



# Responses of winter wheat (*Triticum aestivum* L.) varieties to drought stress and elevated CO<sub>2</sub> levels: a comparative analysis of growth, spike characteristics, and grain yield

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## Abstract

The study highlights the impact of drought stress at different phenological stages and different carbon dioxide concentrations on the growth and productivity of four Hungarian winter wheat varieties ('Mv Ikva', 'Mv Nádor', 'Mv Nemere', 'Mv Kolompos'). The experiments were performed at the HUN-REN Centre for Agricultural Research and the experimental setting contained three different watering regimes (optimal watering as control, water withdrawal at the stem elongation, water withdrawal at the heading developmental stage as drought treatment) and three different carbon dioxide levels (current atmospheric, 700 ppm or 1000 ppm). Our findings contribute to a better understanding of how atmospheric conditions, including elevated CO<sub>2</sub> levels, might interact with drought stress to influence wheat growth. At current atmospheric CO<sub>2</sub> concentration drought experienced during the early developmental stage caused a significant reduction in several measured parameters compared to drought occurring at the heading stage. At elevated CO<sub>2</sub> levels (700 ppm and 1000 ppm), the drought-induced reductions in plant height were generally less severe. Drought stress during stem elongation significantly reduced spike weights, at 700 ppm CO<sub>2</sub> concentration, the early-stage drought had a stronger negative impact on this parameter than the late-stage drought. Early drought significantly reduced the grain number in the main spikes under ambient CO<sub>2</sub> levels, while heading-stage drought primarily affected the secondary spikes.

**Keywords** Abiotic stress · Drought stress · Climate change · Main and secondary spikes

## Introduction

One of the most pressing issues of present era is the assurance of the adequate quantity and quality of food. Hence, in 2022 the global population reached 8 billion and it is expected to reach 10 billion by 2050, it would be a challenging task (Saeed et al. 2023; Sakaguchi 2023; The World Bank Group 2025). Ensuring food security fundamentally relies on food availability, food production and distribution.

While there is a growing need for food, the food supply is being steadily constrained and limited by factors such as urbanization, land degradation, spreading of industrial crops and climate change (Albahri et al. 2023). The effects originated from climate change affect greatly the production of agricultural crops and threaten the provision of food security (Iancu et al. 2022; Tudor et al. 2023). Since the industrial revolution, the atmospheric carbon dioxide concentration has risen from 278 to appr. 417 ppm. A continuous increase in CO<sub>2</sub> levels has been observed since the 1760s, but this upward trend has become much steeper since the 1960s (Betts 2021). Depending on efforts to reduce carbon emissions in the future, the atmospheric concentration of this gas could be between 500 and 1000 ppm by the end of the century (Anwar et al. 2018; Dusenge et al. 2019). The elevated concentration of CO<sub>2</sub>, along with other greenhouse gases, has altered the composition of the atmosphere, causing global warming (Dusenge et al. 2019). The Earth's surface temperature has increased by 0.08 °C per decade since 1880, and since 1981, the rate of increase has accelerated to

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0.18 °C per decade (Lindsey and Dahlman 2021). The intensity of warming shows no uniform distribution around the globe, with higher latitudes experiencing more significant warming than the tropical belt. The expected rate of warming varies by season, with the greatest increase anticipated during winter months (Ciais et al. 2013). Climate change will have a significant impact on the Earth's vegetation. The elevated temperature and the increasing dryness of the atmosphere, coupled with lower relative humidity, may enhance potential evaporation (Ficklin and Novick 2017). Over the past 40 years, an increase in the number of extreme events due to climate change has been observed. This growth has been more pronounced in hydrological (e.g., floods) and meteorological events (e.g., storms) compared to climatological proceedings (e.g., extreme temperatures, droughts, forest fires). The changes in the global climate will have both spatial and temporal impacts on agricultural production. The rising frequency of extreme weather events, such as heat-waves, heavy rainfall and floods, along with soil degradation or a reduction in arable land imposes an increasingly heavy burden on agriculture, exacerbating the already precarious situation of food security (Del Buono 2021; Khadka et al. 2020).

Wheat (*Triticum aestivum* L.) plays a significant role in our civilization, and its importance is well-illustrated by the fact that wheat is ranked second among cereal crops regarding total global production (FAO 2018). The primary causes of losses in wheat production are attributed to abiotic factors such as drought, salinity and heat stress, rather than biotic factors (Abhinandan et al. 2018). Regrettably, recurring drought events pose a significant threat to global wheat production, demanding substantial attention. The impact of water stress varies across different developmental stages of wheat (Daryanto et al. 2016), with the duration and intensity of water stress influencing wheat development at various trait levels (Sarto et al. 2017), ultimately leading to a decrease in grain yield. Reports from various regions worldwide consistently highlight the substantial role of limited water availability in diminishing wheat yield (Khadka et al. 2020). In general, although the overall performance of the crop is greatly influenced by the intensity and frequency of drought, it is equally crucial to consider the specific phenological stage at which these drought events occur (Sarto et al. 2017). Wheat may exhibit increased vulnerability to drought during specific critical growth stages, including germination and seedling phases (Akram 2011); tillering and stem elongation stages (Saeidi et al. 2015; Wang et al. 2015; Ding et al. 2018); as well as heading, anthesis and grain filling stages (Akram 2011; Sarto et al. 2017). Drought stress can have varied effects on different physiological processes. When the decrease in turgor pressure is significant, the size of actively growing cells tends to remain smaller. The reduction in cell size influences the external appearance

of the plant, but differences arise depending on the growth stage at which water shortage occurs. If drought occurs at the beginning of the growth cycle, morphological changes are observed, such as a decrease in leaf area surface, leading to lower carbon dioxide uptake throughout the entire vegetation period. Additionally, drought during the vegetative phase limits shoot development and branching extent (Kato et al. 2008; Barnabás et al. 2008; Lipiec et al. 2013; Aslam et al. 2013; Dietz et al. 2021). Drought stress experienced during stem elongation results in reduced plant height, leaf area index and concurrently observed decreased water-use efficiency (Li et al. 2017). Numerous studies suggest that plants are more sensitive to drought stress during their reproductive phase (Farooq et al. 2014; Ma et al. 2017; Varga et al. 2017), but the severity of drought effects greatly depends on the intensity and duration of the stress. In the early reproductive phase, drought stress leads to pollen and spikelet abortion, resulting in reduced grain number (Kato et al. 2008; Dölfer et al. 2011). Pre-flowering drought reduces the spikelet/spike number (Kato et al. 2008), decreases plant height and the harvest index of plants (Quaseem et al. 2019) and alters flowering time (Foulkes et al. 2007; Cattivelli et al. 2008). Drought during flowering increases the rate of pollen and ovary abortion, hinders pollen development and can cause spike sterility (Praba et al. 2009; Rang et al. 2011; Powell et al. 2012; Aslam et al. 2013). Moreover, drought during grain filling shortens the filling period, reduces grain number, yield and thousand-kernel weight, as well as the harvest index (Samarah 2005; Foulkes et al. 2007; Samarah et al. 2009; Blum 2017). The morphological characteristics influencing the ultimate grain yield vary across different growth stages, and the severity of the stress event is determined by how much these traits are affected by drought (Khadka et al. 2020). Prolonged droughts, particularly those initiating from stem elongation and extending through maturity, lead to a more substantial reduction in yield compared to droughts starting at later phenophases and continuing through maturity (Shamsi and Kobraee 2011). Due to partly anthropogenic influences, the increase in atmospheric carbon dioxide concentration has an impact on the phenology of plants. Alongside the rise in carbon dioxide levels, there is a potential increase in plant biomass production, thousands-kernel weight, harvest index, number of grains and an improvement in water-use efficiency. However, these positive effects are primarily observed in C3 plants (Wu et al. 2004; Kimball 2016; Dunn et al. 2019; Hussien 2020; Gámez et al. 2020; Abdelhakim et al. 2021). The elevated carbon dioxide concentration may reduce stomatal conductance and decrease the transpiration rate; thereby, it will reduce excessive water loss and consequently increase water-use efficiency (Allen et al. 2011; Abdelhakim et al. 2022). By spring wheat higher grain yield and harvest index was found at elevated CO<sub>2</sub> level (~ 800 ppm) compared to the ambient

level (Abdelhakim et al. 2022). Due to increased number of grain per spike increased grain yield (up to 30–40%) can be observed at elevated (950 ppm) CO<sub>2</sub> concentration (Combe 1981).

While temperature, water availability and atmospheric CO<sub>2</sub> play crucial roles in regulating plant growth, function and development, their effects can vary significantly among different species and varieties. In this study, we explored the impacts of varying CO<sub>2</sub> concentrations, coupled with simulated water shortage, at distinct developmental stages across four Hungarian winter wheat varieties. The objective of the present research was to assess the influence of water shortage and different CO<sub>2</sub> concentrations on the phenological and yield parameters of commonly cultivated wheat varieties in the Carpathian Basin and to determine the interaction effects between the CO<sub>2</sub> enrichment and the water stress in different developmental stages on main and secondary spikes.

## Materials and methods

### Experimental design

In a model experiment conducted at the HUN-REN Centre for Agricultural Research in Martonvásár, Hungary, four locally bred winter wheat (*Triticum aestivum* L.) varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') were examined. Our study, performed in climate-controlled greenhouse chambers in 2020, started on February 3rd and ended at the end of June with manual harvesting. Among the varieties, 'Mv Ikva' is classified as extreme early ripening, 'Mv Nemere' and 'Mv Nádor' as early ripening, and 'Mv Kolompos' as a late-ripening variety. The varieties were selected for the trial based on the ripening classes in that those get national registration. The experimental setup included three water-supply treatments: control ('C'), water shortage at stem elongation ('SE') and water shortage at heading ('H') developmental stage. One-third of all tested plants (36 pots, 144 plants in total) represented the control plants and were watered until reaching 60% of soil water holding capacity (WHC). Drought stress was induced by ceasing irrigation at BBCH 31 stage ('SE') for one-third of the plants (36 pots, 144 plants in total) or at BBCH 51 stage ('H') for another one-third (36 pots, 144 plants in total). The developmental stages were defined according to Lancashire et al. (1991). WHC was monitored daily at 9:00 during the stress treatments in the center of the pot by 5TE sensors (Decagon Devices Ltd., Pullman, WA, USA) and the re-watering occurred when the soil water content dropped below 5 v/v%, maintaining consistent stress intensity (Figures 7, ). This study was conducted in three climate-controlled greenhouse chambers with different CO<sub>2</sub> levels:

ambient (~400 ppm) as control and enriched to 700 ppm<sup>8</sup> or 1000 ppm. Pure CO<sub>2</sub> was introduced into the chambers through a perforated pipe network placed 0.5 m above the plants. Uniform gas distribution was achieved by ventilation. The CO<sub>2</sub> concentration was controlled by SH-VT250 device (SH-VT250 CO<sub>2</sub>, Temperature and Humidity Transmitter, Soha Tech Co., Ltd., Soul, Korea), and the CO<sub>2</sub> level was measured and verified by Wöhler CDL 210 (Wöhler CDL Serie 210 CO<sub>2</sub> Messgerät, Wöhler Technik GmbH, Bad Wünnenber, Germany) logger device in the chambers where the plants are grown under elevated CO<sub>2</sub> concentration.

In this experiment, four vernalized plants of each tested variety were planted in plastic pots (depth: 27 cm; diameter: 24 cm) as described by Varga et al. (2017). The experimental design comprised 108 pots in total, distributed across the three greenhouse chambers with different carbon dioxide levels. A total of 432 plants were examined, with 12 plants of each variety subjected to the same treatments under different irrigation and CO<sub>2</sub> levels. Measurements at full maturity included shoot heights, spike lengths and weights, grain number per spike and grain weights per spike. The exact water uptake of the plants/pot was monitored by a digital balance (ICS689g-A15, Mettler Toledo Ltd., Budapest, Hungary) from the planting to the final harvest, while spike and grain weights were measured with a digital scale (440-45N, KERN & SOHN GmbH, Balingen, Germany). Plant heights were determined by adding the length of the shoots and spikes.

Relative changes of the different parameters to elevated carbon dioxide levels were calculated by using Eq. (1):

$$Ex/A \text{ or } Ey/A \quad (1)$$

where A is the different parameters' values at 400 ppm CO<sub>2</sub> level, Ex is the different parameters' values at 700 ppm CO<sub>2</sub> level and Ey is the different parameters' values at 1000 ppm CO<sub>2</sub> level.

### Plant growth conditions

On December 14th in 2019, seeds of each tested variety were prepared for germination. These seeds were placed in plastic boxes in the dark at room temperature (22 °C) for two days. Subsequently, the plants were moved to the vernalization chamber at 4 °C for 48 days. On February 3rd in 2020, four seedlings were transplanted into pots containing 10 L of homogenous mixture of soil, sand and humus in a 3:1: (v/v) ratio. The spring–summer climatic program (Tischner et al. 1997) was employed to automatically regulate climatic conditions. According to the developmental stages, the air temperature was raised from 10–12 °C to 24–26 °C, and the relative humidity was maintained between 60 and 80%. Artificial illumination was used to supplement natural light, reaching

500  $\mu\text{mol m}^{-2} \text{s}^{-1}$  at the start of the vegetation period and gradually increasing to 700  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . A nutrient solution was applied once a week, before watering, and each pot received 200 mL of an 0.322 w/w% water-soluble fertilizer (14% N, 7%  $\text{P}_2\text{O}_5$ , 21%  $\text{K}_2\text{O}$ , 1% Mg, 1% B, Cu, Mn, Fe, Zn; Volldünger Classic; Kwizda Agro Ltd., Vienna, Austria) before irrigation. Watering with tap water occurred twice a week until the tillering stage of the plant and increased to three times a week thereafter. Non-transparent foil was used to cover the soil, preventing evaporation. During the vegetation sulfur (Thiovit Jet) and lambda-cyhalothrin (Karate Zeon 5 CS, Syngenta Ltd. Switzerland) were applied twice based on the manufacturer's recommendations. The use of fungicide and insecticide was necessary to control the powdery mildew and aphid infestation.

## Statistical processing

The experimental design involved four winter wheat varieties, three watering treatments and three  $\text{CO}_2$  levels in three replicates. A Kruskal–Wallis test was performed to determine the effects of the tested factors (variety, water supply and  $\text{CO}_2$ ) and Tukey's post hoc test to compare means. SPSS 16.0 program (IBM, Armonk, NY, USA), and Microsoft Excel (Microsoft, Redmond, WA, USA) were used for the statistical analysis and visualization. The significance level was set at  $P \leq 0.05$ .

## Results

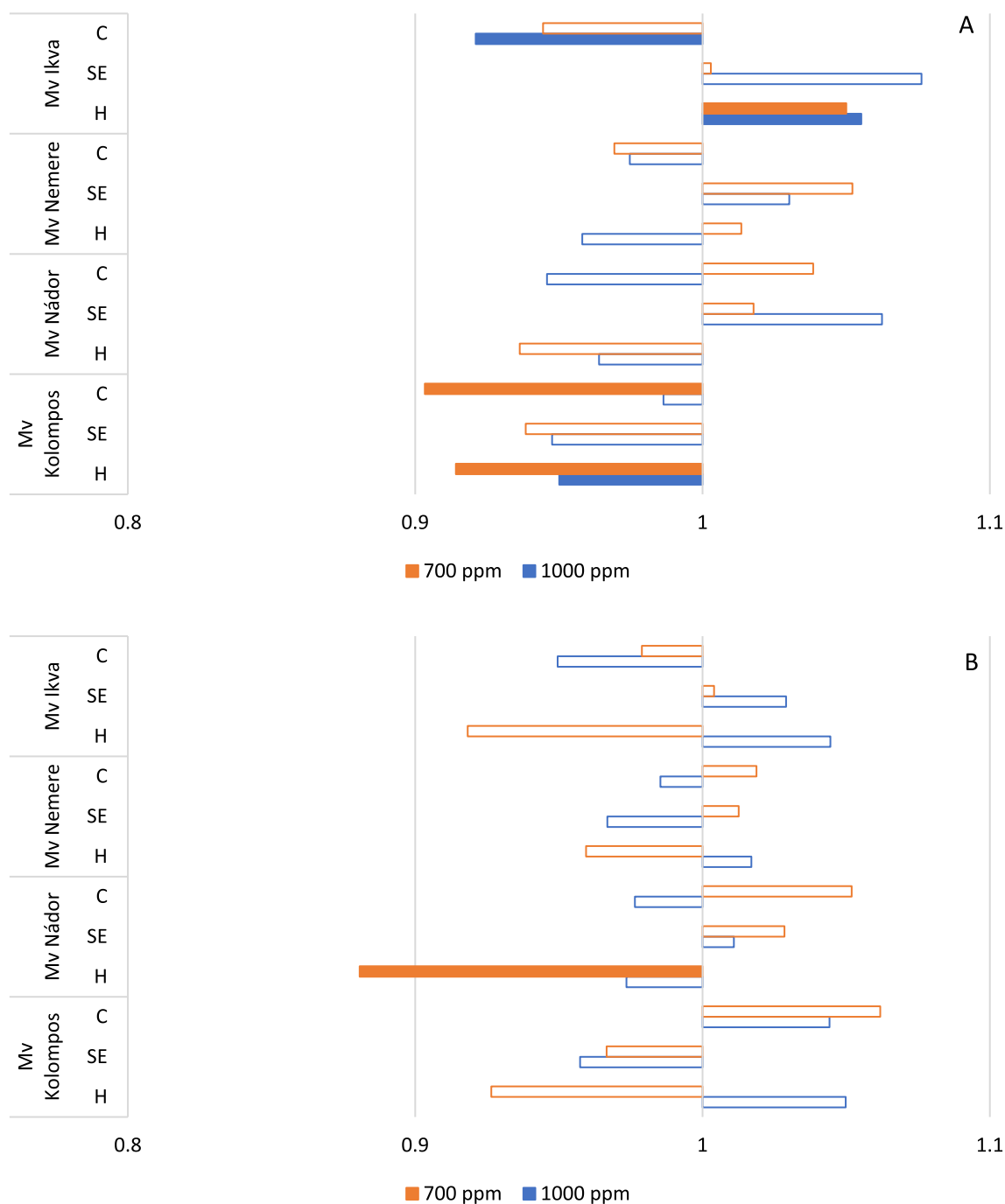
### The effects of the elevated $\text{CO}_2$ concentration combined with drought stress on the plant heights

At the current atmospheric  $\text{CO}_2$  level, compared to the optimal watering, the drought stress at stem elongation phenophase significantly decreased the plant height in the case of the main tillers by 'Mv Ikva' (18%), 'Mv Nemere' (15%) and 'Mv Nádor' (15%) and the water withdrawal at heading stage decreased this parameter with 10% by 'Mv Ikva' and with 9% by 'Mv Nemere' varieties. In the case of the secondary tillers, a significant decrease was observed by early-stage drought stress by 'Mv Ikva' (9%) and by late-stage drought treatment by 'Mv Ikva' (27%), 'Mv Nemere' (15%) and 'Mv Kolompos' (6%) varieties. By the late-ripening variety ('Mv Kolompos'), a significant increase (6%) was observed as an effect of the stem elongation-stage drought (Table 1). At an elevated carbon dioxide level (700 ppm), the early-stage drought decreased the plant height of the 'Mv Nádor' (17%) and 'Mv Ikva' (13%) varieties' main shoot and the heading-stage drought by 'Mv Nádor' (8%), compared to the control. In the case of the heights of the secondary tillers, a 7% decrease was observed by the extreme early

ripening variety ('Mv Ikva') as an effect of the stem elongation-stage drought. The drought simulated at the heading stage decreased this parameter in 'Mv Ikva', 'Mv Nádor', 'Mv Nemere' and 'Mv Kolompos', with 32%, 21%, 20% and 18%, respectively (Table 1). At 1000 ppm  $\text{CO}_2$  level, the drought stress at stem elongation phenophase caused a significant decrease (10%) in the plant height of the main tillers only by the 'Mv Nemere' variety. Drought at the heading stage decreased plant heights of main shoots by the 'Mv Nemere' (11%), by the secondary tillers in the case of 'Mv Ikva' (20%) and 'Mv Nemere' (12%) genotypes (Table 1). In this study, significant differences were observed regarding the plant heights between the main and secondary tillers as an effect of the heading-stage water shortage at the three tested carbon dioxide levels (~400 ppm, 700 ppm, 1000 ppm) by all examined winter wheat varieties. In the case of the late-ripening variety ('Mv Kolompos'), the plant heights differed between the main and secondary tillers in every applied treatment (control, drought at stem elongation or heading developmental stage) (Table 1). Positive impact of  $\text{CO}_2$  was observed in the case of the extreme early ripening variety's ('Mv Ikva') plant heights in the main shoots as an effect of the heading-stage drought stress when the carbon dioxide concentration was elevated from the ambient level up to 700 ppm or 1000 ppm (Fig. 1A). The plant heights of the main tillers in the case of the 'Mv Kolompos' variety reacted negatively to the elevation of  $\text{CO}_2$  level up to 700 ppm level by the optimal watering and late-drought treatment. Compared to the ambient level at 700 ppm  $\text{CO}_2$  concentration, also a negative reaction was observed in the plant height of the late-ripening variety ('Mv Kolompos') when the plants were stressed at the heading phenophase. In the case of the tested winter wheat varieties' secondary tillers, only one significant  $\text{CO}_2$  impact was observed, on 'Mv Nádor' genotype. In the case of the late-stage drought stress at 700 ppm carbon dioxide level, lower plant height was observed than at the ambient level (Fig. 1B).

### The effects of the elevated $\text{CO}_2$ concentration combined with drought stress on the spike length

At the current atmospheric  $\text{CO}_2$  concentration, the drought stress simulated in BBCH31 or BBCH51 phenophases caused no significant differences regarding the lengths neither by the main nor the secondary spikes at any tested winter wheat varieties but by the extreme early ripening genotype's ('Mv Ikva') main spikes. The length of spikes of the main spikes was longer than the secondary spikes in the optimal watering and late-stage drought stress treatment in the case of all tested varieties. As an effect of the early-stage drought, a 10% reduction in spike length was observed by 'Mv Nádor' variety (Table 2). At 700 ppm  $\text{CO}_2$  level, the stem elongation-phase stress decreased by 13% the lengths



**Fig. 1** Reactions of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') to the elevated carbon dioxide levels compared to the current atmospheric concentration regard to the plant heights of main **A** and secondary **B** shoots. 'C' represents control (optimum watering), 'SE' stands for water withdrawal

at the stem elongation developmental stage, 'H' represents the water withdrawal at the heading stage. The filled bars represent the significant difference from the current atmospheric carbon dioxide level at  $P \leq 0.05$  significance level

of the main and secondary spikes of the 'Mv Ikva' genotype and the heading-stage drought increased this parameter by 9% in the case of the 'Mv Nemere' variety. For secondary spikes, only the late-stage drought caused significant

differences, namely a 15% decrease in the spike's length by 'Mv Kolompos' and 'Mv Nádor' varieties. At 700 ppm CO<sub>2</sub> level, the lengths of the spikes were significantly lower by the secondary spikes compared to the main spikes in the



heading-stress treatment in every tested variety. By optimal watering, significant differences occurred by ‘Mv Ikva’ and ‘Mv Nádor’ varieties between the main and secondary tillers. As an effect of the stem elongation-stage drought, the main spikes were longer by the ‘Mv Kolompos’ and ‘Mv Nemere’ varieties (Table 2). At 1000 ppm carbon dioxide concentration, no significant changes were observed by the main ears. However, the applied stem elongation-stage stress increased the length of the secondary spikes by the ‘Mv Ikva’ (18%) and by the ‘Mv Nádor’ (12%) varieties. Significant differences were observed between the main and secondary spikes in the case of the well-watered ‘Mv Ikva’, ‘Mv Nemere’ and ‘Mv Kolompos’ varieties and by ‘Mv Ikva’, ‘Mv Nemere’ and ‘Mv Nádor’ genotypes as an effect of the heading-stage stress (Table 2). As an effect of the elevation of the carbon dioxide level, a positive CO<sub>2</sub> reaction was observed in the case of the late-ripening variety’s (‘Mv Kolompos’) spike’s lengths in all treatments (optimal watering, drought stress at stem elongation or heading phenophase) at 700 ppm level. However, a positive impact of the elevated CO<sub>2</sub> level (1000 ppm) compared to the atmospheric concentration can be detected only by the late-stage drought (Fig. 2A, B). By the ‘Mv Nádor’ variety, in the case of the heading-stage drought, a significant decrease was observed as an effect of the CO<sub>2</sub> enrichment regarding the spike lengths (Fig. 2A, B). Positive impact of CO<sub>2</sub> showed on the lengths of the main spikes by the ‘Mv Ikva’ variety in the early stress and by the ‘Mv Nemere’ genotype by the two applied stress treatments at 700 ppm and by late-stage drought at 1000 ppm (Fig. 2A). By the lengths of the secondary spikes, the well-watered ‘Mv Ikva’ at 700 ppm showed a positive reaction to the carbon dioxide concentration elevation, and by the heading-stage stressed, ‘Mv Nemere’ and ‘Mv Nádor’ genotypes at 1000 ppm level were observed the same effect. But as an effect of the drought simulated in the late developmental stage by the ‘Mv Ikva’, we observed a decrease in this parameter at 1000 ppm compared to the ambient carbon dioxide level (Fig. 2B).

### The effects of the elevated CO<sub>2</sub> concentration combined with drought stress on the spike weight

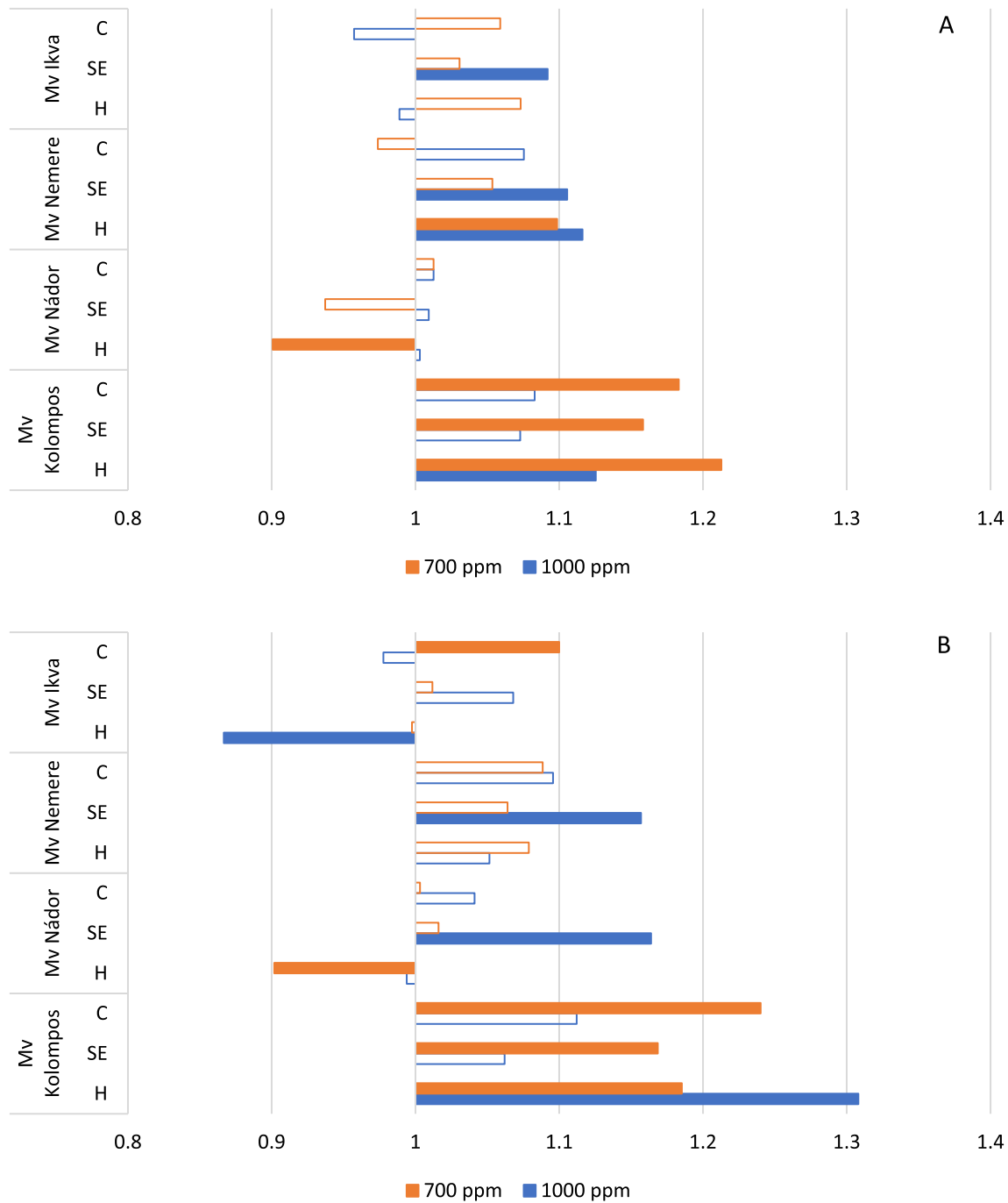
At ambient carbon dioxide level, the drought stress applied by stem elongation phenophase decreased the weights of spikes by main ears in the case of ‘Mv Nemere’ (35%), ‘Mv Nádor’ (28%) and ‘Mv Ikva’ (12%) varieties. By secondary spikes, the BBCH31-stage stress also caused a significant decrease in ‘Mv Nádor’ (22%), ‘Mv Nemere’ (18%) and ‘Mv Ikva’ (17%) varieties. Regarding the weights of the spikes, the heading-stage drought decreased this parameter by the ‘Mv Ikva’ genotype with 9% (main spikes) and by the ‘Mv Nemere’ (13%) variety in the case of the secondary spikes (Table 3). When the carbon dioxide level was elevated up

to 700 ppm, the early-stage drought decreased the spikes’ weights of main ears in every tested variety (‘Mv Nádor’ with 39%, ‘Mv Kolompos’ with 22%, ‘Mv Nemere’ with 16%, ‘Mv Ikva’ with 15%). In the case of secondary spikes, the water withdrawal applied by the stem elongation phase only decreased this parameter by the ‘Mv Nemere’ (20%) variety and the late-stage drought lowered it in the case of ‘Mv Kolompos’ and ‘Mv Nádor’ with 33% and 18%, respectively (Table 3). At 1000 ppm CO<sub>2</sub> concentration, the early-stage drought decreased the spikes’ weights of main spikes in ‘Mv Nádor’ (35%), ‘Mv Nemere’ (28%) and ‘Mv Kolompos’ (20%) genotypes and by secondary spikes, significant differences were observed by ‘Mv Nádor’ (24%) compared to the control treatment (Table 3). At ambient CO<sub>2</sub> level, the weights of the main ears were higher than the tillers’ ears in every tested variety in each treatment, except by the ‘Mv Nemere’ genotype. In this case, as an effect of the early drought, the weight of the main and the secondary tillers were not different. At 700 ppm and 1000 ppm CO<sub>2</sub> concentration, the same phenomenon was observed in the case of the ‘Mv Nádor’ and the ‘Mv Nemere’ variety (Table 3).

The elevation of the carbon dioxide level from the current atmospheric level up to 1000 ppm caused no significant changes regarding the weight of the spikes in the case of main ears in any winter wheat varieties. When the CO<sub>2</sub> concentration was elevated up to 700 ppm, significant increases were observed by this parameter by the late-ripening genotype (‘Mv Kolompos’s main ears) in the case of the well-watered plants and by the heading-phase drought treatment, compared to the ambient CO<sub>2</sub> level. But by ‘Mv Nemere’ variety, as an effect of the elevation of the carbon dioxide level significant decrease was observed in the spike weights under optimal irrigation. By ‘Mv Nádor’ variety, significant decreases were observed by the two applied stress treatments (drought in BBCH31 and BBCH51 phenophase) (Fig. 3A). By the secondary spikes of the tested varieties, significant increases were observed in the ‘Mv Kolompos’ variety in the applied treatments (optimal watering, drought by stem elongation or heading developmental stage) at 700 ppm CO<sub>2</sub> level and by drought treatment at 1000 ppm level (compared to the atmospheric level). In the case of the ‘Mv Nádor’ variety, the CO<sub>2</sub> enrichment up to 700 ppm significantly decreased the spike weights by optimal watering or simulated drought stress in the BBCH51 stage at 1000 ppm CO<sub>2</sub> level (Fig. 3B).

### The effects of the elevated CO<sub>2</sub> concentration combined with drought stress on the grain number

At current atmospheric CO<sub>2</sub> level, the drought stress at stem elongation phenophase significantly decreased the average number of grains of the main spikes by ‘Mv Nemere’ (43%), ‘Mv Nádor’ (29%) and ‘Mv Ikva’ (22%) varieties. Drought

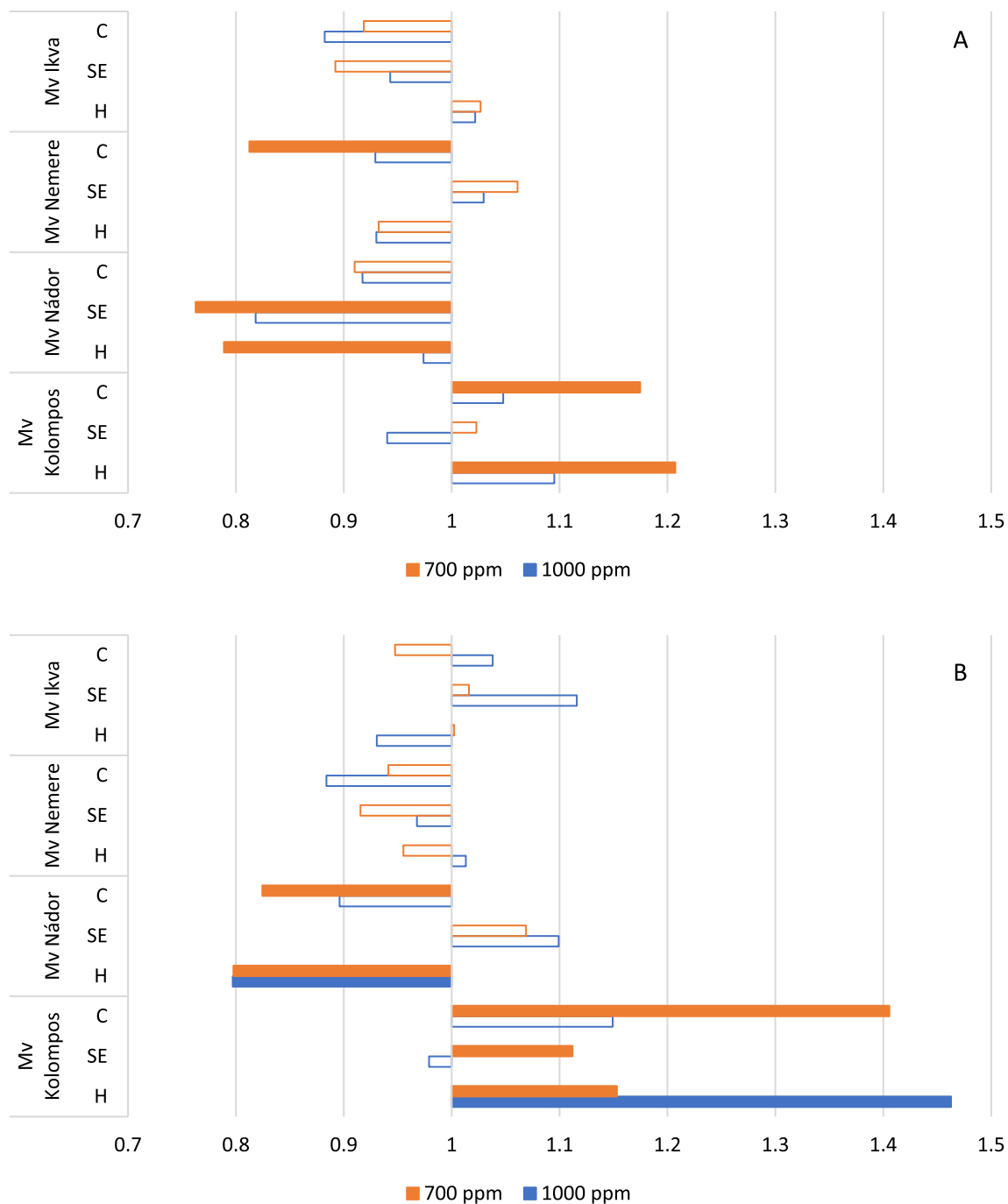


**Fig. 2** Reactions of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') to the elevated carbon dioxide levels compared to the current atmospheric concentration regard to the lengths of main **A** and secondary **B** spikes. 'C' represents control (optimal watering), 'SE' stands for water withdrawal at the stem

elongation developmental stage, 'H' represents the water withdrawal at the heading stage. The filled bars represent the significant difference from the current atmospheric carbon dioxide level at  $P \leq 0.05$  significance level

stress at heading phenophase caused a significant decrease (18%) in the grain number of the secondary spikes by 'Mv Ikva' and 'Mv Kolompos' varieties (Table 4). Under elevated (700 ppm) carbon dioxide concentration, the applied drought stress at the stem elongation phase decreased the grain

number with 16% of main spikes and increased it by 12% on the secondary spikes by 'Mv Ikva' genotype. The early developmental phase drought decreased (23%) the grain number of secondary spikes in the case of 'Mv Nádor' variety. By secondary spikes, decreases were observed by 'Mv



**Fig. 3** Reactions of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') to the elevated carbon dioxide levels compared to the current atmospheric concentration regard to the weights of main **A** and secondary **B** spikes. 'C' represents control (optimal watering), 'SE' stands for water withdrawal at the stem

elongation developmental stage, 'H' represents the water withdrawal at the heading stage. The filled bars represent the significant difference from the current atmospheric carbon dioxide level at  $P \leq 0.05$  significance level

Kolompos' (35%) and 'Mv Ikva' (21%) varieties as an effect of the heading-stage drought (Table 4). At 1000 ppm CO<sub>2</sub> concentration, no significant alterations were observed as an effect of the drought stress treatments in the case of the main spikes. By the secondary spikes, the late stress decreased

the grain number by 'Mv Nádor' (20%) and 'Mv Nemere' (15%) varieties (Table 4). At the current atmospheric carbon dioxide level, significant decreases were observed in the four tested varieties by optimum irrigation and drought stress at the heading stage; the main spikes contained more grains.



When the plans were stressed at the stem elongation phenophase, significantly more grains were found by the main spikes of 'Mv Kolompos' (Table 4). At 700 ppm CO<sub>2</sub> level and optimal watering, the grain number in the main spikes was higher than in the secondary spikes. Drought stress at stem elongation phenophase induced higher grain number in the main spikes of the 'Mv Kolompos' and 'Mv Nemere' varieties. Drought stress at the heading stage induced significant differences between the main and secondary spikes by each genotype except 'Mv Nádor' (Table 4). The main spikes showed significantly higher grain numbers by 'Mv Nemere' and 'Mv Kolompos' varieties at 1000 ppm CO<sub>2</sub> concentration and under optimum watering. Simulated drought stress at stem elongation resulted in a higher grain number only by 'Mv Nemere' variety; however, the late-drought stress induced a significant increase in each genotype (Table 4).

The elevation of CO<sub>2</sub> up to 700 ppm resulted in a negative effect regarding the grain number per ear of the main spikes under optimum watering by 'Mv Nemere', 'Mv Nádor' and 'Mv Ikva' varieties compared to the atmospheric level. Drought stress induced at the stem elongation stage significantly increased the grain numbers of the 'Mv Nemere' variety and drought at the heading stage increased the number of grains by 'Mv Kolompos' and a decreased by 'Mv Nádor' varieties as the effect of the CO<sub>2</sub> enrichment. Lower spike numbers were observed at 1000 ppm than at atmospheric CO<sub>2</sub> level by optimal irrigated 'Mv Ikva' and 'Mv Nádor' genotypes, and the early drought increased the grain numbers (Fig. 4A). In the case of the grain number per spike by the secondary spikes, a less significant CO<sub>2</sub> impact was observed; by the 'Mv Nemere' variety, the drought stress at heading increased the grain number at both elevated carbon dioxide levels (700 ppm or 1000 ppm). By the 'Mv Kolompos' variety, the late drought decreased the grain number at 700 ppm and increased it at 1000 ppm level compared to the atmospheric CO<sub>2</sub> concentration (Fig. 4B).

### The effects of the elevated CO<sub>2</sub> concentration combined with drought stress on the grain weight

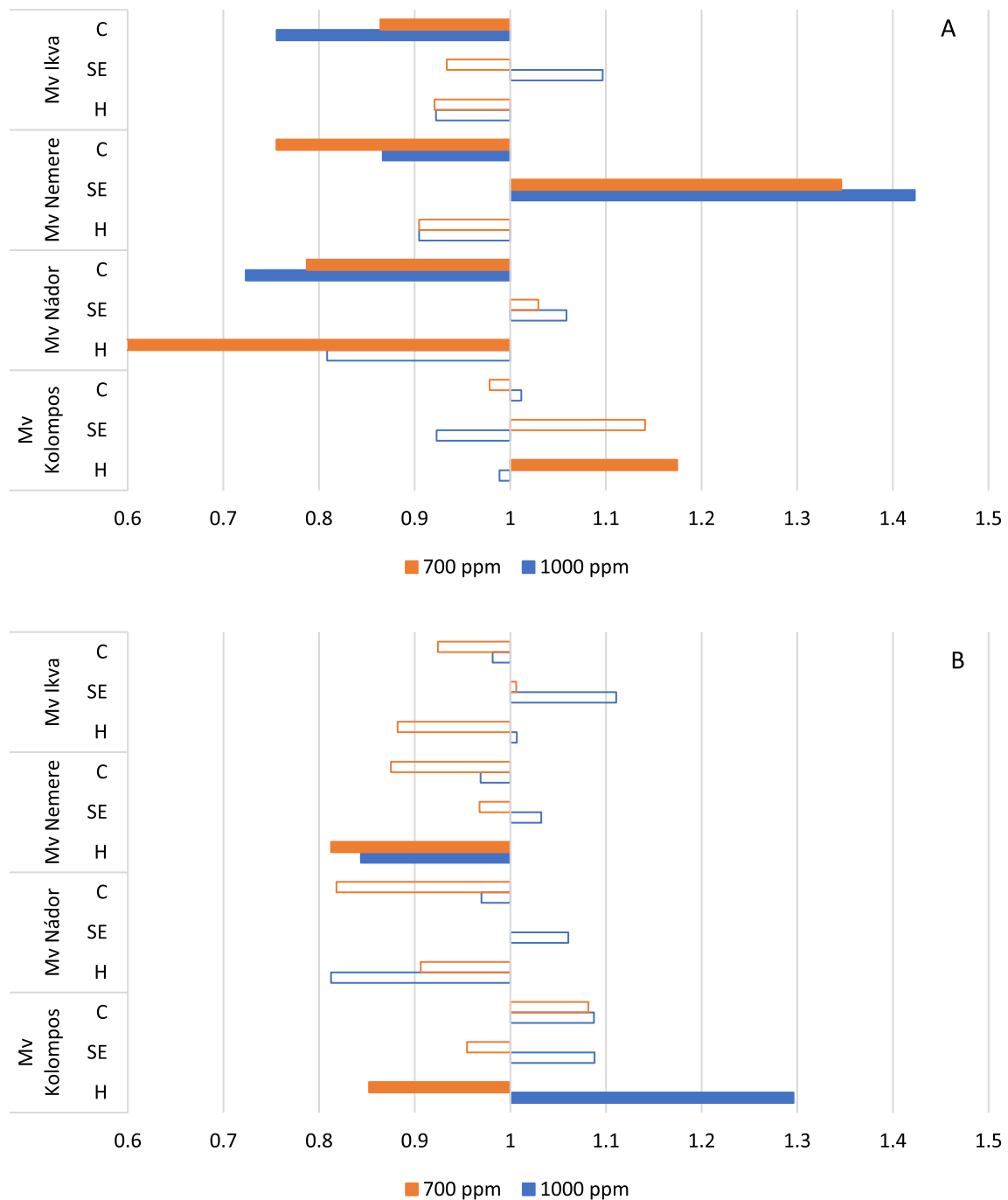
At the atmospheric carbon dioxide level, the water withdrawal at the stem elongation stage decreased the grain weight of the main spikes by 'Mv Nemere', 'Mv Nádor' and 'Mv Ikva' with 37%, 27% and 12%, respectively. Drought at heading phenophase caused a 9% decrease in grain weight of the main spike by 'Mv Ikva', as compared with the well-watered control (Fig. 5). By the grain weight per spikes of secondary spikes, 'Mv Ikva' and 'Mv Nemere' show no significant changes compared to the control. However, by 'Mv Nádor' each applied stress treatment decreased the grain weight of the early and late-drought stress by 26% and 16%, respectively. In the case of the late-ripening genotype ('Mv Kolompos'), a 27% decrease was observed as an effect of

the water shortage at the heading stage (Fig. 5). At 700 ppm CO<sub>2</sub> level, the applied early-drought treatment decreased the grain weight by the main spikes of 'Mv Nádor' (41%) and 'Mv Ikva' (16%) varieties and by the secondary spikes of 'Mv Ikva' (13%). Drought at heading decreased the grain weights of 'Mv Nádor' by 43% and the 'Mv Kolompos' by 37% in the secondary spikes (Fig. 5). At 1000 ppm carbon dioxide concentration, significant decreases (33% 25% 22%) were observed regarding the grain weights of the main spikes by 'Mv Nádor', 'Mv Nemere' and 'Mv Kolompos' genotypes, respectively as an effect of the early-stage drought. By secondary tillers, the drought stress caused changes only by 'Mv Nemere', the water shortage at BBCH31 decreased the grain weight by 13% (Fig. 5). The comparison of the main and secondary spikes showed that the grain weights were higher in each genotype by every treatment except by the 'Mv Nádor' in the early-stage drought treatment when no significant changes were observed on the three carbon dioxide levels (Table 5).

Compared to the atmospheric level, the elevation of the carbon dioxide concentration up to 700 ppm significantly reduced grain weight. In the case of the grain weights per main spikes by the optimal watered 'Mv Nemere' variety, and by the 'Mv Nádor' genotype in the two applied stress treatments. In the case of secondary spikes, the elevation of CO<sub>2</sub> up to 700 ppm caused significant changes only by 'Mv Nádor'; lower grain weight was observed at 700 ppm than the atmospheric CO<sub>2</sub> level. When the carbon dioxide concentration was elevated up to 1000 ppm, higher values were observed in 'Mv Ikva' by both applied stress treatment and by 'Mv Kolompos' as a result of the late-stage stress (Fig. 6A, B).

## Discussion

Drought significantly impacts wheat plant height, a crucial trait. Insufficient moisture during stem elongation leads to reduced photosynthesis and hinders metabolite/nutrient translocation in wheat (Sarto et al. 2017). This decline in height is a result of altered carbon partitioning as plants undergo osmotic adjustment under water stress (Blum and Sullivan 1997). The extent of height reduction depends on both drought intensity and genotype (Mirbahar et al. 2009; Khadka et al. 2020). Drought-tolerant plants tend to maintain shorter plant height and plant area index, minimizing water demand and preventing transpiration-related water loss (Su et al. 2019). Consequently, smaller plants demonstrate proportionally less growth reduction than larger ones, suggesting that smaller plants are less sensitive to water stress (Blum and Sullivan 1997). Unlike the previous findings mentioned, we observed opposite results in our experiment. On the one hand, in this study, the drought stress

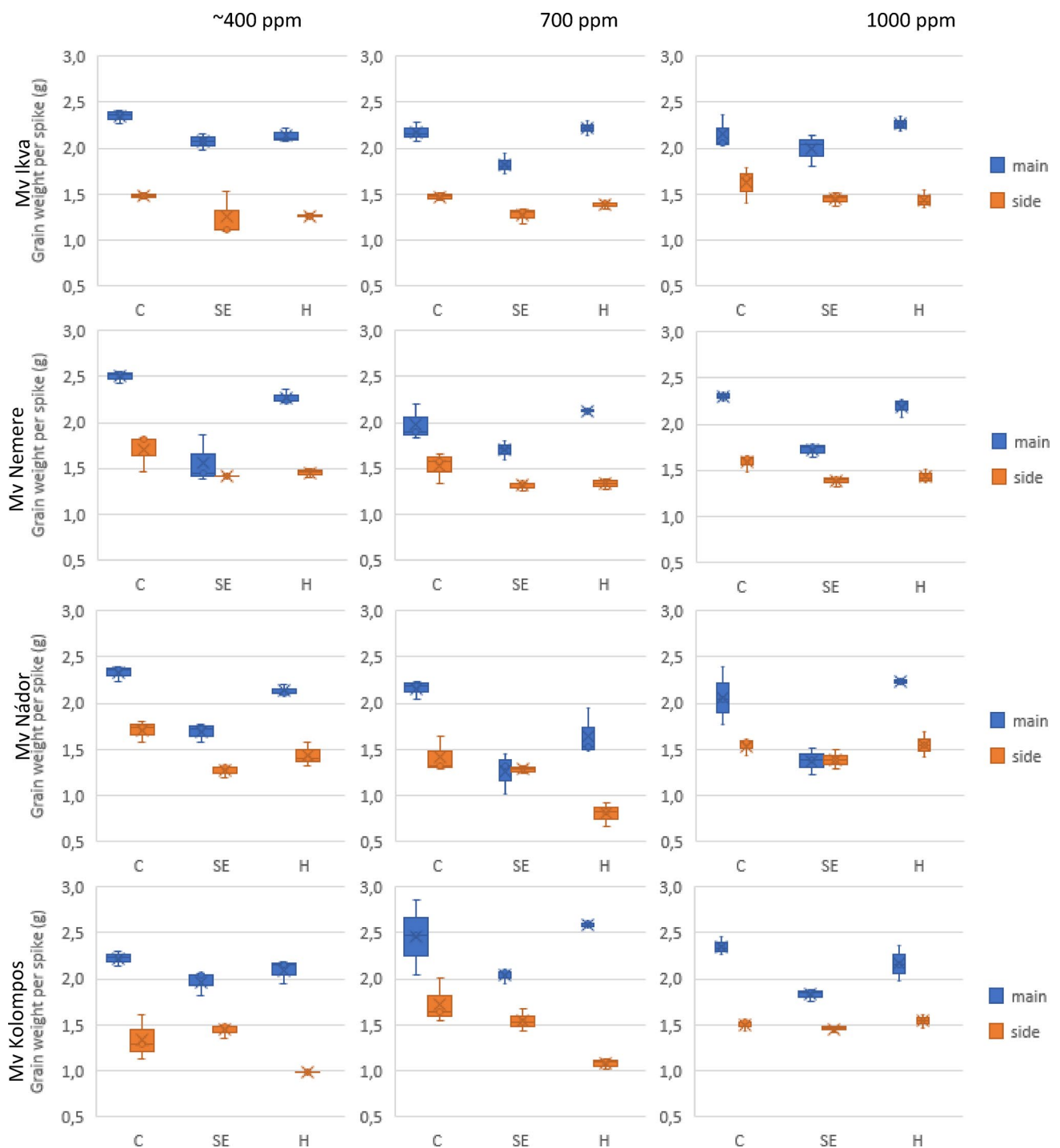


**Fig. 4** Reactions of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') to the elevated carbon dioxide levels compared to the current atmospheric concentration regard to the number of grains of main **A** and secondary **B** spikes. 'C' represents control (optimal water regime), 'SE' stands for water with-

drawal at the stem elongation developmental stage, 'H' represents the water withdrawal at the heading stage. The filled bars represent the significant difference from the current atmospheric carbon dioxide level at  $P \leq 0.05$  significance level

significantly reduced plant height across different wheat varieties, with the magnitude of the decrease depending on both the timing of water withdrawal (stem elongation or heading stage) and the  $\text{CO}_2$  concentration. At current atmospheric carbon dioxide levels, drought during stem elongation

decreased the height of main spikes by 18% and 15% in the extreme early and in the two early ripening wheat varieties, respectively. On the other hand, the tallest plant height was observed in the late-ripening wheat variety, 'Mv Kolompos', and among the tested varieties, this one exhibited the highest

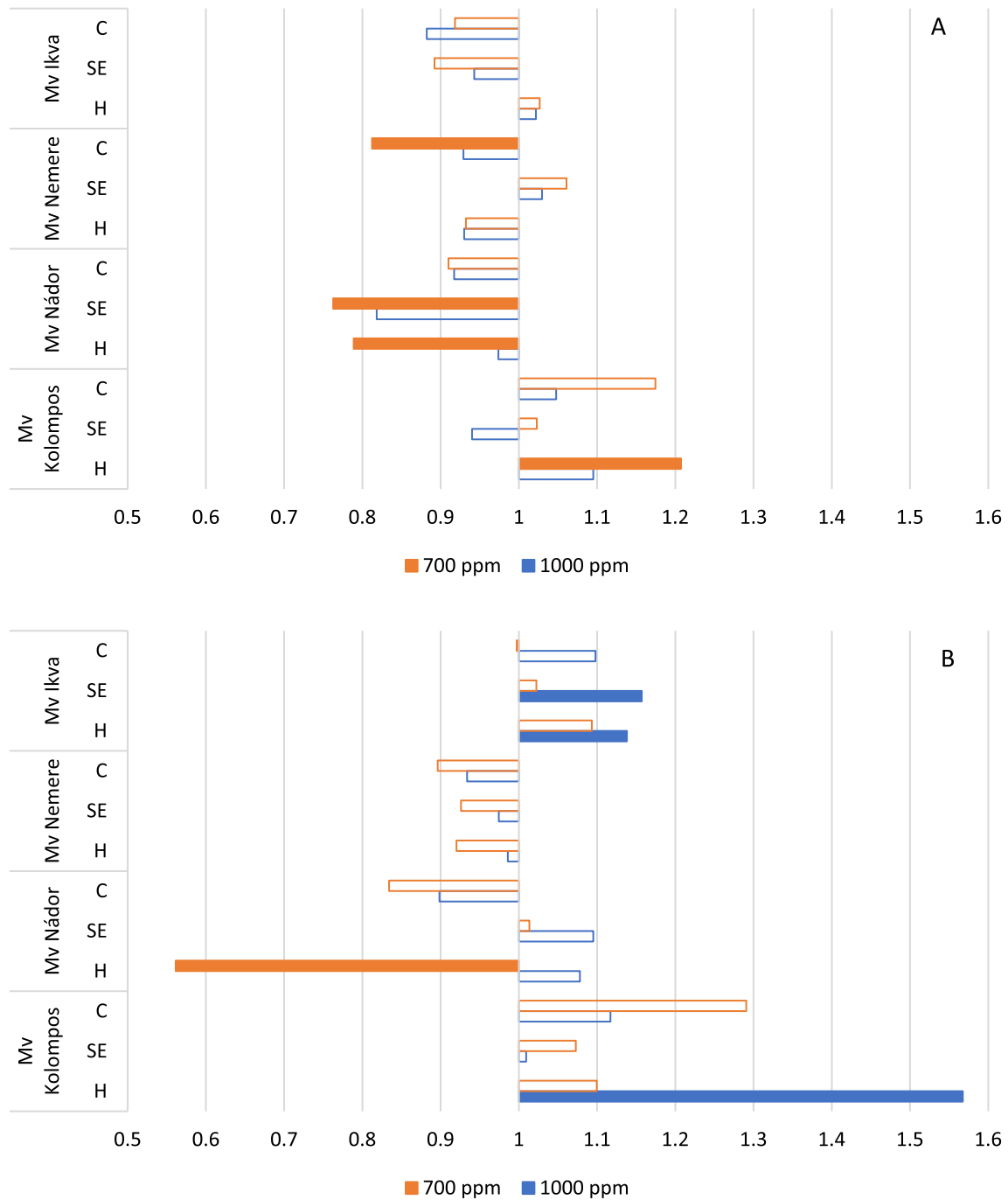


**Fig. 5** Average weight of grains by main (main) and secondary (side) spikes of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') at different carbon dioxide levels

(atmospheric, 700 ppm, 1000 ppm) with different watering levels (optimal 'C', water withdrawal at stem elongation 'SE' or at heading 'H' developmental stage). The significance level was set at  $P \leq 0.05$

drought resistance in terms of plant height. Neither early (stem elongation phase) nor late (heading stage) drought stress caused significant height reduction in this variety. Duvnjak et al. (2023) also found no significant differences regarding the plant height of winter wheat in the case of

stem elongation-stage drought. Xu (2015) found no significant differences in plant height under optimal growth conditions at either 400, 600, 800 or 1000 ppm carbon dioxide levels. In our research, under optimal irrigation, compared to the ambient level, we observed a negative  $\text{CO}_2$  response



**Fig. 6** Reactions of the tested winter wheat varieties ('Mv Ikva', 'Mv Nemere', 'Mv Nádor', 'Mv Kolompos') to the elevated carbon dioxide levels compared to the current atmospheric concentration regard to the weight of grains of main **A** and secondary **B** spikes. 'C' represents the control (optimal water regime), 'SE' stands for water with-

drawal at the stem elongation developmental stage, 'H' represents the water withdrawal at the heading stage. The filled bars represent the significant difference from the current atmospheric carbon dioxide level at  $P \leq 0.05$  significance level

in the late-ripening wheat variety at 700 ppm and the case of the extremely early ripening genotype at 1000 ppm. Interestingly, at 700 ppm  $\text{CO}_2$  concentration, the late-ripening variety showed a significant increase in plant height during early-stage drought stress, suggesting that some genotypes

might exhibit positive growth responses under elevated  $\text{CO}_2$  levels, but only under specific conditions.

The length of spikes plays a critical role in determining the number of grains per spike; longer spike may have the potential to produce a greater number of grains. Spike

length is influenced by genotype, but consistent observations indicate that it is significantly affected by environmental factors (Mirbahar et al. 2009; Frantová et al. 2022). Although several studies (Khan and Naqvi 2011; Khyber et al. 2019; Frantová et al. 2022) claimed that drought negatively affects the length of wheat spikes, in our experiment, we found that only by the extremely early ripening genotype and only in the case of the early-stage drought. However, Wang et al. (2017) claimed that the imposition of drought at the different developmental stages had a moderate effect on the spike length. We found a positive reaction among the tested varieties to the elevation of the carbon dioxide level up to 700 ppm in the case of the late-ripening genotype, in every treatment (control, the early- or late-stage drought) and at 1000 ppm level by the late drought. Although only a few studies deal with this topic, especially with these developmental stages (stem elongation or heading stage), Shokat et al. (2020) found no significant effects of anthesis-stage drought at 800 ppm CO<sub>2</sub> concentration, regarding this parameter. On the other hand, Aljazairi and Nogués (2015) found significant differences between their CO<sub>2</sub> treatments in terms of spike length. Additionally, a consistent pattern of longer spike length in main spikes compared to secondary spikes was observed under optimal watering and drought conditions. Notably, the positive CO<sub>2</sub> impact in spike length was evident on the late-ripening variety, especially at elevated carbon dioxide levels (700 and 1000 ppm), indicating potential genotype-specific responses to CO<sub>2</sub> enrichment.

Studies stated that at the current atmospheric CO<sub>2</sub> concentration, the weight of the spikes was decreased as an effect of the late-stage (pre-anthesis or post-anthesis) or long-lasting drought stress by bread wheat (Fischer and Wood 1979; Yang et al. 2001; Saeedipour 2011; Chen et al. 2021). In our study, we obtained a significant reduction regarding the weight of the spikes as an effect of the late-stage drought in only one genotype but the early, stem elongation-stage drought caused significant decreases in spike's weight in majority of the tested genotypes. González et al. (2002) stated that drought can shorten the stem elongation phase and consequently reduce the dry weight of ears, which was also confirmed in our study for 'Mv Nádor' genotype. Abdelhakim et al. (2022) found a positive impact of CO<sub>2</sub> on the weights of spikes of spring wheat under control conditions at ~770 ppm compared to the current atmospheric concentration. In our experiment, we also observed a positive impact of CO<sub>2</sub> at 700 ppm level in the case of the late-ripening genotype under control conditions and by the water shortage at the heading stage. However, under control conditions, we observed a significant decrease in the weight of the spikes at 700 ppm compared to the current atmospheric carbon dioxide level.

Although numerous studies have investigated the extent to which drought stress experienced during the generative

developmental stage can reduce the number of grains per spike (e.g., Mogensen 1985; Kato et al. 2008; Dolferus et al. 2011; Duvnjak et al. 2023), few studies have focused on the effect of drought stress during early developmental stages (tillering, stem elongation) on grain number. We observed a significant decrease in the number of grains per spike by the extreme early and early ripening varieties. Manderscheid and Weigel (2007) also found that dry conditions (drought stress was started two or three weeks after the first node appearance) significantly decreased the grain numbers per spike at ambient CO<sub>2</sub> level. The numbers of grains per spike reacted negatively to the elevation of the carbon dioxide level up to 700 or 1000 ppm by the extreme early or the early varieties. On the contrary to our findings, Sionit et al. (1980) and Manderscheid and Weigel (2007) found no significant effect of the CO<sub>2</sub> concentration on grain number per spike.

The grain weight per spike greatly affects the formation of wheat yield and depends on one hand on the weather conditions and the other hand on the genetic characteristics of certain varieties (Lozinskiy et al. 2021; Korkhova et al. 2023). According to Fischer (1973), the greatest reduction in grain weight of wheat occurs when the water deficiency starts 15 days before and 5 days after heading while González et al. (2002) reported that drought can reduce the number of fertile florets at late-stage plant development period resulting in lower grain yields. In contrast to this, in our study significant decrease in grain weight per spike was determined only in the extreme early ripening genotype as an effect of the late-stage (heading) drought. However, drought stress in the early developmental stage caused a more severe decrease in the extreme early and early ripening varieties. It has been stated that the grain yield of wheat increase when it is exposed to elevated carbon dioxide concentration before floral initiation (Krenzer and Moss 1975). However, the reports say that the responses of yield components of wheat grain yields under elevated carbon dioxide levels have not been consistent. Combe (1981) reported that the increased grain yield (30–40%) at 950 ppm CO<sub>2</sub> level was due to an increased number of grain per spike and not to more spikes or increased grain weight. On the other hand, we observed negative impact or no impact of the elevation of the CO<sub>2</sub> concentration on the weights of grains.

## Conclusion

This study demonstrates that wheat varieties respond differently to drought stress and elevated CO<sub>2</sub> levels, with significant variations in plant height, spike length, spike weight, grain number and grain weight. Overall, elevated CO<sub>2</sub> concentrations can exacerbate the negative effects of drought, particularly in drought-sensitive genotypes like 'Mv Nádor'. However, some varieties, such as 'Mv Kolompos', may

benefit from increased CO<sub>2</sub>, particularly in non-stress or mild drought conditions. The observed differences between the main and secondary tillers across all treatments highlight the differential adaptation strategies of the tested wheat varieties. In several cases, secondary tillers were more affected by drought, indicating that they may serve as a key determinant of yield stability under future climate scenarios. These findings suggest that future wheat breeding programs should

consider both drought tolerance and CO<sub>2</sub> responsiveness to improve crop resilience in the face of climate change.

## Appendix A

See Tables 1, 2, 3, 4, and 5.

**Table 1** Average heights (cm) of main (main) and secondary (side) shoots per pot of the tested winter wheat varieties at different carbon dioxide levels

| Variety     | Treat | CO <sub>2</sub> concentration |                     |                    |                    |                     |                     |
|-------------|-------|-------------------------------|---------------------|--------------------|--------------------|---------------------|---------------------|
|             |       | ~400 ppm                      |                     | 700 ppm            |                    | 1000 ppm            |                     |
|             |       | Main                          | Side                | Main               | Side               | Main                | Side                |
| Mv Ikva     | C     | 78 <sup>Ba*1</sup>            | 71 <sup>Aa*1</sup>  | 73 <sup>Ba12</sup> | 69 <sup>Aa1</sup>  | 71 <sup>Ba2</sup>   | 67 <sup>Ba1</sup>   |
|             | SE    | 64 <sup>Bb1</sup>             | 64 <sup>Bb1</sup>   | 64 <sup>Bb1</sup>  | 65 <sup>Bb1</sup>  | 68 <sup>Ba*1</sup>  | 66 <sup>Ba*1</sup>  |
|             | H     | 70 <sup>Ab*2</sup>            | 52 <sup>Cc*1</sup>  | 73 <sup>Ba*1</sup> | 47 <sup>Cc*1</sup> | 74 <sup>Ba*1</sup>  | 54 <sup>BCb*1</sup> |
| Mv Nemere   | C     | 74 <sup>BCa*1</sup>           | 68 <sup>Aa*1</sup>  | 72 <sup>Ba1</sup>  | 70 <sup>Aa1</sup>  | 72 <sup>Ba*1</sup>  | 67 <sup>Ba*1</sup>  |
|             | SE    | 63 <sup>Bb1</sup>             | 66 <sup>Ba12</sup>  | 66 <sup>Ba1</sup>  | 67 <sup>Ba1</sup>  | 65 <sup>Bb2</sup>   | 64 <sup>Ba2</sup>   |
|             | H     | 68 <sup>BCb*1</sup>           | 58 <sup>Bb*1</sup>  | 69 <sup>Ca*1</sup> | 56 <sup>Bb*1</sup> | 65 <sup>Cb*1</sup>  | 59 <sup>Bc*1</sup>  |
| Mv Nádor    | C     | 62 <sup>Ba12</sup>            | 57 <sup>Ba1</sup>   | 65 <sup>Ca*1</sup> | 60 <sup>Ba*1</sup> | 59 <sup>Cab2</sup>  | 55 <sup>Ca1</sup>   |
|             | SE    | 53 <sup>Cb1</sup>             | 56 <sup>Ca1</sup>   | 54 <sup>Cc1</sup>  | 57 <sup>Ca1</sup>  | 56 <sup>Cb1</sup>   | 56 <sup>Ca1</sup>   |
|             | H     | 64 <sup>Ca*1</sup>            | 54 <sup>BCa*1</sup> | 60 <sup>Db*1</sup> | 47 <sup>Cb*2</sup> | 62 <sup>Ca*1</sup>  | 52 <sup>Ca*1</sup>  |
| Mv Kolompos | C     | 91 <sup>Aa*1</sup>            | 73 <sup>Ab*1</sup>  | 82 <sup>Aa*2</sup> | 77 <sup>Aa*1</sup> | 90 <sup>Aa*12</sup> | 76 <sup>Aa*1</sup>  |
|             | SE    | 90 <sup>Aa*1</sup>            | 77 <sup>Aa*1</sup>  | 84 <sup>Aa*1</sup> | 75 <sup>Aa*1</sup> | 85 <sup>Aa*1</sup>  | 74 <sup>Aa*1</sup>  |
|             | H     | 94 <sup>Aa*1</sup>            | 68 <sup>Ac*1</sup>  | 86 <sup>Aa*3</sup> | 63 <sup>Ab*1</sup> | 89 <sup>Aa*2</sup>  | 72 <sup>Aa*1</sup>  |

C represents control (optimal watering), SE represents water withdrawal at stem elongation phenophase, H represents water withdrawal at stem elongation phenophase

Capital letters indicate the statistically significant differences between the varieties; lowercase letters indicate the statistically significant differences between the treatments; the numbers in the index show the statistically significant differences between the different CO<sub>2</sub> levels at  $p \leq 0.05$  levels ( $n = 4$ )

**Table 2** Average lengths (cm) of main (main) and secondary (side) spikes per pot of the tested winter wheat varieties at different carbon dioxide levels

| Variety     | Treat | CO <sub>2</sub> concentration |                       |                        |                        |                         |                         |
|-------------|-------|-------------------------------|-----------------------|------------------------|------------------------|-------------------------|-------------------------|
|             |       | ~400 ppm                      |                       | 700 ppm                |                        | 1000 ppm                |                         |
|             |       | Main                          | Side                  | Main                   | Side                   | Main                    | Side                    |
| Mv Ikva     | C     | 8.200 <sup>Aa*12</sup>        | 6.961 <sup>Aa*2</sup> | 8.683 <sup>ABa*1</sup> | 7.657 <sup>Ba*1</sup>  | 7.850 <sup>Ba*2</sup>   | 6.806 <sup>Bb*2</sup>   |
|             | SE    | 7.342 <sup>Ab2</sup>          | 7.549 <sup>Aa1</sup>  | 7.567 <sup>Cb12</sup>  | 7.639 <sup>Ba1</sup>   | 8.017 <sup>Aa1</sup>    | 8.063 <sup>Aa1</sup>    |
|             | H     | 8.200 <sup>Aa*1</sup>         | 7.267 <sup>Aa*1</sup> | 8.800 <sup>Aa*1</sup>  | 7.249 <sup>BCa*1</sup> | 8.108 <sup>Ba*1</sup>   | 6.298 <sup>Cb*2</sup>   |
| Mv Nemere   | C     | 8.292 <sup>Aa*12</sup>        | 7.256 <sup>Aa*1</sup> | 8.075 <sup>Bb2</sup>   | 7.897 <sup>Ba1</sup>   | 8.917 <sup>Aa*1</sup>   | 7.950 <sup>Aa*1</sup>   |
|             | SE    | 7.892 <sup>Aa2</sup>          | 7.367 <sup>Aa1</sup>  | 8.314 <sup>Bb*12</sup> | 7.839 <sup>Ba*1</sup>  | 8.725 <sup>Aa1</sup>    | 8.523 <sup>Aa2</sup>    |
|             | H     | 8.033 <sup>Aa*2</sup>         | 7.368 <sup>Aa*1</sup> | 8.825 <sup>Aa*1</sup>  | 7.949 <sup>Aa*1</sup>  | 8.967 <sup>Aa*1</sup>   | 7.748 <sup>ABa*1</sup>  |
| Mv Nádor    | C     | 7.933 <sup>Aa*1</sup>         | 7.454 <sup>Aa*1</sup> | 8.033 <sup>Ba*1</sup>  | 7.478 <sup>Ba*1</sup>  | 8.033 <sup>ABa1</sup>   | 7.761 <sup>ABb1</sup>   |
|             | SE    | 8.100 <sup>Aa*1</sup>         | 7.483 <sup>Aa*2</sup> | 7.592 <sup>Ca1</sup>   | 7.603 <sup>Ba2</sup>   | 8.175 <sup>Aa1</sup>    | 8.710 <sup>Aa1</sup>    |
|             | H     | 8.050 <sup>Aa*1</sup>         | 7.087 <sup>Aa*1</sup> | 7.250 <sup>Ba*2</sup>  | 6.390 <sup>Cb*2</sup>  | 8.075 <sup>Ba*1</sup>   | 7.044 <sup>BCb*12</sup> |
| Mv Kolompos | C     | 8.142 <sup>Aa*2</sup>         | 7.365 <sup>Aa*2</sup> | 9.633 <sup>Aa1</sup>   | 9.133 <sup>Aa1</sup>   | 8.817 <sup>ABa*12</sup> | 8.190 <sup>Aa*12</sup>  |
|             | SE    | 8.000 <sup>Aa2</sup>          | 7.352 <sup>Aa2</sup>  | 9.267 <sup>Aa*1</sup>  | 8.591 <sup>Aab*1</sup> | 8.583 <sup>Aa2</sup>    | 7.809 <sup>Aa12</sup>   |
|             | H     | 7.908 <sup>Aa*2</sup>         | 6.588 <sup>Aa*2</sup> | 9.592 <sup>Aa*1</sup>  | 7.809 <sup>ABb*1</sup> | 8.900 <sup>Aa*2</sup>   | 8.618 <sup>Aa*1</sup>   |

C represents control (optimal watering), SE represents water withdrawal at stem elongation phenophase, H represents water withdrawal at stem elongation phenophase

Capital letters indicate the statistically significant differences between the varieties; lowercase letters indicate the statistically significant differences between the treatments; the numbers in the index show the statistically significant differences between the different CO<sub>2</sub> levels at  $p \leq 0.05$  levels ( $n = 4$ )



**Table 3** Average weight (g) of main (main) and secondary (side) spikes per pot of the tested winter wheat varieties at different carbon dioxide levels

| Variety     | Treat | CO <sub>2</sub> concentration |                         |                        |                        |                        |                        |
|-------------|-------|-------------------------------|-------------------------|------------------------|------------------------|------------------------|------------------------|
|             |       | ~ 400 ppm                     |                         | 700 ppm                |                        | 1000 ppm               |                        |
|             |       | Main                          | Side                    | Main                   | Side                   | Main                   | Side                   |
| Mv Ikva     | C     | 2.760 <sup>Aa*1</sup>         | 1.758 <sup>ABa*1</sup>  | 2.535 <sup>Ba*1</sup>  | 1.665 <sup>Ba*1</sup>  | 2.435 <sup>Aa*1</sup>  | 1.824 <sup>Aa*1</sup>  |
|             | SE    | 2.427 <sup>ABb*1</sup>        | 1.461 <sup>Bb*1</sup>   | 2.165 <sup>Bb*1</sup>  | 1.484 <sup>Ca*1</sup>  | 2.288 <sup>ABa*1</sup> | 1.630 <sup>Aa*1</sup>  |
|             | H     | 2.525 <sup>Ab*1</sup>         | 1.547 <sup>Bab*1</sup>  | 2.593 <sup>Ba*1</sup>  | 1.550 <sup>ABa*1</sup> | 2.580 <sup>Ba*1</sup>  | 1.440 <sup>Ba*1</sup>  |
| Mv Nemere   | C     | 3.003 <sup>Ba*1</sup>         | 2.140 <sup>Aa*1</sup>   | 2.439 <sup>Ba*2</sup>  | 2.015 <sup>ABa*1</sup> | 2.790 <sup>Aa*1</sup>  | 1.892 <sup>Aa*1</sup>  |
|             | SE    | 1.942 <sup>Cb1</sup>          | 1.754 <sup>ABb1</sup>   | 2.060 <sup>Bb*1</sup>  | 1.605 <sup>BCb*1</sup> | 1.999 <sup>Bb*1</sup>  | 1.697 <sup>Aa*1</sup>  |
|             | H     | 2.733 <sup>Aa*1</sup>         | 1.865 <sup>Ab*1</sup>   | 2.548 <sup>Ba*1</sup>  | 1.781 <sup>Aab*1</sup> | 2.542 <sup>Ba*1</sup>  | 1.889 <sup>Aa*1</sup>  |
| Mv Nádor    | C     | 2.837 <sup>ABa*1</sup>        | 2.092 <sup>ABa*1</sup>  | 2.582 <sup>Ba*1</sup>  | 1.725 <sup>Ba*2</sup>  | 2.603 <sup>Aa*1</sup>  | 1.875 <sup>Aa*12</sup> |
|             | SE    | 2.054 <sup>BCb*1</sup>        | 1.623 <sup>ABb*1</sup>  | 1.567 <sup>Cb2</sup>   | 1.735 <sup>Ba1</sup>   | 1.681 <sup>Bb12</sup>  | 1.784 <sup>Aa1</sup>   |
|             | H     | 2.619 <sup>Aa*1</sup>         | 1.782 <sup>ABab*1</sup> | 2.066 <sup>Cab*2</sup> | 1.421 <sup>Bb*2</sup>  | 2.551 <sup>Ba*12</sup> | 1.420 <sup>Bb*2</sup>  |
| Mv Kolompos | C     | 2.826 <sup>ABa*2</sup>        | 1.662 <sup>Ba*2</sup>   | 3.319 <sup>Aa*1</sup>  | 2.337 <sup>Aa*1</sup>  | 2.961 <sup>Aa*12</sup> | 1.910 <sup>Aa*12</sup> |
|             | SE    | 2.535 <sup>Aa*1</sup>         | 1.850 <sup>Aa*2</sup>   | 2.593 <sup>Ab*1</sup>  | 2.058 <sup>Aa*1</sup>  | 2.383 <sup>Ab*1</sup>  | 1.812 <sup>Aa*1</sup>  |
|             | H     | 2.682 <sup>Aa*2</sup>         | 1.351 <sup>Ca*3</sup>   | 3.238 <sup>Aa*1</sup>  | 1.558 <sup>ABb*2</sup> | 2.937 <sup>Aa*12</sup> | 1.976 <sup>Aa*1</sup>  |

C represents control (optimal watering), SE represents water withdrawal at stem elongation phenophase, H represents water withdrawal at stem elongation phenophase

Capital letters indicate the statistically significant differences between the varieties; lowercase letters indicate the statistically significant differences between the treatments; the numbers in the index show the statistically significant differences between the different CO<sub>2</sub> levels at  $p \leq 0.05$  levels ( $n=4$ )

**Table 4** The average number of grains per pot of main (main) and secondary (side) spikes of the tested winter wheat varieties at different carbon dioxide levels

| Variety     | Treat | CO <sub>2</sub> concentration |                     |                     |                     |                     |                     |
|-------------|-------|-------------------------------|---------------------|---------------------|---------------------|---------------------|---------------------|
|             |       | ~ 400 ppm                     |                     | 700 ppm             |                     | 1000 ppm            |                     |
|             |       | Main                          | Side                | Main                | Side                | Main                | Side                |
| Mv Ikva     | C     | 54 <sup>Aa*1</sup>            | 38 <sup>Aa*1</sup>  | 47 <sup>Aa2*</sup>  | 35 <sup>Ab*1</sup>  | 41 <sup>Ba2</sup>   | 37 <sup>ABab1</sup> |
|             | SE    | 42 <sup>ABb1</sup>            | 39 <sup>Aa1</sup>   | 39 <sup>Bc1</sup>   | 39 <sup>Aac1</sup>  | 46 <sup>Aa1</sup>   | 43 <sup>Aa1</sup>   |
|             | H     | 53 <sup>Aa*1</sup>            | 31 <sup>Ab*1</sup>  | 49 <sup>ABa*1</sup> | 27 <sup>Ac*1</sup>  | 49 <sup>Aa*1</sup>  | 31 <sup>Ab*1</sup>  |
| Mv Nemere   | C     | 45 <sup>Ca*1</sup>            | 32 <sup>Aa*1</sup>  | 34 <sup>Ba*2</sup>  | 28 <sup>Ba*1</sup>  | 39 <sup>Ba*2</sup>  | 31 <sup>Ba*1</sup>  |
|             | SE    | 26 <sup>Cb2</sup>             | 31 <sup>Ba1</sup>   | 35 <sup>Ca*1</sup>  | 30 <sup>Ba*1</sup>  | 37 <sup>Ba*1</sup>  | 32 <sup>Ba*1</sup>  |
|             | H     | 42 <sup>Ba*1</sup>            | 32 <sup>Aa*1</sup>  | 39 <sup>BCa*1</sup> | 26 <sup>Aa*2</sup>  | 38 <sup>Ba*1</sup>  | 27 <sup>Bb*2</sup>  |
| Mv Nádor    | C     | 47 <sup>BCa*1</sup>           | 33 <sup>Aa*1</sup>  | 37 <sup>Ba*2</sup>  | 27 <sup>Bb*1</sup>  | 34 <sup>Ba2</sup>   | 32 <sup>ABa1</sup>  |
|             | SE    | 34 <sup>BCb1</sup>            | 33 <sup>Ba1</sup>   | 32 <sup>Ca1</sup>   | 33 <sup>Ba1</sup>   | 36 <sup>Ba1</sup>   | 35 <sup>Ba1</sup>   |
|             | H     | 47 <sup>ABa*1</sup>           | 32 <sup>Aa*1</sup>  | 28 <sup>Ca2</sup>   | 29 <sup>Aab1</sup>  | 38 <sup>Ba*12</sup> | 26 <sup>Bb*1</sup>  |
| Mv Kolompos | C     | 50 <sup>ABa*1</sup>           | 35 <sup>Aa*1</sup>  | 49 <sup>Aa*1</sup>  | 38 <sup>Aa*1</sup>  | 51 <sup>Aa*1</sup>  | 38 <sup>Aa*1</sup>  |
|             | SE    | 46 <sup>Aa*12</sup>           | 36 <sup>ABa*1</sup> | 52 <sup>Aa*1</sup>  | 34 <sup>ABa*1</sup> | 42 <sup>ABa2</sup>  | 39 <sup>Aa1</sup>   |
|             | H     | 47 <sup>ABa*2</sup>           | 29 <sup>Ab*2</sup>  | 56 <sup>Aa*1</sup>  | 25 <sup>Aab*3</sup> | 47 <sup>Aa*2</sup>  | 38 <sup>Aa*1</sup>  |

C represents control (optimal watering), SE represents water withdrawal at stem elongation phenophase, H represents water withdrawal at stem elongation phenophase

Capital letters indicate the statistically significant differences between the varieties; lowercase letters indicate the statistically significant differences between the treatments; the numbers in the index show the statistically significant differences between the different CO<sub>2</sub> levels at  $p \leq 0.05$  levels ( $n=4$ )

**Table 5** Average weights of grain (g) per pot of main (main) and secondary (side) spikes of the tested winter wheat varieties at different carbon dioxide levels

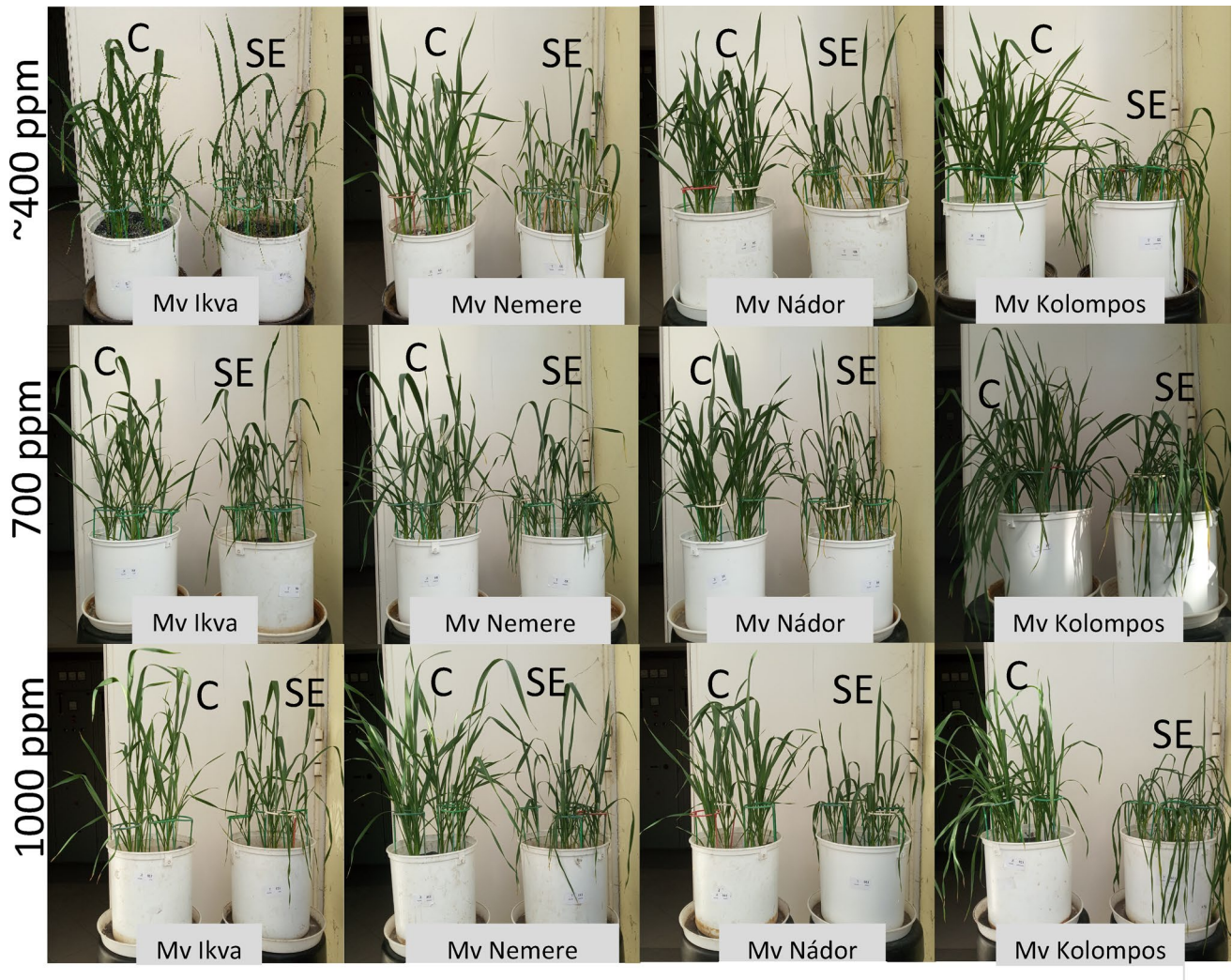
| Variety     | Treat | CO <sub>2</sub> concentration |                        |                        |                         |                       |                        |
|-------------|-------|-------------------------------|------------------------|------------------------|-------------------------|-----------------------|------------------------|
|             |       | ~ 400 ppm                     |                        | 700 ppm                |                         | 1000 ppm              |                        |
|             |       | Main                          | Side                   | Main                   | Side                    | Main                  | Side                   |
| Mv Ikva     | C     | 2.348 <sup>Aba*1</sup>        | 1.475 <sup>Aa*1</sup>  | 2.172 <sup>Aa*1</sup>  | 1.471 <sup>Aa*1</sup>   | 2.151 <sup>Aa*1</sup> | 1.619 <sup>Aa*1</sup>  |
|             | SE    | 2.071 <sup>Ab*1</sup>         | 1.249 <sup>Aa*2</sup>  | 1.820 <sup>Ab*1</sup>  | 1.277 <sup>Bb*12</sup>  | 1.993 <sup>Aa*1</sup> | 1.445 <sup>Aa*1</sup>  |
|             | H     | 2.137 <sup>Ab*1</sup>         | 1.265 <sup>Ba*2</sup>  | 2.219 <sup>Ba*1</sup>  | 1.382 <sup>Aab*12</sup> | 2.261 <sup>Aa*1</sup> | 1.439 <sup>Aa*1</sup>  |
| Mv Nemere   | C     | 2.498 <sup>Aa*1</sup>         | 1.700 <sup>Aa*1</sup>  | 1.977 <sup>Aab*2</sup> | 1.524 <sup>Aa*1</sup>   | 2.298 <sup>Aa*2</sup> | 1.588 <sup>Aa*1</sup>  |
|             | SE    | 1.565 <sup>Bb*1</sup>         | 1.417 <sup>Aa*1</sup>  | 1.701 <sup>Ab*1</sup>  | 1.312 <sup>Ba*1</sup>   | 1.721 <sup>Ab*1</sup> | 1.381 <sup>Ab*1</sup>  |
|             | H     | 2.272 <sup>Aa*1</sup>         | 1.452 <sup>Aa*1</sup>  | 2.128 <sup>Ba*1</sup>  | 1.336 <sup>Aa*1</sup>   | 2.186 <sup>Aa*1</sup> | 1.431 <sup>Aab*1</sup> |
| Mv Nádor    | C     | 2.330 <sup>Aba*1</sup>        | 1.706 <sup>Aa*1</sup>  | 2.153 <sup>Aa*1</sup>  | 1.423 <sup>Aa*1</sup>   | 2.064 <sup>Aa*1</sup> | 1.532 <sup>Aa*1</sup>  |
|             | SE    | 1.691 <sup>ABb1</sup>         | 1.267 <sup>Ab1</sup>   | 1.264 <sup>Bb2</sup>   | 1.284 <sup>Ba1</sup>    | 1.373 <sup>Bb12</sup> | 1.387 <sup>Aa1</sup>   |
|             | H     | 2.137 <sup>Aa*1</sup>         | 1.435 <sup>ABb*1</sup> | 1.648 <sup>Cab*2</sup> | 0.805 <sup>Bb*2</sup>   | 2.230 <sup>Aa*1</sup> | 1.546 <sup>Aa*1</sup>  |
| Mv Kolompos | C     | 2.223 <sup>Ba*1</sup>         | 1.339 <sup>Aab*1</sup> | 2.456 <sup>Aa*1</sup>  | 1.728 <sup>Aa*1</sup>   | 2.352 <sup>Aa*1</sup> | 1.496 <sup>Aa*1</sup>  |
|             | SE    | 1.968 <sup>ABa*1</sup>        | 1.442 <sup>Aa*1</sup>  | 2.038 <sup>Aa*1</sup>  | 1.547 <sup>Aa*1</sup>   | 1.830 <sup>Ab*1</sup> | 1.455 <sup>Aa*1</sup>  |
|             | H     | 2.095 <sup>Aa*2</sup>         | 0.982 <sup>Cb*2</sup>  | 2.585 <sup>Aa*1</sup>  | 1.080 <sup>Bb*2</sup>   | 2.164 <sup>Aa*2</sup> | 1.540 <sup>Aa*1</sup>  |

*C* represents control (optimal watering), *SE* represents water withdrawal at stem elongation phenophase, *H* represents water withdrawal at stem elongation phenophase

Capital letters indicate the statistically significant differences between the varieties; lowercase letters indicate the statistically significant differences between the treatments; the numbers in the index show the statistically significant differences between the different CO<sub>2</sub> levels at  $p \leq 0.05$  levels ( $n=4$ )

## Appendix B

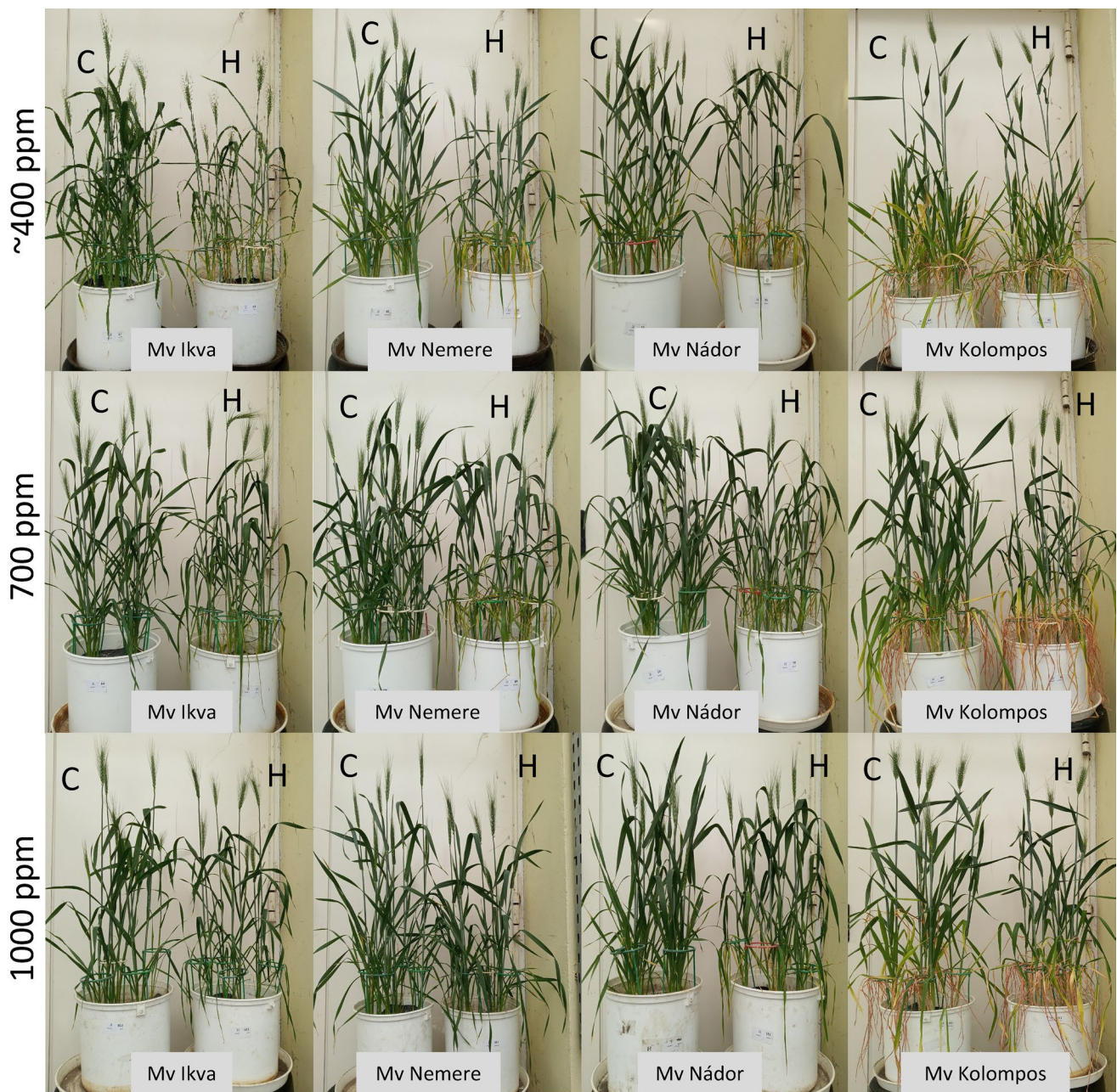
See Figs. 7 and 8.



**Fig. 7** The effects of the water shortage at stem elongation phenophase compared to the optimal watering regime at different carbon dioxide levels. The photos was taken by the first author at the ending

of the stress treatment. 'C' represents the control (optimal watering) and 'SE' represents water withdrawal at stem elongation phenophase





**Fig. 8** The effects of the water shortage at heading phenophase compared to the optimal watering regime at different carbon dioxide levels. The photos were taken by the first author at the ending of the

stress treatment. 'C' represents the control (optimal watering) and 'H' represents water withdrawal at heading phenophase

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## Declarations

**Conflict of interest** The authors of this manuscript declare no conflict of interest.

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## References

- Abdelhakim LO, Palma CFF, Zhou R, Wollenweber B, Ottosen C-O, Rosenqvist E (2021) The effect of individual and combined drought and heat stress under elevated CO<sub>2</sub> on physiological responses in spring wheat genotypes. *Plant Physiol Biochem* 162:301–314. <https://doi.org/10.1016/j.plaphy.2021.02.015>
- Abdelhakim LOA, Mendanha T, Palma CFF, Vrobel O, Šteflová N, Čavar Zeljković S, Tarkowski P, De Diego N, Wollenweber B, Rosenqvist E, Ottosen C-O (2022) Elevated CO<sub>2</sub> improves the physiology but not the final yield in spring wheat genotypes subjected to heat and drought stress during anthesis. *Front Plant Sci* 13:824476. <https://doi.org/10.3389/fpls.2022.824476>
- Abhinandan K, Skori L, Stanic M, Hickerson NMN, Jamshed M, Samuel MA (2018) Abiotic stress signaling in wheat—An inclusive overview of hormonal interactions during abiotic stress responses in wheat. *Front Plant Sci* 9:734. <https://doi.org/10.3389/fpls.2018.00734>
- Akram M (2011) Growth and yield components of wheat under water stress of different growth stages. *Bangladesh J Agric Res* 36:455–468. <https://doi.org/10.3329/bjar.v36i3.9264>
- Albahri G, Alyamani AA, Badran A, Hijazi A, Nasser M, Maresca M, Baydoun E (2023) Enhancing essential grains yield for sustainable food security and bio-safe agriculture through latest innovative approaches. *Agronomy* 13:1709. <https://doi.org/10.3390/agronomy13071709>
- Aljazairi S, Nogués S (2015) The effects of depleted, current and elevated growth [CO<sub>2</sub>] in wheat are modulated by water availability. *Environ Exp Bot* 112:55–66. <https://doi.org/10.1016/j.envexpbot.2014.12.002>
- Allen LH Jr, Kakani VG, Vu JCV, Boote KJ (2011) Elevated CO<sub>2</sub> increases water use efficiency by sustaining photosynthesis of water-limited maize and sorghum. *J Plant Physiol* 168(16):1909–1918. <https://doi.org/10.1016/j.jplph.2011.05.005>
- Anwar MN, Fayyaz A, Sohail NF, Khokhbar MF, Baqar M, Khan WD, Rassol K, Rehan M, Nizami AS (2018) CO<sub>2</sub> capture and storage: a way forward for sustainable environment. *J Environ Manag* 226:131–144. <https://doi.org/10.1016/j.jenvman.2018.08.009>
- Aslam M, Zamir MSI, Afzal I, Yaseen M, Mubeen M, Shoi BA (2013) Drought stress, its effect on maize production and development of drought tolerance through potassium application. *Cercet Agronomice Mold* 46(2):99–114
- Barnabás B, Jäger K, Fehér A (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant Cell Environ* 31:11–38. <https://doi.org/10.1111/j.1365-3040.2007.01727.x>
- Betts R (2021) Carbon dioxide (CO<sub>2</sub>) in the atmosphere is now reaching levels 50% higher than when humanity began large-scale burning of fossil fuels during the industrial revolution. Met Office: Atmospheric CO<sub>2</sub> now hitting 50% higher than pre-industrial levels. <https://www.carbonbrief.org/met-office-atmospheric-co2-now-hitting-50-higher-than-pre-industrial-levels/>. (Available:17.03.2025.)
- Blum A (2017) Osmotic adjustment is a prime drought stress adaptive engine in support of plant reproduction. *Plant Cell Environ* 40(1):4–10. <https://doi.org/10.1111/pce.12800>
- Blum A, Sullivan CY (1997) The effect of plant size on wheat response to agents of drought stress. I. Root Drying. *Aust J Plant Physiol* 24:35–41. <https://doi.org/10.1071/PP96022>
- Cattivelli L, Rizza F, Badeck FW, Mazzucotelli E, Mastrangelo AM, Francia E, Mare C, Tondelli A, Stanca AM (2008) Drought tolerance improvement in crop plants: an integrated view from breeding to genomics. *Field Crop Res* 105:1–14. <https://doi.org/10.1016/j.fcr.2007.07.004>
- Chen X, Zhu Y, Pan R, Shen W, Yu X, Xiong F (2021) The relationship between characteristics of root morphology and grain filling in wheat under drought stress. *PeerJ* 9:e12012. <https://doi.org/10.7717/peerj.12015>
- Ciais P, Sabine C, Bala G, Bopp L, Brovkin V, Canadell J, Chhabra A, DeFries R, Galloaway J, Heimann M, Jones C, Le Quéré C, Myneni RB, Piao RB, Thorton P (2013): Carbon and other biogeochemical cycles. In: Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM. (eds) *Climate Change 2013 - the Physical Science Basis Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK and New York, NY, USA, pp 465–570. <https://doi.org/10.1017/CBO9781107415324.015>
- Combe L (1981) Effect of carbon dioxide and culture under artificial climate on the growth and yield of a winter wheat. *Agronomie* 1:177–186
- Daryanto S, Wang L, Jacinthe PA (2016) Global synthesis of drought effects on maize and wheat production. *PLoS ONE* 11:e0156362. <https://doi.org/10.1371/journal.pone.0156362>
- Del Buono D (2021) Can biostimulants be used to mitigate the effect of anthropogenic climate change on agriculture? It is time to respond. *Sci Total Environ* 751:141763. <https://doi.org/10.1016/j.scitotenv.2020.141763>
- Dietz K-J, Zörb C, Geilfus C-M (2021) Drought and crop yield. *Plant Biol* 23(6):881–893. <https://doi.org/10.1111/plb.13304>
- Ding J, Huang Z, Zhu M, Li C, Zhu X, Guo W (2018) Does cyclic water stress damage wheat yield more than a single stress? *PLoS ONE* 13:e0195535. <https://doi.org/10.1371/journal.pone.0195535>
- Dolferus R, Ji X, Richards RA (2011) Abiotic stress and control of grain number in cereals. *Plant Sci* 181:331–341. <https://doi.org/10.1016/j.plantsci.2011.05.015>
- Dunn J, Hunt L, Afsharinfar M, Al Meselmani M, Mitchell A, Howells R, Wallington E, Fleming AJ, Gray JE (2019) Reduced stomatal density in bread wheat leads to increased water-use efficiency. *J Exp Bot* 70(18):4737–4748. <https://doi.org/10.1093/jxb/erz248>
- Dusenge ME, Duarte AG, Waw DA (2019) Plant carbon metabolism and climate change: elevated CO<sub>2</sub> and temperature impacts on photosynthesis, photorespiration and respiration. *New Phytol* 221:32–49. <https://doi.org/10.1111/nph.15283>
- Duvnjak J, Lončarić A, Brkljačić L, Šamec D, Šarčević H, Salopek-Sondi B, Španić V (2023) Morpho-physiological and hormonal response of winter wheat varieties to drought stress at stem elongation and anthesis stages. *Plants* 12(3):418. <https://doi.org/10.3390/plants12030418>
- FAO (2018) Crop prospects and food situation. Quarterly global report. Food and Agriculture Organization of the United Nations, Rome
- Farooq M, Hussain M, Siddique KH (2014) Drought stress in wheat during flowering and grain-filling periods. *Crit Rev Plant Sci* 33:331–349. <https://doi.org/10.1080/07352689.2014.875291>
- Ficklin DL, Novick KA (2017) Historic and projected changes in vapour pressure deficit suggest a continental-scale drying of the United States atmosphere. *J Geophys Res Atmos* 122:2061–2079. <https://doi.org/10.1002/2016JD025855>
- Fischer RA (1973) The effect of water stress at various stages of development on yield process in wheat. *Aus J Agric Res* 29:897–912. <https://doi.org/10.1071/AR9780897>



- Fischer RA, Wood JT (1979) Drought resistance in spring wheat cultivars. III. \* Yield associations with morpho-physiological trait. *Aus J Agric Res* 30(6):1001. <https://doi.org/10.1071/ar9791001>
- Foulkes MJ, Sylvester-Bradley R, Weightman R, Snape JW (2007) Identifying physiological traits associated with improved drought resistance in winter wheat. *Field Crop Res* 103:11–24. <https://doi.org/10.1016/j.fcr.2007.04.007>
- Frantová N, Rábek M, Elzner P, Středa T, Jovanović I, Holková L, Martinek P, Smutná P, Prášil IT (2022) Different drought tolerance strategy of wheat varieties in spike architecture. *Agronomy* 12(10):2328. <https://doi.org/10.3390/agronomy12102328>
- Gámez AL, Vicente R, Sanchez-Bragado R, Jauregui I, Morcuende R, Giocoechea N, Aranjuelo I (2020) Differential flag leaf and ear photosynthetic performance under elevated [CO<sub>2</sub>] conditions during grain filling period in durum wheat. *Front Plant Sci* 11:587958. <https://doi.org/10.3389/fpls.2020.587958>
- González FG, Slafer GA, Miralles DJ (2002) Vernalization and photoperiod responses in wheat pre-flowering reproductive phases. *Field Crops Res* 74:183–195. [https://doi.org/10.1016/S0378-4290\(01\)00210-6](https://doi.org/10.1016/S0378-4290(01)00210-6)
- Hussen A (2020) Review on: response of cereal crops to climate change. *Adv Biosci Bioeng* 8(4):63–72. <https://doi.org/10.11648/j.abb.20200804.11>
- Iancu T, Tudor VC, Dumitru EA, Sterie CM, Micu MM, Smedescu D, Marcu L, Tonea E, Stoicea P, Vintu C, Jitareanu AF, Costuleanu LC (2022) A scientometric analysis of climate change adaptation studies. *Sustainability* 14:12945. <https://doi.org/10.3390/su141912945>
- Kato Y, Kamoshita A, Yamagishi J (2008) Preflowering abortion reduces spikelet number in upland rice under water stress. *Crop Sci* 48:2389–2395. <https://doi.org/10.2135/cropsci2007.11.0627>
- Khadka K, Earl HJ, Raizada MN, Navabi A (2020) A physio-morphological trait-based approach for breeding drought tolerant wheat. *Front Plant Sci* 11:715. <https://doi.org/10.3389/fpls.2020.00715>
- Khan N, Naqvi FN (2011) Effect of water stress in bread wheat hexaploids. *Curr Res J Biol Sci* 3(5):487–498
- Khyber JA, Soomro F, Sipio WD, Balcoh AW, Soothar JK, Soothar MK, Ali Z (2019) Evaluation of bread wheat (*Triticum aestivum* L.) genotyped for drought tolerance through selection indices. *J Hortic Plant Res* 7:40–52. <https://doi.org/10.18052/www.scipress.com/JHPR.7.40>
- Kimball BA (2016) Crop responses to elevated CO<sub>2</sub> and interactions with H<sub>2</sub>O, N and temperature. *Curr Opin Plant Biol* 31:36–43. <https://doi.org/10.1016/j.pbi.2016.03.006>
- Korkhova M, Panfilova A, Domaratkiy Y, Smirnova I (2023) Productivity of winter wheat (*T. aestivum*, *T. durum*, *T. spelta*) depending on varietal characteristics on the context of climate change. *Ecol Eng Environ Technol* 24(4):236–244. <https://doi.org/10.12912/27197050/163124>
- Krenzer EG Jr, Moss DN (1975) Carbon dioxide enrichment effects upon yield and yield components in wheat. *Crop Sci* 15:71–74. <https://doi.org/10.2135/cropsci1975.0011183X001500010020x>
- Lancashire PD, Bleiholder H, van den Boom T, Langelüddeke P, Stauss R, Weber E, Witzemberger A (1991) A uniform decimal code for growth stages of crops and weeds. *Ann Appl Biol* 119:561–601. <https://doi.org/10.1111/j.1744-7348.1991.tb04895.x>
- Li Y, Li X, Yu J, Liu F (2017) Effect of the transgenerational exposure to elevated CO<sub>2</sub> on the drought response of winter wheat: Stomatal control and water use efficiency. *Environ Exp Bot* 136:78–84. <https://doi.org/10.1016/j.envexpbot.2017.01.006>
- Lindsey R, Dahlman L (2021) Climate Change: Global Temperature. Sciences & information for a climate-smart nation (NOAA). <https://www.climate.gov/news-features/understanding-climate/climate-change-global-temperature>
- Lipiec J, Doussan C, Nosalewicz A, Kondracka K (2013) Effect of drought and heat stresses on plant growth and yield: a review. *Int Agrophys* 27:463–477. <https://doi.org/10.2478/intag-2013-0017>
- Lozinskiy M, Lozinska T, Sabadyn V, Sidorova I, Panchenko T, Fedoruk Y, Kumanska Y (2021) Evaluation of selected soft winter wheat lines for main ear grain weight. *Agron Res* 19(2):540–551. <https://doi.org/10.15159/AR.21.071>
- Ma J, Li R, Wang H, Li D, Wang X, Zhang Y, Zhen W, Duan H, Yan G, Li Y (2017) Transcriptomics analyses reveal wheat responses to drought stress during reproductive stages under field conditions. *Front in Plant Sci* 8:592. <https://doi.org/10.3389/fpls.2017.00592>
- Manderscheid R, Weigel H-J (2007) Drought stress effects on wheat are mitigated by atmospheric CO<sub>2</sub> enrichment. *Agron Sustain Dev* 27:79–87. <https://doi.org/10.1051/agro:2006035>
- Mirbahar AA, Markhand GS, Mahar AR, Abro AA, Kanhar NA (2009) Effect of water stress on yield and yield component of wheat (*Triticum aestivum* L.) varieties. *Pak J Bot* 41:1303–1310
- Mogensen VO (1985) Growth rate of grain and grain yield of wheat in relation to drought. *Acta Agric Scand* 35:353–360. <https://doi.org/10.1080/00015128509442046>
- Powell N, Ji X, Ravash R, Edlington J, Dolferus R (2012) Yield stability for cereals in a changing climate. *Funct Plant Biol* 39(7):539–552. <https://doi.org/10.1071/FP12078>
- Praba ML, Cairns JE, Babu RC, Lafitte HR (2009) Identification of physiological traits underlying cultivar differences in drought tolerance in rice and wheat. *J Agron Crop Sci* 195:30–46. <https://doi.org/10.1111/j.1439-037X.2008.00341.x>
- Quaseem MF, Qureshi R, Shaheen H (2019) Effects of pre-anthesis droughts, heat and their combination on the growth, yield and physiology of diverse wheat (*Triticum aestivum* L.) genotypes varying in sensitivity to heat and drought stress. *Sci Rep* 9:6955. <https://doi.org/10.1038/s41598-019-43477-z>
- Rang ZW, Jagadish SVK, Zhou QM, Craufurd PQ, Heuer S (2011) Effect of high temperature and water stress on pollen germination and spikelet fertility in rice. *Environ Exp Bot* 70:58–65. <https://doi.org/10.1016/j.envexpbot.2010.08.009>
- Saeed F, Chaudhry UK, Raza A, Charagh S, Bakhsh A, Bohra A, Ali S, Chitkineni A, Saeed Y, Visser RGF, Siddique VRK (2023) Developing future heat-resilient vegetable crops. *Funct Integr Genom* 23:47. <https://doi.org/10.1007/s10142-023-00967-8>
- Saeedipour S (2011) Effect of drought at the post-anthesis stage on remobilization of carbon reserves in two wheat cultivars differing in senescence properties. *Int J Plant Physiol Biochem* 3:15–24. <https://doi.org/10.5539/jas.v3n3p81>
- Saeidi M, Ardalani S, Jalali-Honarmand S, Ghobadi ME, Abdoli M (2015) Evaluation of drought stress at vegetative growth stage on the grain yield formation and some physiological traits as well as fluorescence parameters of different bread wheat cultivars. *Acta Biol Szeged* 59:35–44
- Sakaguchi H (2023) Asian states and the Arctic ocean. *Asia Policy* 18(1):3–4. <https://doi.org/10.1353/asp.2023.0001>
- Samarah NH (2005) Effects of drought stress on growth and yield of barley. *Agron Sustain Dev* 25:145–149. <https://doi.org/10.1051/agro:2004064>
- Samarah NH, Alqudah AM, Amayreh JA, McAndrews GM (2009) The effects of late-terminal drought stress on yield components of four barley cultivars. *J Agron Crop Sci* 195:427–441. <https://doi.org/10.1111/j.1439-037X.2009.00387.x>
- Sarto MVM, Sarto JRW, Rampim L, Bassegio D, da Costa PF, Inagaki AM (2017) Wheat phenology and yield under drought: a review. *Aust J Crop Sci* 11:941–946. <https://doi.org/10.21475/ajcs.17.11.08.pne351>
- Shamsi K, Kobraee S (2011) Bread wheat production under drought stress conditions. *Ann Biol Res* 2:352–358



- Shokat S, Großkinsky DK, Liu F (2020) Impact of elevated CO<sub>2</sub> on two contrasting wheat genotypes exposed to intermediate drought stress at anthesis. *J Agron Crop Sci* 207(1):20–33. <https://doi.org/10.1111/jac.12442>
- Sionit N, Hellmers H, Strain BR (1980) Growth and yield of wheat under CO<sub>2</sub> enrichment and water stress. *Crop Sci* 20:687–690. <https://doi.org/10.2135/cropsci1980.0011183X002000060003x>
- Su Y, Wu F, Ao Z, Jin S, Qin F, Liu B, Pang S, Liu L, Guo Q (2019) Evaluating maize phenotype dynamics under drought stress using terrestrial lidar. *Plant Methods* 15:11. <https://doi.org/10.1186/s13007-019-0396-x>
- The World Bank Group (2025) Population estimates and projections. <https://databank.worldbank.org/source/health-nutrition-and-population-statistics:-population-estimates-and-projections> (Available: 17.03.2025.)
- Tischner T, Kőszegi B, Veisz O (1997) Climatic programs used in the Martonvásár phytotron most frequently in recent years. *Acta Agric Hung* 45:85–104
- Tudor VC, Stoicea P, Chiurciu IA, Soare E, Iorga AM, Dinu TA, David L, Micu MM, Smedescu DI, Dumitru EA (2023) the use of fertilizers and pesticides in wheat production in the main european countries. *Sustainability* 15:3038. <https://doi.org/10.3390/su15043038>
- Varga B, Vida G, Varga-László E, Hoffman B, Veisz O (2017) Combined effect of drought stress and elevated atmospheric CO<sub>2</sub> concentration on the yield parameters and water use properties of winter wheat (*Triticum aestivum* L.) genotypes. *J Agron Crop Sci* 203:192–205. <https://doi.org/10.1111/jac.12176>
- Wang X, Vignjevic M, Liu F, Jacobsen S, Jiang D, Wollenweber B (2015) Drought priming at vegetative growth stages improves tolerance to drought and heat stresses occurring during grain filling in spring wheat. *Plant Growth Regul* 75:677–687. <https://doi.org/10.1007/s10725-014-9969-x>
- Wang J-Y, Xiong Y-C, Li F-M, Siddique KHM, Turner NC (2017) Effects of drought stress on morphophysiological traits, biochemical characteristics, yield, and yield components in different ploidy wheat. *Adv Agron* 143:139–173. <https://doi.org/10.1016/bs.agron.2017.01.002>
- Wu D-X, Wang G-X, Bai Y-F, Liao J-X (2004) Effects of elevated CO<sub>2</sub> concentration on growth, water use, yield and grain quality of wheat under two soil water levels. *Agr Ecosyst Environ* 104:493–507. <https://doi.org/10.1016/j.agee.2004.01.018>
- Xu M (2015) The optimal atmospheric CO<sub>2</sub> concentration for the growth of winter wheat (*Triticum aestivum*). *J Plant Physiol* 184:89–97. <https://doi.org/10.1016/j.jplph.2015.07.003>
- Yang J, Zhang J, Wang Z, Zhu Q, Liu L (2001) Water deficit-induced senescence and its relationship to the remobilization of pre-stored carbon in wheat during grain filling. *Agron J* 93(1):196. <https://doi.org/10.2134/agronj2001.931196x>