



Yield and grain weight responses to post-anthesis increases in maximum temperature under field grown wheat as modified by nitrogen supply

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ABSTRACT

High-temperatures reduce yield of wheat and with global warming episodes of heat waves (only few days of high maximum temperatures) during grain filling will become more frequent. It has been recently reported that the magnitude of the yield penalties imposed by high temperatures under field conditions may interact with nitrogen (N) availability both in barley and maize. We determined, under field conditions, the penalties imposed by post-anthesis high-temperatures waves (increased maximum –but not minimum– temperatures during part of the grain filling period) on wheat yield under contrasting soil N supply during two consecutive years. The high temperature treatment was imposed for 10 d starting 10 d after anthesis by placing over the crops transparent polyethylene film (125 μm) mounted on wood structures of 1.5 m height above the ground. This high-temperature and the unheated controls were imposed on 5 modern and well adapted cultivars under contrasting N availabilities (376, 268 and 68 KgN ha^{-1}). Averaged across N conditions, high-temperature treatments reduced yield by c. 1.5 Mg ha^{-1} (a loss of c. 17%) even though the treatment was rather mild in terms of different average temperature during grain filling. The magnitude of the loss was consistently shaped by the N condition in which the treatment was imposed: yield penalty produced by high-temperature increased from less than 1 to 2.6 Mg ha^{-1} (which represents losses from 10 to 25%) in parallel with the increased N supply. The penalties were related to both yield components (grain number and average grain weight) which also were more severely penalised under high than under low N supply. As episodes of high-temperature waves will become more frequent in the future the tools used to establish the needs of N fertilisation should be revised as the rates maximising yield (or gross margin) might induce higher sensitivities to these episodes. Also simulation models used to upscale physiological responses to regional or even global domains might need to be revised to include the effect of heat waves (which would be larger per $^{\circ}\text{C}$ increase than what is estimated from experiments increasing temperature during the whole day and over longer periods) as well as the interaction with N supply.

1. Introduction

There is an urgent need to increase global wheat yields. In the relatively near future the population will increase to at least 9 billion people (UN, 2015) and the per capita income growth will increase the individual demands simultaneously (Fischer et al., 2014). Projections suggest that a cereal production increase of at least 50% (Fischer et al., 2014), or even more (Hall and Richards, 2013; Ray et al., 2012) will be needed by 2050. And these remarkable increases must be achieved in the context of serious inconveniences: no major contributions may be expected in acreage cropped with cereals (Albajes et al., 2013) and thus future agricultural growth will be more reliant than ever on raising yields (Reynolds et al., 2012; Fischer et al., 2014) at a time when we expect changes in climate which will make crops more frequently

exposed to higher temperatures (Battisti and Naylor, 2009; Lobell et al., 2011; Cairns et al., 2013; Challinor et al., 2014). In this context, not only average global temperatures, but also heat waves are predicted to increase under future climate scenarios (Asseng et al., 2011; Rahmstorf and Coumou, 2011; Semenov and Shwery, 2011; Barlow et al., 2015). And this increase in frequency (and severity) of heat waves are expected in regions characterised to be relatively warm like the Mediterranean Basin (Sánchez et al., 2004) as well as in relatively cool regions (Semenov, 2007). In fact, Semenov and Shwery (2011) concluded that an increase in frequency and magnitude of heat stress around flowering in wheat will seriously increase the vulnerability of the crop (more so than drought).

Wheat plays a major role in food security (Reynolds et al., 2012) as it is the crop most widely grown worldwide, and is the main source of

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calories and proteins for the world population (Braun et al., 2010; Shewry and Hey, 2015). As wheat is grown minimising the likelihood of frost events during flowering, it is rather common that in most environments grain filling takes place with some likelihood of heat stress, and this likelihood will only increase during the next decades (IPCC, 2014). It has been repeatedly shown that exposure to higher temperatures does reduce yield of cereals (Prasad and Djanaguiraman, 2014; Prasad et al., 2006; Jagadish et al., 2007; Lobell and Field, 2007; Prasad et al., 2008; Hatfield et al., 2011; Asseng et al., 2015; García et al., 2015), and physiological factors behind the yield penalty imposed have been studied for a long time (e.g. Slafer and Miralles, 1992; Jenner 1994; Wardlaw and Wrigley 1994; Calderini et al., 1999), including cases in which the effect of heat waves (only few days of high maximum temperatures) were considered (Jenner 1991; Stone and Nicolas 1994, 1995; Savin et al., 1996; Savin and Nicolas 1996; Wallwork et al., 1998; Passarella et al., 2002, 2005). It is therefore critical to identify breeding and/or management tools to mitigate post-anthesis heat effects on wheat yield (Prasad et al., 2017).

Management studies have almost only focused on the possibility of escaping (at least partly) the stress, reducing the likelihood of heat waves during grain filling, through advancing anthesis (with changes in sowing dates and cultivars). Although this could be possible in some cases, in most growing conditions anthesis is optimised when occurring immediately after the last frosts, and therefore other management tools, more directly related to the mitigation of the heat penalty should be identified. It has been recently reported that the magnitude of the effects of high temperatures on yield or its components may interact with nitrogen (N) availability both in barley and maize under field conditions (Passarella et al., 2008; Ordoñez et al., 2015). Regrettably, as far as we are aware, there is only one study analysing this interaction in the field for wheat, but with the high temperatures imposed throughout the whole growing season, and particularly over the winter (Liu et al., 2013); which means that high temperature was beneficial, rather than stressful, for the crop, at least during the winter period. There are, however, very few examples of studies under controlled conditions reporting that interaction in wheat may also exist. For instance, Altenbach et al. (2003) found that grain weight of plants exposed to heat stressed was decreased, but the magnitude of the effect was milder under low- than under high-N availability. Slightly later, Zahedi et al. (2004) and Dupont et al. (2006) confirmed that N status may modify the magnitude of the penalty imposed by heat stress on wheat grain weight. Earlier, Mitchell et al. (1993) had grown in chambers a wheat cultivar under a combination of two CO₂ concentrations two temperatures and two levels of N supply, and overall both CO₂ levels heat reduced yield more under high than under low N supply. But extrapolations from controlled conditions to field and upscaling from individual plants to crop canopies is completely uncertain (Passioura, 2010; Sadras and Richards, 2014), particularly for complex traits. Furthermore, most of the studies mentioned in controlled conditions (i) imposed relatively strong temperature treatments, and (ii) provided data for grain weight and quality but not for yield. Therefore even if the risky extrapolation from controlled conditions to field crops were assumed, there are virtually no results on yield penalties produced by a heat stress consisting of few days of higher-than-normal maximum temperatures (a sort of “heat waves”), which is more common in the real field conditions, considering inter-annual variations, than a very long period (e.g. the whole period from anthesis to maturity) of consistently higher temperatures.

We determined, for the first time under field conditions, the penalties imposed by post-anthesis high-temperatures waves (i.e. increased maximum – but not minimum- temperatures during part of the grain filling period) on wheat yield under contrasting soil N growing conditions in well adapted, modern wheat cultivars. The hypothesis is that a high soil N supply would produce crops that are not only higher yielding but also more sensitive to high-temperature waves when they occur. The hypothesis is not only original but also agronomically

relevant. It owes its novelty to the fact that it has never been tested in wheat grown under field conditions. The support for the hypothesis comes from what has been found in the very few examples on which high-temperature and N treatments were factorially combined in the field (for maize and barley). The relevance is because, should it be accepted, the tools we use to recommend N fertilisation rates might need to be revisited, as episodes of high-temperature waves will become more frequent in the near future.

2. Materials and methods

2.1. Experimental setup and treatments

Field experiments were carried out close to Bell-lloc d'Urgell (41.64°N, 0.79°E), Catalonia, North-East Spain, in real fields rented to farmers to install the experiments in the most realistic possible background conditions. All experiments were conducted under potential conditions, with the exception of the soil N level, they were fully irrigated to avoid any water stress and biotic interferences were avoided through controlling weeds, insects and diseases following usual practices. In all cases sowing dates (22/11/2012 or experiment 1, EXP1 and 12/11/2013, for experiment 2, EXP2) and rates (300–350 seeds m⁻²) were optimal. Temperature data were obtained from a government meteorological station located close to the experimental field (agro-meteorological network of Catalonia, XEMA, Generalitat de Catalunya). In both experiments, plots were 1.2 m wide (6 rows 0.20 m apart) and 4 m long; and treatments were arranged in a randomized complete block design with three replications.

EXP1 (2012/13) was sown in a field with rather high soil N availability at sowing (176 ± 43 KgN ha⁻¹ in the first meter depth). We therefore did not impose a “low-N” treatment in this year and fertilised it with another 200 KgN ha⁻¹, “N1”), in order to have an environment with a likely excess of soil N supply (a relatively widespread condition in many European agroecosystems). In the next season (2013/14) we selected a field with relatively low N availability at sowing (68 ± 12 kg N ha⁻¹ in the first meter depth) and carried out EXP2, under two contrasting N fertilisation management: unfertilised (“N0”) and fertilised with 200 KgN ha⁻¹ (“N1”). Therefore we created three levels of soil N supply: a case with an excessive (though not rare) condition of 376 KgN ha⁻¹ available (EXP1 – N1), a case with a clear deficiency with only 68 KgN ha⁻¹ available (EXP2 – N0), and an intermediate situation with a high, though unlikely excessive, N supply (268 KgN ha⁻¹; EXP2 – N1). All these values are supply considering soil mineral N at sowing plus fertilised N, but actual availabilities values had been higher due to the contribution of mineralisation.

Within these three different N-supply conditions treatments were the factorial combination of five modern, well adapted, wheat cultivars and two high-temperature conditions, a control and a heated treatment during 10 days starting 10 days after anthesis. To impose these treatments we assessed anthesis plot by plot and imposed the treatments based on the phenology of each individual plot in each of the growing seasons (Fig. 1).

Cultivars chosen were Tribat, Nogal, Ingenio, Sensas, and Rodolfo. All of them are high-yielding, modern, well adapted hexaploid wheat cultivars. They are a selection of a slighter larger range of cultivars we grew in previous experiments (Elía et al., 2016) that were selected for best performance across different conditions of that study.

The post-anthesis heat treatment was imposed through enclosing the canopy area designated for the treatments with transparent polyethylene film (125 µm) mounted on wood structures of 1.5 m height above the soil level (with c. 0.5 m of each leg buried; as illustrated in Fig. 2, top panels), but leaving the bottom 30 cm of the four sides of each structure open, in order to facilitate free gas exchange through that area. Temperature sensors (connected to dataloggers EM5b Decagon Devices) were regularly distributed in order to monitor air temperatures inside and outside the structures at the height of the

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