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Interactive effects of high temperature and drought stress during stem elongation, anthesis and early grain filling on the yield formation and photosynthesis of winter wheat

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ABSTRACT

Heat waves and drought periods are expected to become more frequent due to climate change. This may cause a critical decline in future crop yields. However, insufficient knowledge of the interactive effects of high temperature and drought stress at specific growth stages is the cause of numerous uncertainties in modeling impacts of climate change on field crop growth and yield. Hence, the aim of this study was to investigate the effects of interactions between the short-term exposure (3 and 7 days) of two winter wheat genotypes to elevated temperature and drought stress on yield formation and photosynthetic parameters. Winter wheat plants grown under ambient conditions were subjected to four temperature regimes (with maxima at 26, 32, 35 and 38 °C) and drought in growth chambers at three critical growth stages (beginning of stem elongation – DC 31, beginning of anthesis – DC 61, and medium milk ripe – DC 75). The response of yield formation parameters was obviously modulated by variety and growth stage. Grain number was more affected by drought at DC 31 and by the temperature at DC 61. Grain weight per spike was reduced by drought stress similarly at all growth stages, but the results indicated the increasing sensitivity of this parameter to a temperature at the later growth stage. Although yield parameters only changed slightly with the length of heat and drought stress, the photosynthetic parameters were strongly affected, particularly by longer drought and the interactive effect of high temperature and drought stress. Higher temperature significantly increased the negative impact of drought on CO_2 assimilation rate. Photosynthetic parameters were less affected by combined high temperatures and drought stress at DC 61 as compared to other growth stages investigated. The larger effect at the later growth stage (DC 75) can be attributed to induced senescence, among other factors, particularly in the Bohemia variety. The Tobak variety appears to be more tolerant to combined high temperatures and drought stress in terms of photosynthetic parameters. Based on the relationships between heat degree-days (HDD) and grain weight per spike we demonstrated the potential of HDD to integrate length and intensity of heat stress at different growth stages, particularly for estimation effects on yield parameters. It can be summarized that although the short-term combination of high temperatures and drought causes significant reductions in photosynthetic parameters, the impact on yield formation is much lower, indicating fast recovery of photosynthetic processes and compensation in yield formation parameters.

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1. Introduction

Drought as well as heat stress (high temperature stress) represent the major abiotic stress factors affecting growth, development and production of plants (Noohi et al., 2009; Hasanuzzaman et al., 2012; Hossain et al., 2012; Bilal et al., 2015; Lobell et al., 2015). Moreover, these stresses often occur at the same time (Rizhsky et al., 2004) and are physically intertwined at least in some regions (Hirschi et al., 2011).

The annual global temperature is predicted to increase by 1.8–4.0 °C until the end of the 21st century (Bita and Gerats, 2013). The increase in occurrences of extreme weather events (Zheng et al., 2012) such as short periods of very high temperatures (> 33 °C) (Wardlaw et al., 1989; Stone and Nicolas, 1994) and drought spells (Li et al., 2009) is also expected under future climate scenarios (e.g., Trnka et al., 2011), and it represents a significant risk for crop production (Wardlaw et al., 1989; Stone and Nicolas, 1994; Zheng et al., 2012). Wheat, as the globally second most widely grown cereal crop (Reyer et al., 2013), is very susceptible to drought stress, particularly at the developmental stages of anthesis and grain-filling (Trnka et al., 2014). Moreover, the susceptibility is likely to increase in future climate conditions across large portions of European wheat-producing regions (Trnka et al., 2015) including the Czech Republic (Trnka et al., 2016a). The damage temperature threshold for wheat is estimated to be 31 °C during the flowering stage and 35 °C during the grain filling stage (Niwas and Khichar, 2016).

Both heat and drought stress directly or indirectly regulate a number of biochemical and physiological processes. In addition to directly affecting plant growth (Skirycz and Inzé, 2010), the most affected processes are related to photosynthesis (Chaves et al., 2009; Sharkey, 2005). The direct effect on photosynthesis is mediated by stomatal closure or mesophyll conductance (Flexas et al., 2007) and occurs much earlier, while the indirect effect is due to downregulation of photosynthetic metabolism occurring under prolonged or more severe stress (Lawlor and Cornic, 2002; Salvucci and Crafts-Brandner, 2004). Drought and/or heat stress reduce membrane integrity and increase lipid peroxidation, leading to a reduction of chlorophyll content (Bolhar-Nordenkampf et al., 1991; Mafakheri et al., 2010) and functionality of leaves (Al-Khatib and Paulsen, 1984) and stress-induced premature senescence (Silva et al., 2010). Heat stress thus accelerates not only whole plant senescence but also the grain filling process, leading to an earlier maturation and a shorter reproductive phase (Farooq et al., 2011), which result in a significant yield loss (Barnabas et al., 2008). The leaf senescence in wheat was found to be accelerated at temperatures above 31 °C shortly after anthesis and during grain filling (Asseng et al., 2011).

The responses of plants to drought and heat stress are often species-specific, but there are also differences among varieties within a species (Ristic and Cass, 1992; Demirevska et al., 2008; Vassileva et al., 2011). It is evident that the evaluation of photosynthetic responses and changes in chlorophyll content may provide relevant selection criteria for breeding new genotypes that are tolerant to higher temperatures and drought stress (Mohammadi et al., 2009; Monneveux et al., 2006; Camejo et al., 2005).

Field crops are known to be more prone to heat stress in reproductive developmental stages compared to vegetative phases (Vara Prasad et al., 2017); in addition, the response of each yield component of wheat depends on the specific crop and the developmental stage in which the stress occurs (Stone and Nicolas, 1995; Ferris et al., 1998; Calderini et al., 1999; Gibson and Paulsen, 1999). Nevertheless, the information on responses of various field crops to heat stress during reproductive stages (especially anthesis) at a finer scale of exposure to this stress is still less known (Vara Prasad et al., 2017). Moreover, studies about the responses of yield components of various wheat varieties to heat stress at different developmental stages are still rare (Kumar et al., 2016). While a retrospective approach based on regional yield statistics across Europe does not allow one to disentangle individual influences completely (e.g., Trnka et al., 2016b), there seems to be a shift towards an increasing sensitivity of wheat to heat and drought stress over the past 120 years, as Trnka et al. (2012) suggested.

Complete knowledge of the responses of wheat varieties to the most serious abiotic factors such as drought or heat stress and their interactions is necessary for ensuring sustainable crop production under the future climate conditions. Therefore, the aim of this study was to assess how short-term exposure (3 and 7 days) to heat and drought stress and their combination, as a simulation of heat waves that are expected to be more frequent during vegetation seasons under future climate conditions, affect the photosynthetic parameters and yield formation components (grain number, spike productivity) at different growth stages. The main hypotheses tested were as follows: (1) Under short-term exposure to drought and heat stress, the photosynthetic recovery and compensation between yield formation parameters result in a non-proportional reduction of individual yield parameters. (2) Wheat genotypes differing in yield formation have different sensitivities to heat and drought stress at individual critical growth stages for yield formation. (3) The sensitivities of yield formation parameters to heat and drought stress and their interaction change with growth stage.

2. Material and methods

2.1. Plant material

Two of the most widely grown winter wheat varieties (*Triticum aestivum* L.) in the Czech Republic were sown (2 seeds per pot) in plastic pots (10.5 × 10.5 × 21 cm). The plants were cultivated under ambient weather conditions in a vegetation hall at the Mendel University in Brno (235 m a.s.l.; 16°36′48.64716“N, 49°12′36.62892“E). The soil used for cultivation was a topsoil (0–30 cm) from the Polkovice experimental station (199 m a.s.l.). The soil is a Luvic Chernozem with a silt-clay texture (26% clay, 68% loam, 6% sand); pH_{CaCl_2} 7.4; C_{tot} 2.66%; N_{tot} 0.25%; and the contents of P, Ca, Mg and K (Mehlich III) were 143, 6045, 252 and 567 mg kg^{-1}, respectively. The floor of the vegetation hall was concrete and the hall was covered with a wire netting roof to enable exposure of the pots to the ambient weather conditions. The plants in the vegetation hall were (1) irrigated (in total, 80 mm per month in the vegetation hall) to prevent the plants from drought stress and (2) protected against pests and diseases using recommended plant protection products and fertilized (see Table A in Supplementary materials) during their placement in the vegetation hall.

2.2. Environmental conditions during temperature and drought stress treatment in growth chambers

The responses of the wheat plants to heat and drought stress were assessed under fully controlled environmental conditions in growth chambers at three developmental stages: beginning of stem elongation (DC 31), beginning of anthesis (DC 61) and the early grain filling period (DC 75) at two exposure lengths (three and seven days). The protocols used in the growth chambers provided a daily schedule of air temperature (T), photosynthetically active radiation (PAR), and relative humidity (RH) close to the natural conditions. The temperature regimes differed in temperature maxima (T_{max}): 26, 32, 35 and 38 °C. The RH and PAR protocols were the same in each treatment (Table 1). Drought stress was established by splitting the pots into two subtreatments within each temperature treatment: (1) well-watered (*control*), where the soil volumetric moisture was maintained at approximately 30% and (2) drought-stressed, where the volumetric soil moisture was maintained at approximately 15–20%. Each combination of temperature and drought treatment was replicated in 7 pots, and the replications were randomized in space and time. After the heat and temperature treatment at each growth stage, the plants were moved back to the vegetation hall and regularly irrigated. The plants grew in the vegetation hall up to the full ripening stage (DC 92), when the manual harvest was