Photosynthetic response of spring oilseed rape to heat, drought, nutrient deficiency and combined stress

Dikšaitytė A[1,2,*], Viršilė A.[1], Januškaitienė I.[2], Žaltauskaitė J.[2]

[1]Institute of Horticulture, Lithuanian Research Centre for Agriculture and Forestry, Kauno St. 30, LT-54333, Babtai, Kaunas distr., Lithuania
[2]Department of Environmental Sciences, Faculty of Natural Sciences, Vytautas Magnus University, Vileikos St. 8, LT-44404 Kaunas, Lithuania

*corresponding author: austra.diksaityte@vdu.lt

Abstract
This study aimed to determine the photosynthetic response of spring oilseed rape to heatwave (HW), drought, nutrient deficiency (N-D) and combined stress. HW and drought acted in a different manner. Under both adequate and deprived soil nutrient conditions, in the presence of adequate water supply, HW up regulated the photosynthetic performance of rape. However, drought-induced stress was highly exacerbated under HW, leading to the incomplete recovery that was additionally impaired by nutrient deficiency.
Keywords: photosynthesis, oilseed rape, heat, drought, nutrient deficiency

1. Introduction

Under natural conditions, crops are subjected to a combination of different abiotic stressors. Among them, drought and heat represent the most frequent abiotic stress combination that are predicted to increase in frequency and severity in many regions of the world due to global climate change (Mittal et al., 2014). In addition to this, plants nutrient availability will also likely change with climate warming. However, the trajectory of terrestrial nitrogen availability is still uncertain (Craine et al., 2018). The objective of this study was to examine the photosynthetic performance of spring oilseed rapes grown under single and combined treatments of heatwave and drought under adequate or deprived soil nutrient conditions and to evaluate their capability to recover after the treatments.

2. Materials and methods

Spring oilseed rape seeds (*Brassica napus* L., var. 'Fenja') were sown in plastic pots filled with a mixture of field topsoil, perlite, and fine sand (5:3:2, by volume). Plants were grown in the growth chambers under controlled environment (a day/night air temperature was 21.1±0.02 / 14.1±0.02 °C, CO_2 concentration averaged 406±1.2 µmol mol^{-1}, RH − 56±0.1% during the day and 73±0.3% at night, PAR was ~270 µmol m^{-2} s^{-1}, the day length − 14 h). Plants grown under adequate nutrient (N-A) conditions were fertilized twice with the complex nutrient (NPK 12-11-18 + microelements) solution to the final N level of 160 kg ha^{-1}. At the same time, nutrient deprived ones (N-D) received 60 kg ha^{-1} of nitrogen.

The heatwave (HW, 33/26 *vs.* 21/14 ºC, day/night) and drought treatments were imposed at BBCH 13 growth stage. Drought stress was applied by withholding water for a period of 7 days in both ambient air temperature (AT) and HW treatments. After that, drought-stressed plants were re-watered to the control level of 30% of volumetric soil water content and, upon relief of HW and drought, a 7-day recovery period under AT conditions was applied.

LI-6400XT (LiCor Biosciences, USA) portable photosynthesis system was used for light-saturated leaf gas exchange measurements that were conducted under the same block temperature as was in each treatment chamber, either 21 ºC for AT or 33 ºC for HW. The airflow rate through the assimilation chamber was maintained at 500 µmol s$^{−1}$. PAR and CO_2 were set at 1500 and 400 µmol m$^{−2}$ s$^{−1}$, respectively. The measurements were taken on the most recent fully developed lit leaves.

LSD tests were used to evaluate statistically significant differences (at $p \leq 0.05$) between the means of investigated parameters. All statistical analyses were performed by STATISTICA 8 software.

3. Results and discussion

At the end of the treatment, drought as single stressor significantly reduced photosynthetic rate (A_{sat}), stomatal conductance (g_s), transpiration (E) and intercellular CO_2 concentration (C_i), while water use efficiency (WUE) increased. In contrast, under HW, A_{sat}, g_s and E of well-watered plants were up regulated, while C_i and WUE decreased (Fig. 1A−E). Even so, the adverse effect of drought was highly exacerbated under HW with the combined stress leading to the significant greater reduction of A_{sat}, g_s and C_i and decreased WUE. These results are in consistent with other studies (Elferjani and Soolanayakanahally, 2018), were the effect of combined stress on A was far stronger than the effect of single treatments, even when HW and drought, in this study, acted in a different manner.

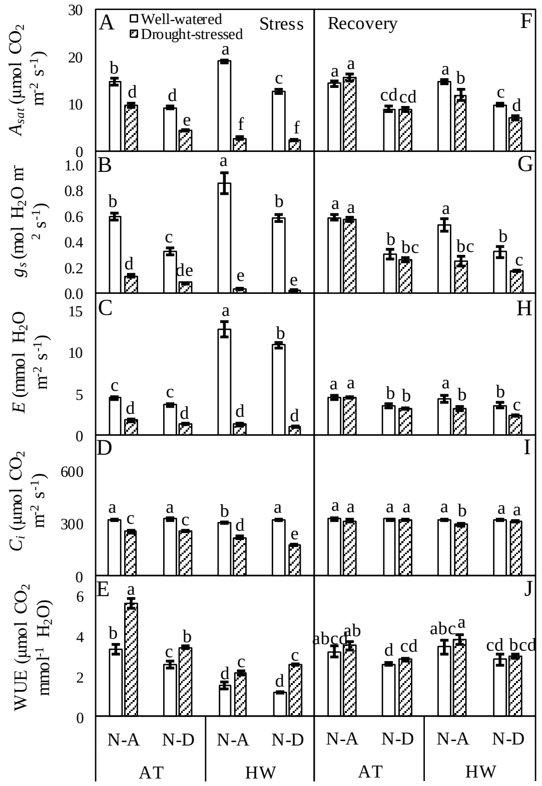

Figure 1. Leaf gas exchange of well-watered and drought-stressed spring oilseed rapes (*Brassica napus* L.) grown under ambient air temperature (AT) or heatwave (HW) and under adequate (N-A) or deprived (N-D) soil nutrient conditions at the end of the stress (left panels) and after recovery (right panels). Values are means ±SE (n = 9)

Nutrient deficiency had the same effect on A_{sat} as drought (p>0.05), however the response of other leaf exchange parameters was different. Reduction of g_s was smaller, E and C_i did not change, while WUE decreased. Under N-D conditions, the responses of plants to drought, HW and their combined treatment, in general terms, mirrored the same patterns as under N-A conditions. The plants affected by single drought exhibited decreases of A_{sat}, g_s, E and C_i and increase in WUE, while those subjected to single HW treatment showed higher A_{sat}, g_s and E and reduced WUE. The same as under N-A, under N-D conditions, combined drought and HW stress resulted in a far greater reduction of A_{sat}, compared to drought alone, however, no significant difference between these treatments was found on g_s (Fig. 1A,B).

After recovery, in AT treatment, none of gas exchange parameters of plants pre-exposed to single drought under either N-A or N-D conditions differ significantly from their respective controls (Fig. 1F−J). While, under bot N-A and N-D conditions, the gas exchange parameters of plants previously subjected to combined drought and HW treatment not fully levelled off after recovery. Plants grown under N-A conditions had still significantly lower values of A_{sat}, g_s, E and C_i, while under N-D conditions – the lower values of g_s and E, compared with their respective controls.

Nutrient deficiency has largely aggravated the A_{sat} of drought-stressed plants. Moreover, this was more expressed in HW treatment. When compare to AT treatment, there was found a significantly stronger effect of nutrient deficiency on drought-stressed plants in HW treatment, even under N-A conditions. On the other hand, in HW treatment nutrient deficiency, as second stressor to drought, did not add additional stress on A_{sat} (p>0.05). However, after recovery, drought-stressed plants grown under N-A conditions in HW treatment differed significantly from drought-stressed and nutrient-deprived ones both grown in AT and HW treatments with markedly better regeneration of A_{sat}, keeping the drought-stressed plants grown under N-A conditions in AT treatment as control. (Fig. 1A,F).

Conclusions

Temperature increases up to 12 ºC can positively affect the photosynthetic performance of well-watered oilseed rapes grown under adequate soil nutrient conditions, at least at the early vegetative stage. However, drought might fully negate all the advantages gained from warmer climate and lead to the incomplete recovery of gas exchange following stress. Further, the recovery of leaf gas exchange might be additionally impaired by nutrient deficiency in both AT and HW treatments.

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