield in response to elevated canopy air temperature treatment were magnified by the N availability. The effect of N on emphasising the penalties seemed not to be a direct effect of this nutrient but an indirect effect through affecting growth. The effect was through affecting the capacity of the plants to set grains and to a lesser extent to allow grain weight to be maximised; and it was independent of any (potentially additional) effects on either uncoupling anthesis and silking or on pollen amount and viability.

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1. Introduction

Yield of cereals must increase dramatically in the next few decades. This need is based on predictions of population increase to some 10 billion people and on the simultaneous growth of individual demands. Maize demand would also increase noticeably due to the expected increase in its use in biofuel production towards 2050 (Fischer et al., 2014). These remarkable increases must be achieved in the context of a climate change which will imply that crops will

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be more frequently exposed not only to relatively higher temperatures but also to periods of heat stress (Battisti and Naylor, 2009; Lobell et al., 2011; Cairns et al., 2013).

Yield in maize is the consequence of the interaction between the number of grains and their average weight. Grain number is mainly determined during the critical period of 30 d bracketing silking (Vega et al., 2001; Andrade et al., 2002; Westgate et al., 2004) when the number of grains per plant is determined in line with the rate of growth of the crop during that period (Vega et al., 2001), because it is during this period when the juvenile ear, where the female florets are developing, grow (Otegui and Bonhomme, 1998) and then the abortion process affects a proportion of the pollinated florets. Grain weight potential is largely determined during the same period (Gambín et al., 2006) and formally realised during the “lag phase” (Maddoni et al., 1998); but final grain weight is realised during the effective period of grain filling (Cirilo and Andrade, 1996; Borrás and Otegui, 2001).

High-temperature effects on yield may affect either of the two components, depending on the timing of occurrence of the heat (Rattalino Edreira and Otegui, 2013). In principle, if the penalty imposed by the increased temperature operates, at least partly, through reductions in crop growth, yield would be more affected when the heat occurs during the grain number determination period (around silking) as grain number determination is clearly source-limited (Gambín et al., 2006; Slafer and Savin, 2006) whilst grain weight seems more limited by the sink strengths (Gambín et al., 2008), at least if severe defoliations or very low levels of incoming radiation do not occur during the effective period of grain filling (Borrás et al., 2004). The consequently higher responsiveness of grain number than grain weight to changes in resource availability (Slafer et al., 2014) explains why grain number is more plastic and grain weight more heritable (Sadras, 2007; Sadras and Slafer, 2012) and consequently yield is more related to grain number than to grain weight in most grain crops (Slafer et al., 2006), including maize (Otegui, 1995; Borrás et al., 2004). If the effects were not mediated by reducing crop growth, the magnitude of the penalty would be similar whether the stress occurs around silking or during the effective period of grain filling. It seems likely to hypothesise that high-temperature effects may be indirect, mediated by reducing growth (e.g. Cicchino et al., 2010b), though direct effects not mediated by reductions in growth are possible (Rattalino Edreira and Otegui, 2013). High temperature induce shortening of developmental phases, reduced light interception, increased respiration, reduced photosynthesis, and cause pollen sterility (e.g. Wahid et al., 2007; Barnabás et al., 2008; Cairns et al., 2013). It has been demonstrated that female tissues have greater tolerance while pollen production and/or viability is strongly sensitive to high temperatures. However, the sensitivity of the female reproductive tissues has also recently been highlighted as a critical (Cicchino et al., 2010b; Rattalino Edreira et al., 2011), as the damage produced by high temperatures on reproductive output remained when fresh pollen was used to pollinate ears of plants exposed to high temperatures around silking (Cicchino et al., 2010b).

A major inconvenience of studies aimed to uncover high-temperature effects on crop productivity is that, due to the difficulties in imposing the treatments under field conditions, they are most frequently conducted under controlled conditions. These controlled studies are extremely useful for understanding detailed mechanisms of action of particular factors at relatively low levels of organisation. The problem is that results can hardly be extrapolated to field conditions (Passioura, 2006), where the practical consequences are expected. Scaling up from controlled conditions experiments to application in realistic field conditions may present several constraints (Passioura, 2010).

Recently a number of studies were conducted in the experimental field of the Univ of Buenos Aires by the group of Prof. Otegui

enclosing for particular periods the maize canopy with transparent polyethylene film mounted wood structures build up a priori (Cicchino et al., 2010a; Rattalino Edreira et al., 2011). Normally the approach of studying this type of stresses in the field is that the errors increase noticeably compared with controlled conditions, but the increase in reliability on the extrapolation of conclusions makes them indispensable. A step forward in direction to increase the actual value of the conclusions to realistic system is to run such experiment in real farmer fields (instead than in a field experimental facility) and in interaction with very common management practices, such as nitrogen (N) fertilisation, a step we pursued in this study. This again increases the errors while increasing the dependability of conclusions.

Several agronomic and genetic strategies for increased tolerance to high temperatures will be necessary (Rosenzweig and Parry, 1994). The likelihood of mitigations through using plant growth regulators (Cicchino et al., 2013), or adequate management of magnesium (Mengutay et al., 2013) are being discussed. Around the world, food production increased linearly with the increment of N use in the agricultural systems (Tilman, 1999), and N fertilisation is likely one of the most common management practices implemented in maize production worldwide. High yields in maize are closely associated with N fertilisation (Setiyono et al., 2010), mainly through affecting grain number (Cárcova et al., 2000; Paponov et al., 2005) by modifying crop growth during the critical period around silking (Andrade et al., 2002; D’Andrea et al., 2008).

To the best of our knowledge, the interaction between heat stress and N availability has not been tested in maize. Both in wheat (Altenbach et al., 2003; Zahedi et al., 2004) and in barley (Passarella et al., 2008) it has been shown that the penalty on yield imposed by exposure to high temperatures were affected by the level of N availability: the higher the availability the more damaging the high-temperature effect (Altenbach et al., 2003; Zahedi et al., 2004; Passarella et al., 2008). Although the mechanisms involved are not understood, reporting evidences of this type of interaction would be relevant in practical terms. If a similar sort of interaction were also apparent in maize, it may have relevant practical implications as in the future, when maize would be more often exposed to heat stresses. In this scenario, decisions on rates of N fertilisation should be taken not only considering the potential beneficial effects on crop growth but also the potential trade off on the magnitude of the penalty produced by heat stresses.

The main objective in this study was to explore under field conditions of real farms whether the magnitude of yield penalty imposed by high temperature around flowering or during early grain filling is affected by N availability. In particular we aimed to (i) quantify the magnitude of yield losses by heat stress in these two phases, (ii) determine whether N fertilisation affects these magnitudes, and (iii) identify whether the effects are indirect (through affecting growth) or direct on the grain set and/or grain growth capacity.

2. Materials and methods

2.1. General conditions

Field experiments were conducted on actual farmer’s paddocks (part of which were rented for the experiments to be established using the normal sowing and management of the farmer, with the exception of the N fertilisation) close to Algerri (41°47’41”N; 0°38’52”E), province of Lleida (Catalonia, north-eastern Spain) in 2009 (exp. 1), 2010 (exp. 2), 2011 (exp. 3), and 2012 (exp. 4), within the irrigated Mediterranean region of the Ebro River Valley. The region has a semiarid continental climate, with low annual precipitations (374 mm annual, mostly in winter and early spring),

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