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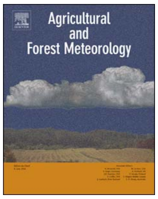

Research paper

Acclimation to higher VPD and temperature minimized negative effects on assimilation and grain yield of wheat

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ABSTRACT

Adapting to climate change and minimizing its negative impact on crop production requires detailed understanding of the direct and indirect effects of different climate variables (i.e. temperature, VPD). We investigated the direct (via heat stress) and indirect effects (through increased VPD) of high temperature on growth, physiology and yield of two wheat cultivars (Taifun and Vinjett) at two watering levels; well-watered: WW (100% evapotranspiration (ET)) and drought stress: DS (50% of WW ET). Three climate treatments were applied for five days, starting at one week after anthesis. Treatments included hot humid (HH: 36° C; 1.96 kPa VPD), hot dry (HD: 36° C; 3.92 kPa VPD) and normal (NC: 24° C; 1.49 kPa VPD). Difference between HH and HD was considered as the indirect effect of temperature through increased VPD. HD increased transpiration by 2–22% and decreased photosynthetic water-use efficiency (WUE_p) by 24–64% over HH during stress but whole-plant WUE at final harvest was not affected. HD reduced grainfilling duration (3 days), resulted in relatively lower green leaf area (GLA) after the stress and showed a tendency of lower net assimilation rate during the stress compared to HH. However, yield and yield components were not affected under WW conditions due to two reasons (i) acclimation of the photosynthesis, stomatal conductance and rubisco carboxylation efficiency to high temperature and VPD and (ii) translocation of assimilates from stem/leaf to grains after the stress episode. Five days of high temperature stress alone (HH) reduced GLA, grainfilling duration (5 days) and thousand-grain weight (17%), which ultimately reduced grain yield by 17%. DS mainly affected GLA, grainfilling duration and reduced grain yield by 7% vis-à-vis WW. Two cultivars differed only for GLA (lower for Vinjett under HH) and WUE_p (higher for Vinjett under DS). This indicates that the temperature induced increase in VPD has little effect on growth and yield, if sufficient soil moisture is available, because acclimation and tolerance mechanisms tend to alleviate stress effects. These compensatory mechanisms should also be considered when modelling climate effects on crops. However, heat waves and drought events during sensitive crop developmental stages (i.e. anthesis, grainfilling) are important climate variables that need to be considered for adaption to climate change.

1. Introduction

Global annual mean temperature is expected to rise between 1.5 and 6 °C by the end of this century (IPCC, 2013), which could very well interfere with growth and yield of crops (Asseng et al., 2015). Increased overall climatic variability, i.e. frequency, intensity, timing and duration of certain events, are expected to be the common feature of future climate, and large regions are expected to become exposed to higher frequencies of both extreme heat waves and drought periods (IPCC, 2012; Schar et al., 2004; Trnka et al., 2014). Wheat is one of the most

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Abbreviations: A_n, net photosynthesis; CE_i, instantaneous carboxylation efficiency of rubisco; DS, drought stress; GLA, green leaf area; g_s, stomatal conductance; HH, hot humid; HD, hot dry; LWR, leaf weight ratio; NC, normal climate; PAR, photosynthetically active radiation; PM, physiological maturity; QC_i, instantaneous quantum cost; SD, stress-day; SLA, specific leaf area; SPAD, chlorophyll content index; StWR, stem weight ratio; SWR, spike weight ratio; TAGB, total aboveground biomass; T_r, transpiration; VPD, vapor pressure deficit; WUE, water-use efficiency; WUE_{GY}, WUE for grain yield; WUE_i, intrinsic WUE; WUE_p, photosynthetic WUE; WUE_{TY}, WUE for total aboveground biomass; WW, well-watered; Ψ_L, leaf water potential

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sensitive crops to high temperature (Satorre and Slafer, 1999). It may experience heat stress during all phenological stages, but anthesis and grainfilling phases (end-of-season stress or terminal stress) are generally more sensitive (Wollenweber et al., 2003). The terminal heat stress is expected to rise due to changes in climatic variability (Semenov, 2009). The upper optimum temperature limit for wheat during anthesis and grainfilling has been reported to be around 34° C (Farooq et al., 2011), and temperature higher than this seriously reduces grain yield (Ferris et al., 1998).

The effects of higher seasonal mean temperature (Asseng et al., 2015; Porter and Gawith, 1999) and extreme high and variable temperatures (Asseng et al., 2011; Ferris et al., 1998; Wollenweber et al., 2003) on wheat physiology, growth, and other yield determinants have been extensively studied; however, in order to develop climate resilient management practices and crop cultivars, detailed understanding of the actual mechanisms behind these effects is required. The effects of extreme heat waves on some of the yield determinants in wheat viz. accelerated and premature senescence, reduction in grain weight have been documented (Farooq et al., 2011; Vignjevic et al., 2015), but attributing these negative effects exclusively to temperature is not straight forward. This is because of the hidden and confounding effects of vapor pressure deficit (VPD), which increases exponentially with increasing temperature at constant absolute humidity. High VPD amplifies the evaporative power of the surrounding environment and serves as the major driving force behind evaporative and transpirational water losses. Certainly, it is not possible to deny the direct heat effects, but high temperatures also acts indirectly by changing plant water-use and intensifying drought effects through higher VPD (Will et al., 2013). A comprehensive meta-analysis study by Gourdji et al. (2013) revealed that heat tolerance in wheat is influenced by changes in daily VPD. Under extreme heat stress, VPD not only increases plant water demand due to high transpiration rates but also reduces the future soil water supply (Lobell et al., 2013), and it thereby acts as dual stress. However, this notion cannot be taken as absolute because of the fact that VPD driven high transpiration can also serve as a negative feedback by lowering crop canopy temperature and consequently VPD is reduced, which ultimately may mitigate heat stress (Gourdji et al., 2013).

The effect of heat stress through enhanced VPD also depends on plant stomatal behavior which is crucial for regulating leaf gas exchange (H_2O loss and CO_2 influx). Crop species or cultivars may differ in their stomatal response to VPD and drought (Schoppach and Sadok, 2012), which leads to different water-use efficiency (CO_2 uptake vs. H_2O loss). Cultivars showing little control over water loss are termed as anisohydric (McDowell et al., 2008) as revealed for peanut genotypes (Devi et al., 2009). These cultivars could be ideal if soil water is not a limiting factor. In contrast, isohydric cultivars show conservative behavior and tend to close stomata in order to maintain plant water status (McDowell et al., 2008) as observed for pearl millet (Kholová et al., 2010) and chickpea (Zaman-Allah et al., 2011). Nonetheless, irrespective of plant stomatal behavior, high VPD may amplify the physiological stress under water limiting conditions, either by reduced CO_2 influx (isohydric) or by enhanced transpirational water loss (anisohydric) (McDowell et al., 2008). Thus, cultivars with isohydric nature may exhibit higher water-use efficiency under stress conditions, but at an expense in terms of total biomass production. However, suitability of these two groups of cultivars also depends on timing and duration of drought. Generally, isohydric cultivars are suggested to be more suitable under terminal drought while anisohydric under intermittent drought (Polania et al., 2016).

Heat and drought stresses are, therefore, interlinked through VPD with the two factors reinforcing each other. Previous model-based analyses on maize (Lobell et al., 2013) showed that a significant proportion of the heat effects may be attributed to indirect effects of changes in VPD, which modulates plant water use and carbon assimilation. However, models differ in their description of crop responses to temperature and VPD, and they mostly do not account for acclimation responses to changes in these conditions. Therefore, despite ongoing efforts to improve the modelling of crop responses to increased temperatures and drought, large uncertainties still remain (Asseng et al., 2015; Cammarano et al., 2016). Other studies have suggested a positive impact of VPD on crop yield, and associated this with higher solar radiation on days with high VPD (Lobell, 2007; Roberts et al., 2012). Experimental work by Will et al. (2013) on forest species, Schoppach and Sadok (2012); Schoppach and Sadok (2013) on wheat and Yang et al. (2012) on maize considered the effect of VPD, but they focused mainly on transpiration. Furthermore, extreme heat was not in focus in either of these studies.

Nonetheless, due to contrasting results and lack of experimental evidence, VPD effects on grain yield of wheat at high temperature need to be better understood. We therefore aimed to investigate the combined effects of high temperature and high VPD on growth and yield of two wheat cultivars at two watering levels. We hypothesize that, as a consequence of high temperature, higher VPD will reduce grain yield by increasing crop water demand, restricting CO_2 assimilation, hastening leaf senescence and crop maturity. Since at high temperature plants can suffer from heat as well as high VPD, we further hypothesize that the effects of high temperature and high VPD will be additive and more severe than the temperature effects alone. The objectives of this study were (1) to estimate the effects of post-anthesis heat wave at low and high VPD on growth, physiology and yield of two wheat cultivars under drought and well-watered conditions, and (2) to quantify the effects of high VPD on growth and physiology of wheat, and to what extent these effects actually translate into yield loss.

2. Materials and methods

2.1. Experiment introduction

This experiment was designed to serve three purposes (1) to study the effects of post-anthesis heat wave on growth and physiology of wheat thus a high temperature treatment with low VPD was designed to be applied for five days starting from six days after the mid-flowering stage (GS65) (2) To separate the direct (through heat stress) and indirect (through increased VPD) effects of high temperature, therefore a second high temperature treatment was designed with high VPD. A third treatment with normal temperature- and VPD was included as a control. Temperature and VPD treatments collectively were termed as "climate treatments" (3) the above mentioned climate treatments were meant to be studied under well-watered and drought stress conditions for two cultivars (see Table 1 and section 2.3 for treatment details).

2.2. Plant material and cultivation

A controlled environment experiment was conducted in growth chambers at Research Centre Foulum, Aarhus University, Denmark. Thirty seeds of two wheat cultivars of Scandinavian origin, namely *Taifun* and *Vinjett*, were sown at 2.5–3 cm depth in plastic pots (cap.

Table 1
Set points for climate treatments in climate chambers.

Chamber	Treatment notation	Time	T (°C)	RH (%)	VPD (kPa)	CO_2 (ppm)
I	Normal climate	day	24	50	1.49	400
	(NC)	night	12	76	0.34	400
II	Hot humid climate	day	36	67	1.96	400
	(HH)	night	26	90	0.34	400
III	Hot dry climate	day	36	34	3.92	400
	(HD)	night	26	80	0.67	400

T, temperature; RH, relative humidity; VPD, vapor pressure deficit; NM, HH and HD are the notations for treatments in text.