Field Crops Research 223 (2018) 137–149

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Combined effects of drought and high temperature on photosynthetic characteristics in four winter wheat genotypes

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ARTICLE INFO

Keywords:
Chlorophyll fluorescence
Heat stress
Interactive effect
Photosynthesis
Triticum aestivum
Water use efficiency

ABSTRACT

Terrestrial ecosystems are expected to experience more intense and longer drought and heat-waves in the future. How these environmental factors and their interaction influence photosynthetic activity and water use efficiency remains, however, an open question. Since the photosynthetic activity determines yield response, we investigated gas-exchange and chlorophyll fluorescence traits of flag leaves in four winter wheat cultivars, including two genotypes widely grown in Central Europe and two genotypes considered as drought tolerant. Pot-grown plants were cultivated under natural field conditions until anthesis (DC 61). Subsequently, the plants were exposed to a set of temperature regimes with daily maxima of 26–41 °C (temperature treatment) and maximum soil water holding capacity above 70% and below 30% (drought treatment) using laboratory growth chambers. Primary photochemical reactions after 7 and 14 days of acclimation, measured as maximum quantum yield of photosystem II photochemistry and total chlorophyll content, showed typical interactions of temperature and water availability resulting in an amplified response under combined influence of drought and temperatures above 35 °C. In contrast, drought and temperature treatment had only minor effects on content of epidermal flavonols. A dominant effect of drought over temperature on stomatal conductance (G_{Smax}) was observed. Although substantial genotype-specific responses were found, reduced stomatal conductance resulted in significant decrease in light-saturated rates of CO_2 assimilation (A_{max}) in all genotypes studied. The G_{Smax}–A_{max} relationship, however, revealed limitation of CO_2 uptake by other, non-stomatal processes at temperatures above 32 °C, particularly in the sensitive genotypes. Strong interaction of combined drought and temperature treatments was found on water use efficiency (WUE). Decline in WUE with increasing temperature was steeper in water-deficit than well-watered plants of all genotypes studied. Our results thus document a strong interactive effect of elevated temperature and drought on photosynthetic carbon uptake. Detected thresholds of sensitivity to combined drought and heat stress will contribute to improved modelling of wheat growth and production under expected future climate conditions.

1. Introduction

Anthropogenic changes in the chemistry of the atmosphere have a potential to perturb its thermodynamic equilibrium (IPCC, 2013) and to contribute to an increase in global temperature by 0.3 °C to as much as 4.8 °C according to the RPC 2.6 and RCP 8.5 scenarios, respectively, as compared to the 1989–1999 epoch. In addition, increased frequency, intensity, and/or duration of extreme climatic events such as heat waves (Screen and Simmonds, 2014) and drought periods (Dore, 2005; Trenberth, 2011) are predicted for the 21st century by global coupled climate models. These changes already have been observed over wide agricultural areas of Central Europe (e.g., Trnka et al., 2016) and are leading to marked decline in yields over relatively large regions (e.g., Trnka et al., 2012). Trnka et al. (2015) have shown substantially increased risk of drought and heat events across most of the current crop area of Europe.

High sensitivity to climatic and environmental variations has been demonstrated in wheat (Porter and Semenov, 2005), which is the most

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https://doi.org/10.1016/j.fcr.2018.02.029
Received 2 September 2017; Received in revised form 22 January 2018; Accepted 26 February 2018

important crop in Europe. In particular, temperature and water availability play determining roles in wheat yields. Although some modelling studies have shown stronger effect of heat than drought on wheat yields (Semenov and Shewry, 2011), studies analyzing the variability in winter wheat yields over recent decades show a decisive effect of drought episodes, particularly in Central Europe (Hlavinka et al., 2009; Trnka et al., 2012) and the Mediterranean basin (Cossani et al., 2009). Such discrepancies may be caused by difficulties in predicting drought impacts inasmuch as temporal variability of precipitation, not its total amount, is expected to change (Dore, 2005; Konapala et al., 2017). In Europe, the precipitation pattern during summer, typically associated with anticyclonic circulation types (Trnka et al., 2009), is further negatively correlated with temperature anomalies (Trenberth, 2011), thus leading to a high probability for co-occurrence of heat and drought stress. Both heat and drought stress have been identified as main causes of stagnating wheat yield in Europe (Brisson et al., 2010; Trnka et al., 2016).

Although effects of high temperature and drought have been studied intensively in recent decades, interactive effects of these two factors on wheat physiology and production have received only limited attention. Because both heat and drought may affect a number of physiological and reproductive processes, including a number of interactions (summarized by Barnabás et al., 2008; Prasad et al., 2008), the reliable prediction of yield responses requires a deeper understanding of adjustment in individual processes in response to mutual effects of heat and drought. In particular, modification of photosynthesis by temperature and water availability leads to potential changes in plant metabolism, growth, productivity and/or carbon allocation within plant organs (Gargallo-Garriga et al., 2014, 2015).

Photosynthetic processes are relatively more tolerant to heat stress than to drought. Photosynthesis is often reported to be a process relatively resistant to drought occurring at leaf water potential (Ψ_{leaf}) above −1.0 MPa (reviewed in Larcher, 2003). Insufficient soil moisture and high vapor pressure deficit (VPD) values may, however, lead to a reduction of stomatal aperture followed by decreased CO_2 concentrations at both chloroplast and intercellular levels (Flexas et al., 2004; Chaves et al., 2009), thereby causing CO_2 uptake to decline (Wong et al., 1979; Lichtenthaler et al., 2007). Severe and long lasting drought periods have been reported to result in impaired metabolic activities (Farquhar et al., 1989; Sage and Kubien, 2007) including de-carbamylation of Rubisco (ribulose-1,5-bisphosphate carboxylase/oxygenase), the primary enzyme of the photosynthetic cycle, followed by substantially reduced carboxylation activity (Flexas et al., 2004).

It has been shown in most plant species of the temperate zone that the carboxylation activity of Rubisco increases exponentially at temperatures between 10 and 30 °C. Possible mechanisms connected with carboxylation activity declining at temperatures above 30 °C include the following: (i) decrease in CO_2 concentration in chloroplasts, (ii) reduction of Rubisco activation state, and (iii) limitation of ATP (adenosine triphosphate) production (Roy and Andrews, 2000). Moreover, CO_2 assimilation rate at high temperatures is further reduced by stimulated Rubisco oxygenation activity, which leads to increased photorespiration rates (Muraoka et al., 2000).

Despite the fact that quite good knowledge exists today of photosynthetic responses to both heat and drought if applied separately, deeper understanding of their interactive effects remains insufficient. Different sensitivity of photosynthetic processes to drought and heat stress suggests the occurrence of interactive effects. The interactions of increasing temperature and reduced water availability may thus be additive, synergistic, or even antagonistic inasmuch as the responses of photosynthetic processes to increasing temperature may be positive up to relatively high temperatures.

Accordingly, the aim of this study was to determine the interactive effects of drought and a wide range of temperatures on photosynthetic traits in four wheat genotypes differing in their geographic origins and in their sensitivity to drought and high temperatures. It was hypothesized that high temperature combined with drought would lead to a synergistic enhancement of photosynthesis reduction due to a reduced dissipation of latent heat via transpiration under water-limited conditions. To test this hypothesis, four wheat genotypes, including cultivars widely grown in Central Europe and cultivars considered as drought tolerant,were used. Pot-grown plants were cultivated under natural field conditions until the DC 61 (anthesis) stage and subsequently exposed to a set of daily air temperature maxima (26–41 °C; temperature treatment) and soil moisture (30–70% of maximum water holding capacity; drought treatment) under controlled environmental conditions inside laboratory growth chambers. Photosynthesis-related processes, including CO_2 and H_2O fluxes, photochemical reactions, water use efficiency, and pigment compositions, were investigated after 7 and 14 days from the onset of treatment.

2. Material and methods

2.1. Plant material

Four winter wheat (*Triticum aestivum* L.) genotypes (Tobak, Bohemia, Pannonia, and Syrian line S46–IG142780, hereafter referred to as S46) were selected for this study. S46 and Pannonia are regarded as potentially drought and temperature tolerant, while Bohemia and Tobak achieve the highest yields under moderate climate conditions of Central Europe.

Two seeds per pot (0.1 × 0.1 × 0.2 m) were sown in October 2014. Pots had been filled with natural soil (luvic chernozem with loess as a mother substrate) originating from a wheat-growing experimental station at Polkovice, Czech Republic (49°23′ N, 17°15′ E). The pots were exposed to ambient weather conditions of a vegetation hall at Mendel University Brno, Czech Republic until heading stage (DC 57–59). The plants were regularly irrigated and fertilized (total dose of 90 kg N ha^{-1}) between tillering and the end of stem elongation phases to encourage their growth and to avoid their becoming drought-injured.

The pots were then transported to six growth chambers (model FS-SI 3400; Photon Systems Instruments, Brno, Czech Republic) at the Global Change Research Institute Brno, Czech Republic. All genotypes were acclimated for 7 days to day/night air temperatures and relative humidities of 26/18 °C and 45/90%, respectively, and maximum photosynthetic photon flux density of 1500 µmol photons $m^{-2} s^{-1}$. All pots were regularly irrigated to keep soil moisture at 70% of maximum water holding capacity.

When anthesis stage (DC 61) was reached, the plants were exposed to a set of five temperature treatments with daily air temperature maxima of 26, 29, 32, 35, 38, and 41 °C and two levels of drought treatment characterized by keeping soil moisture above 70% (control) and below 30% (water deficit) of maximum water holding capacity. Fig. 1 depicts in detail the microclimatic characteristics of the treatments applied. Each combination of genotype, temperature regime, and water availability was replicated six times. The replications were randomized in time and space to avoid chamber artefacts. Such growing conditions led to changes in flag leaf water content (LWC) calculated as the ratio of leaf fresh minus dry weight after lyophilisation divided by leaf fresh weight. While LWC ranged between 0.65 and 0.75, it amounted 0.55–0.65 and 0.35–0.55 after 7 and 14 day treatment. The statistically significant differences in LWC among individual temperature treatments were not observed. Measurements of physiological parameters related to photosynthetic CO_2 assimilation were taken after 7 and 14 days of these treatments.

2.2. Physiological measurements

All physiological measurements presented were performed on intact flag leaves of six plants per treatment under actual (minimum) air relative humidity and actual (maximum) of the given temperature treatment (see Fig. 1), as well as under the ambient CO_2 concentration