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Different drought resistance mechanisms between two buckwheat species *Fagopyrum esculentum* and *Fagopyrum tataricum*

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Abstract

Water availability is one of the main factors affecting crop production and the occurrence of drought periods is expected to increase in the context of ongoing climate change. We investigated the impact of water stress on two pseudocereal species, common buckwheat (*Fagopyrum esculentum*) and Tartary buckwheat (*Fagopyrum tataricum*). Plants were grown under greenhouse conditions under two water regimes: control (40–50% soil humidity) and water stress (<20% soil humidity). Although closely related, both species differed by their resistance to water stress. The vegetative growth was affected in *F. esculentum* but not in *F. tataricum* as water stress decreased leaf production, leaf fresh, and dry weight, stomatal conductance, transpiration rate, and photosynthesis rate in the former but not in the latter. However, chlorophyll fluorescence parameters were not affected by water stress, whatever the species, and the chlorophyll content increased in water-stressed plants in both species. Oxidative stress was observed in both species in response to water stress, and antioxidant content was increased in *F. tataricum*. The reproductive phase was affected by water stress in both species: the number of inflorescences and pollen production decreased, mainly in *F. esculentum*. Seed set was maintained in *F. tataricum* while this parameter was not investigated in *F. esculentum* due to its self-incompatibility. Our results suggested that *F. tataricum* was more resistant to water stress than *F. esculentum* and that *F. esculentum* had characteristics of drought avoidance, while *F. tataricum* exhibited traits of drought tolerance.

1 | INTRODUCTION

In the face of climate change, extreme events, such as drought are expecting to become more frequent and more intense (IPCC, 2014). It will have many negative impacts on crop production. Indeed, water availability is one of the main factors impacting crop production (Barnabás et al., 2008; Gray and Brady, 2016). When the water supply is inferior to the water demand, plants encounter water stress (Salehi-Lisar and Bakhshayeshan-Agdam, 2016). Water stress can have many impacts on plants at every life stage. It can decrease the germination rate (Prasad et al., 2008; Farooq et al., 2009). It can cause a reduction in vegetative growth (Prasad et al., 2008; Farooq et al., 2009; Gray and Brady, 2016), photosynthesis rate can be reduced (Cornic and Massacci, 1996; Prasad et al., 2008; Farooq et al., 2009) and reproduction parameters, such as female and male sterility, fertilization can be affected. This can result in a lower yield (Barnabás et al., 2008; Prasad et al., 2008; Farooq et al., 2009; Gray and Brady, 2016). Water stress can also lead to the production of reactive oxygen species (ROS) (Farooq et al., 2009).

But, over time, plants have developed resistance strategies to cope with drought. Some escape by growing and reproducing before the drought-period (Chaves et al., 2003; Hu and Xiong, 2014;

Abbreviations: Ai, instantaneous net photosynthesis rate; CCI, chlorophyll content index; Ci, intercellular CO_2 concentration; DW, dry weight; Ei, instantaneous transpiration rate; FRAP, ferric reducing antioxidant power; FW, fresh weight; gs, leaf stomatal conductance; MDA, malondialdehyde; NPQ, non-photochemical quenching; pq, photochemical quenching; ROS, reactive oxygen species; WC, water content; WS, water stress; WUEi, instantaneous water use efficiency; WW, well-watered; φPSII, photosystem II efficiency.

Kooyers, 2015). Others became avoiders by maintaining their water status. In this case, plants reduce their transpiration rate by closing their stomata allowing them to limit water loss. They also extend their root system to increase their water uptake (Chaves et al., 2003; Hu and Xiong, 2014; Kooyers, 2015). Finally, tolerant plants manage to keep their growth and reproduction afloat by, for example, producing more osmolytes or antioxidants (Chaves et al., 2003; Hu and Xiong, 2014; Kooyers, 2015). These strategies are not exclusive and one plant can exhibit adaptations coming from different strategies. Depending on the duration and severity of the stress, the effects can be different (Salehi-Lisar and Bakhshayeshan-Agdam, 2016).

Buckwheat (*Fagopyrum* sp.) is a species gaining in interest but yet not much cultivated. It has three main qualities. First, buckwheat grows well on poor soils, does not need fertilizers or biocides (Sharma, 1986; Myers and Meinke, 1994; Campbell, 1997; Small, 2017). It is sustainable for organic and environmental-friendly farming (Small, 2017). Second, buckwheat belongs to the Polygonaceae family and is a pseudocereal with high nutritional qualities (Myers and Meinke, 1994; Campbell, 1997; Small, 2017). Seeds are rich in lysine, dietary fibers, minerals, and are gluten-free (Campbell, 1997; Alvarez-Jubete et al., 2010) and can be used as Poaceae seeds (Sharma, 1986; Campbell, 1997; Small, 2017). Third, buckwheat is recognized for its medicinal qualities. It contains high concentrations in fagopyritols and antioxidants, such as phenolic compounds (Alvarez-Jubete et al., 2010; Zhu, 2016). Among these molecules, rutin is the most important one found in buckwheat and is involved in the prevention of several diseases, such as diabetes, hypertension, liver damage (Kreft, 2016; Zhu, 2016). But, compared to other crops, buckwheat is not much cultivated (FAOSTAT, 2018). There are several reasons for that low production. First, buckwheat has been the subject of few breeding programs in contrast to major crops like wheat or rice (Myers and Meinke, 1994; Small, 2017). Then, it has an indeterminate flowering, low seed set, and extended seed maturation over time (Cawoy et al., 2007; Jacquemart et al., 2012; Słomka et al., 2017). Moreover, buckwheat is also sensitive to some environmental conditions, such as frost and has a high water requirement (Jacquemart et al., 2012).

Two buckwheat species are cultivated, *Fagopyrum esculentum* Moench. (common buckwheat) and *Fagopyrum tataricum* (L.) Gaertn. (Tartary buckwheat). Both originated from China, *F. esculentum* is more largely cultivated than *F. tataricum* (Myers and Meinke, 1994; Campbell, 1997). The two species differ for their reproduction. *F. esculentum* is a self-incompatible species mainly pollinated by insects (Sharma, 1986; Campbell, 1997; Miljuš-Đukić et al., 2010). It produces two morphs of flowers: pin and thrum flowers. Pin flowers have a style being longer than the stamens. Thrum flowers have a style shorter than the stamens (Sharma, 1986; Campbell, 1997; Miljuš-Đukić et al., 2010). *F. tataricum* produces one type of flower that can self-pollinate and self-fertilize (Sharma, 1986; Campbell, 1997). The two species also differ by their antioxidant production. *F. esculentum* contains fewer antioxidants than *F. tataricum* (Fabjan et al., 2003; Zhu, 2016). For example, for rutin, *F. esculentum* has values 100 times lower than the ones of *F. tataricum* (Fabjan et al., 2003; Zhu, 2016). This high concentration in antioxidants gives a bitterer taste to *F. tataricum* (Fabjan et al., 2003). That could explain why *F. esculentum* counts for 90% of the buckwheat production (Small, 2017).

Although some researchers investigated the impacts of water stress on the early stages of *F. esculentum* (Delpérée et al., 2003; Cawoy et al., 2006), the mechanisms underlying its resistance remain largely unknown. Moreover, the impacts of water stress on *F. tataricum* have not been much investigated so far. In this prospect, we compared the response of *F. esculentum* and *F. tataricum* to water stress during their life-span. This study aims to answer these questions: (1) What are the impacts of water stress on the vegetative, reproductive, and antioxidant parameters of *F. esculentum* and *F. tataricum?* (2) Do the two species show mechanisms of resistance to drought? (3) Are these mechanisms the same between the two species? Because of its poor root system, we expected *F. esculentum* to be drought-sensitive (Sharma, 1986; Myers and Meinke, 1994; Campbell, 1997). *F. tataricum* is expected to show drought-tolerant mechanisms such as an increase in antioxidants, maintenance of its growth and reproduction (Chaves et al., 2003; Hu and Xiong, 2014; Kooyers, 2015).

2 | MATERIAL AND METHODS

2.1 | Plant material and growth conditions

Seeds of *F. esculentum* var. Darja and of *F. tataricum* var. Zlata were received from Prof. Dr. Ivan Kreft (University of Ljubljana, Slovenia). They were sowed in peat compost (DCM, Amsterdam, the Netherlands) and 2 weeks later, the seedlings were transplanted into 2 l pots filled with the same peat compost. Plants were grown under greenhouse conditions (temperature of 22 ± 2°C, relative humidity of 65 ± 5% and 16 h-photoperiod). Four weeks after sowing, 20 plants of each species were placed under control conditions with a water supply every 3 days and 20 others were placed under water stress with a water supply every 2 weeks. Soil moisture was measured every week to certify the well-watered (WW, 40–50% soil humidity) or the water stress (WS, < 20% soil humidity) condition by using ProCheck sensor handheld reader (Decagon Devices). The experiment lasted 74 days.

2.2 | Vegetative and reproductive growth parameters

Every week, on 10 plants per species and treatment, were counted the number of leaves (unfolded) and the number of inflorescences in anthesis on the main stem. The node of the first inflorescence was noted to evaluate the flowering time (the nodes were counted acropetally and the cotyledonary node was disregarded). At the end of the experiment, the total number of leaves and inflorescences per plant were counted on the 10 plants.

Ten inflorescences (between the 12th and 14th nodes) per species and condition were collected and placed in FAA (formaldehyde: acetic

acid: 70% alcohol, 1:1:18) after 6 weeks of treatment. The inflorescences of buckwheat are racemes of cymes (Quinet et al., 2004). Therefore, the number of cymes, flowers, and seeds per inflorescence were counted using a stereomicroscope. The seed set was obtained by dividing the number of seeds by the number of flowers per inflorescence.

Ten non-opened flower buds of well-watered or water-stressed *F. esculentum* were also collected in FAA. Two anthers per flower buds were opened separately on a microscope slide and colored with 10 µl of Alexander's dye (Alexander, 1969). Under a light microscope, the number of pollen grains per anther was counted.

The leaves and stems of three plants per species and condition were harvested separately after 6 weeks of treatment and weighed to obtain the fresh weight (FW). Then, they were placed in an oven at 70°C for 2 days and weighed again to obtain the dry weight (DW). The water content (WC) was calculated as WC = [(FW−DW)/FW] * 100.

2.3 | Physiological parameters

After 2 weeks of treatment, parameters linked to the photosynthesis and water status of the plants were taken on the youngest expanded leaf of five plants per species and condition. The chlorophyll content index (CCI) was measured with a chlorophyllometer (Opti-Sciences, CCM-200) four consecutive times per leaf at different spots. Chlorophyll fluorescence parameters and more precisely the photosystem II efficiency (φPS2), the photochemical quenching (qP) and the non-photochemical quenching (NPQ) were measured thanks to a fluorescence monitoring system (FMS II; Hansatech Instruments) according to Descamps et al. (2018). The instantaneous net photosynthesis rate (Ai), the instantaneous transpiration rate (Ei), the leaf stomatal conductance (gs) and the intercellular CO_2 concentration (Ci) were quantified by using an InfraRed Gas Analyzer (IRGA, ADC BioScientific LCI-SD system). The instantaneous water-use efficiency (WUEi) was calculated as WUEi = Ai/Ei.

2.4 | Antioxidant parameters

The leaves of five plants per species and treatment were collected after 6 weeks of treatment. They were crushed in liquid nitrogen to analyze the concentration in malondialdehyde (MDA, membrane peroxidation byproduct), the antioxidant capacity by FRAP method (ferric reducing antioxidant power) and the concentrations in polyphenols and flavonoids according to Aubert et al. (2020).

The MDA concentration was measured by spectrophotometry using the trichloroacetic acid method from 250 mg of plant material. Results were expressed in nmol g^{-1} FW. For antioxidant capacity, the hydrophilic antioxidants (AOAM fraction) were extracted by methanol and the hydrophobic antioxidants (AOAD fraction) by dichloromethane from 1 g of plant material. After reaction with the FRAP solution, absorbance was read at 593 nm by a spectrophotometer (UV 1800, Shimadzu) and results were expressed in µM equivalent Trolox g^{-1} FW. Polyphenols were quantified using the Folin–Ciocalteu colorimetric method from 100 mg of plant material. Results were read at 760 nm using a spectrophotometer and expressed in mg equivalent gallic acid g^{-1} FW. The flavonoids concentration was quantified thanks to the aluminum chloride chelation method and the absorbance was read at 440 nm using a spectrophotometer. Results were expressed in mg equivalent quercetin g^{-1} FW.

2.5 | Statistical analyses

All of the analyses were conducted in R studio. Counting data were analyzed by Poisson regression testing the effects of the species, the water treatment and their interactions. The remaining data were analyzed by ANOVA testing the same effects but first, the normality of the residues and the variance homoscedasticity were verified using Shapiro–Wilk tests and Levene's tests, respectively. When the homoscedasticity was not met, Kruskal–Wallis tests were performed. Differences are significant when *P*-values were inferior at 0.05.

3 | RESULTS

3.1 | The effect of water stress on vegetative growth differed between buckwheat species

Regarding the number of leaves on the main stem, a difference between the two species appeared during the 2nd and the 4th week of stress with *F. esculentum* producing more leaves than *F. tataricum* (Figure 1; $F_{1,16}$ = 12.73, P = 0.0026). The effect of WS was not the same for the two species ($F_{1,16}$ = 11.02, P = 0.0043). From the second week of stress, *F. esculentum* produced more leaves under control condition than under WS ($F_{1,10}$ = 9.5, P = 0.011), while there was no effect on the production of leaves of *F. tataricum*. At the end of the experiment, the total number of leaves per plant was 44.6 ± 8.1 and 23.2 ± 3.4 for *F. esculentum* under control condition and under WS, respectively, whereas it was 43.7 ± 11 and 35.5 ± 3.5 for *F. tataricum* under control condition and under WS, respectively.

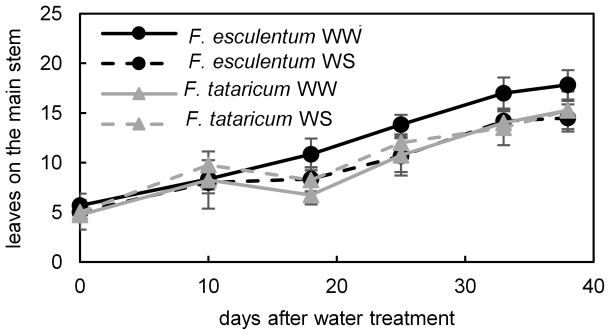

FIGURE 1 Effect of water stress on the production of leaves on the main stem of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*. The plants were either well-watered (WW) or under water stress (WS) for six weeks. Data are presented as mean ± standard error (n = 10)

The water treatment had an impact on the fresh weight ($F_{1,4}$ = 17.55, P = 0.014) and dry weight ($F_{1,4}$ = 33.67, P = 0.0044) of the leaves of *F. esculentum* (Table 1). The weights were higher under control condition than under WS but the leaf water content was not affected. There was no effect on the weights (FW and DW) and water content of the leaves of *F. tataricum* and neither on the weights and water content of the stems of the two species (Table 1).

3.2 | The effect of water stress on physiological parameters differed between buckwheat species

3.2.1 | Water status

The instantaneous transpiration rate (Ei) and the leaf stomatal conductance (gs) of *F. tataricum* was not affected by the water treatment (Table 2; Ei: χ^2_1 = 0.33, P = 0.56; gs: $F_{1,6}$ = 0.089, P = 0.77) but there was a difference between the two water treatments for *F. esculentum* (Table 2; Ei: χ^2_1 = 6.82, P = 0.009; gs: χ^2_1 = 7.07, P = 0.0078). The plants WW had higher values for these two parameters than the plants under WS. Finally, Ei was also different between the two species with *F. esculentum* having a lower Ei than *F. tataricum* (Table 2; χ^2_1 = 9.41, P = 0.0022).

3.2.2 | Photosynthetic status

The water treatment had no effect on the intercellular CO_2 concentration (Ci) and on the instantaneous net photosynthesis rate (Ai) of *F. tataricum* (Table 2; $F_{1,6}$ = 0.89, P = 0.38; $F_{1,6}$ = 0.053, P = 0.83). In the contrary, for *F. esculentum*, Ci and Ai were higher under control condition than under WS (Table 2; $F_{1,8}$ = 317.92, P < 0.001; $F_{1,8}$ = 84.36, P < 0.001).

TABLE 1 Effect of water stress on the fresh weight, dry weight and the water content of leaves and stems of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*

Species		*F. esculentum*		*F. tataricum*	
Water treatment		WW	WS	WW	WS
Fresh weight (g)	Leaves	15.8 ± 4.2[a]	4.8 ± 1.6[b]	4.3 ± 0[a]	4.2 ± 0[a]
	Stems	32.1 ± 14.2[a]	15.6 ± 2.6[a]	11.0 ± 0[a]	7.3 ± 0[a]
Dry weight (g)	Leaves	3 ± 0.5[a]	1.0 ± 0.3[b]	1.0 ± 0.6[a]	0.8 ± 0.05[a]
	Stems	5.5 ± 2.3[a]	2.2 ± 0.1[a]	1.1 ± 0.7[a]	1.3 ± 0.4[a]
Water content (%)	Leaves	80.6 ± 4.7[a]	78.1 ± 3.0[a]	85.3 ± 0[a]	80.9 ± 0[a]

Note: The plants were either well-watered (WW) or under water stress (WS) for 6 weeks. Data are presented as mean ± standard error (n = 3). Different letters mean a significant difference (P < 0.05) between the two water treatments for a same species according to ANOVA test.

TABLE 2 Effect of water stress on the instantaneous transpiration rate (Ei), the leaf stomatal conductance (gs), the intercellular CO_2 concentration (Ci), the instantaneous net photosynthesis rate (Ai) and the instantaneous water use efficiency (WUEi) of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*

Species	*F. esculentum*		*F. tataricum*	
Water treatment	WW	WS	WW	WS
Ei (mmol H_2O m^2 s^{-1})	2.90 ± 0.54[a]	0.39 ± 0.13[b]	4.16 ± 0.51[a]	3.74 ± 1.28[a]
gs (mol H_2O m^2 s^{-1})	0.89 ± 0.38[a]	0.02 ± 0.01[b]	0.47 ± 0.13[a]	0.43 ± 0.23[a]
Ci (µmol CO_2 mol^{-1})	420.0 ± 5.2[a]	288.2 ± 15.7[b]	400.2 ± 6.4[a]	394.2 ± 11.0[a]
Ai (µmol CO_2 m^2 s^{-1})	6.7 ± 0.6[a]	1.6 ± 0.8[b]	1.8 ± 0.8[a]	1.7 ± 0.6[a]
WUEi (µmol CO_2 $mmol^{-1}$ H_2O)	2.37 ± 0.35[b]	4.02 ± 0.72[a]	0.46 ± 0.22[a]	0.48 ± 0.12[a]

Note: The plants were either well-watered (WW) or under water stress (WS) for 6 weeks. Data are presented as mean ± standard error (n = 5). Different letters mean a significant difference (P < 0.05) between the two water treatments for a same species according to ANOVA test.

TABLE 3 Effect of water stress on the chlorophyll content index (CCI), the photosystem II efficiency (φPS2), the photochemical quenching (qP) and the non-photochemical quenching (NPQ) of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*.

Species	*F. esculentum*		*F. tataricum*	
Water treatment	WW	WS	WW	WS
CCI	44.1 ± 5.7[b]	53.2 ± 6.1[a]	31.8 ± 2.9[b]	37.1 ± 6.8[a]
φPS2	0.71 ± 0.06[a]	0.71 ± 0.06[a]	0.75 ± 0.04[a]	0.73 ± 0.05[a]
qP	0.90 ± 0.06[a]	0.88 ± 0.04[a]	0.91 ± 0.05[a]	0.88 ± 0.04[a]
NPQ	0.53 ± 0.16[a]	0.55 ± 0.29[a]	0.21 ± 0.07[a]	0.20 ± 0.07[a]

Note: The plants were either well-watered (WW) or under water stress (WS) for 6 weeks. Data are presented as mean ± standard error (n = 5). Different letters mean a significant difference (P < 0.05) between the two water treatments for a same species according to ANOVA test.

The instantaneous water use efficiency (WUEi) was different between the two species with the WUEi of *F. esculentum* being higher than the WUEi of *F. tataricum* (Table 2; χ^2_1 = 12.63, P < 0.001). There was an impact of the water treatment on the WUEi only in *F. esculentum*, which was lower under WW condition than under WS (Table 2; $F_{1,8}$ = 20.73, P = 0.0019).

The chlorophyll content index (CCI) was higher for *F. esculentum* than for *F. tataricum* (Table 3; $F_{1,50}$ = 84.28, P < 0.001) and it was higher for the plants under WS than for the ones under control condition for both species ($F_{1,50}$ = 23.36, P < 0.001).

About the chlorophyll fluorescence, there was no impact of the water treatment (Table 3). There was only a difference between the two species for the non-photochemical quenching (Table 3; $F_{1,14}$ = 18.66, P < 0.001). The NPQ of *F. esculentum* was higher than the one of *F. tataricum*.

3.3 | Water stress affected reproductive growth in both species

The node of the first inflorescence was different between the two species ($F_{1,16}$ = 17.04, P < 0.001). The first inflorescence of *F. esculentum* appeared at the 6.0 ± 1.0 node, while it appeared at the 8.4 ± 1.4 for *F. tataricum*. There was no effect of the water treatment on this parameter ($F_{1,16}$ = 0.031, P = 0.86).

Regarding the number of inflorescences in anthesis on the main stem, *F. esculentum* had more inflorescences than *F. tataricum* whatever the treatment (Figure 2(A); $F_{1,16}$ = 43.91, P < 0.001). The impact of water treatment on this parameter appeared the second week of treatment for *F. esculentum* with the plants under control condition having more inflorescences in anthesis on the main stem than the plants under WS ($F_{1,16}$ = 5.93, P = 0.027). A different trend was observed in *F. tataricum* where the WS plants had more inflorescences at anthesis on the main stem than WW plants even though the difference was only significant 38 days after the start of treatment. At the end of the experiment, the number of inflorescences at anthesis on the main stem dropped in *F. tataricum* plants under WS as the flowers already set seeds or have wilted, while flowers at anthesis were still present under control condition and in *F. esculentum*.

The total number of inflorescences per plant (Figure 2(B); $F_{1,12}$ = 13.03, P = 0.0036), the number of cymes per inflorescence (Figure 2(C); $F_{1,29}$ = 93.51, P < 0.001) and the number of flowers per inflorescence (Figure 2(D); $F_{1,29}$ = 159.59, P < 0.001) were higher in *F. esculentum* than in *F. tataricum*. However, although the plants WW produced more inflorescences than the plants under WS ($F_{1,12}$ = 16.17, P = 0.0017), there was no effect of the water treatment on the number of cymes ($F_{1,29}$ = 0.63, P = 0.43) and flowers ($F_{1,29}$ = 1.75, P = 0.2) per inflorescence. The seed set of *F. tataricum* was not affected by the water treatment and was of 31.7% ± 13.4 ($F_{1,14}$ = 0.24, P = 0.63). Because *F. esculentum* needs a cross-pollination by insects to produce seeds, no seeds were obtained during this experiment but pollen quantity was investigated. The number of pollen grains per anther of *F. esculentum* was impacted by the lack of water ($F_{1,38}$ = 14.42, P < 0.001). The plants WW produced more pollen grains per anther (108 ± 16) than the plants under WS (94 ± 6).

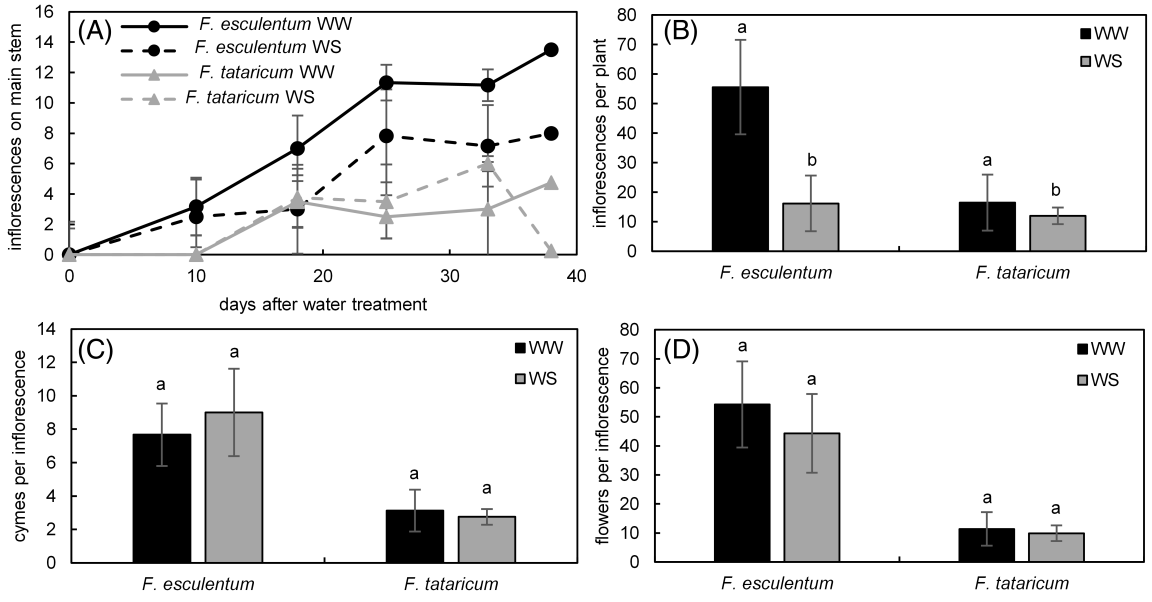

FIGURE 2 Effect of water stress on reproductive parameters of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*. (A) Number of inflorescences in anthesis on the main stem, (B) total number of inflorescences, (C) number of cymes per inflorescence, (D) number of flowers per inflorescence. The plants were either well-watered (WW) or under water stress (WS) for 6 weeks. Data are presented as mean ± standard error (vertical bars) (n = 10). Different letters mean a significant difference (P < 0.05) between the two water treatments for a same species according to Poisson regression

3.4 | Water stress increased antioxidants production in *F. tataricum*

The water stress increased the concentration of malondialdehyde in the leaves mainly for *F. tataricum* (Figure 3(A); χ^2_1 = 10.59, P = 0.0011). Regarding the total content of hydrophilic antioxidants in the leaves, there was no impact of the water treatment for *F. esculentum* (Figure 3(B); $F_{1,4}$ = 0.16, P = 0.71) but it increased with the WS in *F. tataricum* ($F_{1,4}$ = 14.45, P = 0.019). This increase could be related to the higher content of polyphenols (Figure 3(C); $F_{1,6}$ = 12.46, P = 0.012) and flavonoids (Figure 3(D); $F_{1,2}$ = 30.98, P = 0.031) observed in *F. tataricum* in response to WS. However, the concentration of hydrophobic antioxidants (Figure 3(E); $F_{1,8}$ = 0.086, P = 0.78) was not affected by WS whatever the species.

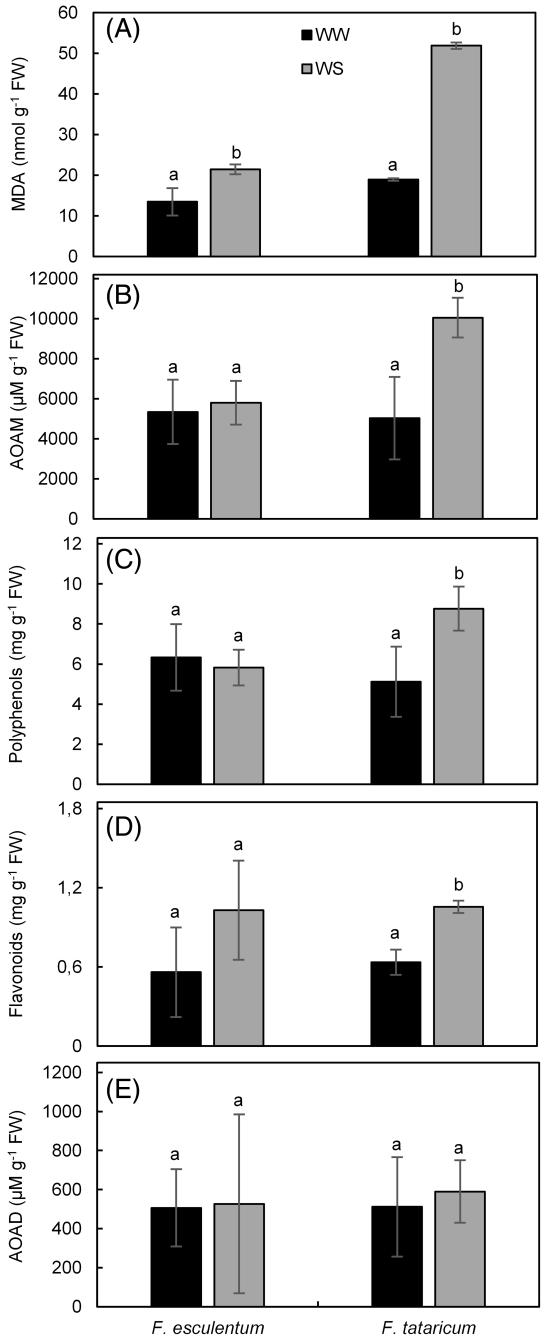

FIGURE 3 Effect of water stress on the oxidative status of leaves of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*. (A) Concentration of malondialdehyde (MDA), (B) activity of hydrophilic antioxidants (AOAM), (C) polyphenols concentrations, (D) flavonoids concentrations, (E) activity of hydrophobic antioxidants (AOAD). The plants were either well-watered (WW) or under water stress (WS) for 6 weeks. Data are presented as mean ± standard error (vertical bars) (n = 5). Different letters mean a significant difference (P < 0.05) between the two water treatments for a same species according to ANOVA test

4 | DISCUSSION

Regarding the results of our study, *F. esculentum* var. Darja and *F. tataricum* var. Zlata seem to have developed different resistance strategies to cope with a water deficit (Figure 4). *F. esculentum* had characteristics of drought avoidance, while *F. tataricum* exhibited traits of drought tolerance. *F. esculentum* showed changes in parameters linked to the water status to maintain its water content. *F. tataricum* showed no changes in its vegetative growth, water status nor photosynthetic status but an increase in oxidative defense. However, the two species shared the same resistance strategy that consisted of the maintenance of the photosynthesis light phase. Indeed, the chlorophyll content of *F. esculentum* and *F. tataricum* was higher under water stress. This has also been shown in *F. esculentum* var. La Harpe in response to water stress (Delpérée et al., 2003). The chlorophyll content has been reported as an index of drought resistance in dicotyledons such as *Solanum tuberosum* or *Arachis hypogaea* as well as in the monocotyledons *Hordeum vulgare* and *Triticum durum* (van der Mescht et al., 1999; Li et al., 2006; Arunyanark et al., 2008; Talebi, 2011). Indeed, the maintenance or increase of chlorophyll content allowed the maintenance of photosynthesis and plant productivity (Li et al., 2006; Talebi, 2011; Anithakumari et al., 2012). However, we observed a decrease in plant growth in *F. esculentum* in response to water stress. In their study, Delpérée et al. (2003) observed also a decrease in leaf area due to water stress. The increase in chlorophyll content index could thus be partly explained by these decreases and could result from a concentration effect. We also observed that water stress had no impact on the chlorophyll fluorescence of *F. esculentum* and *F. tataricum*, meaning that the photosynthesis light phase machinery was not affected by water stress. The stability of the photosynthetic apparatus has been considered as another index of drought resistance (van der Mescht et al., 1999; Li et al., 2006; Nakayama et al., 2007). Although both species shared the same resistance strategy regarding the photosynthesis light phase, they differ in their response to water stress regarding the photosynthesis dark phase. Indeed, the net photosynthesis rate was not affected in *F. tataricum* but decreased with water stress in *F. esculentum*. Such discrepancy could be explained by their difference in the management of water status and stomata opening in response to water stress.

Fagopyrum esculentum showed drought avoidance adaptations to maintain its water status, while *F. tataricum* was less affected by water stress. Water stress reduced leaf production and leaf fresh and dry weights

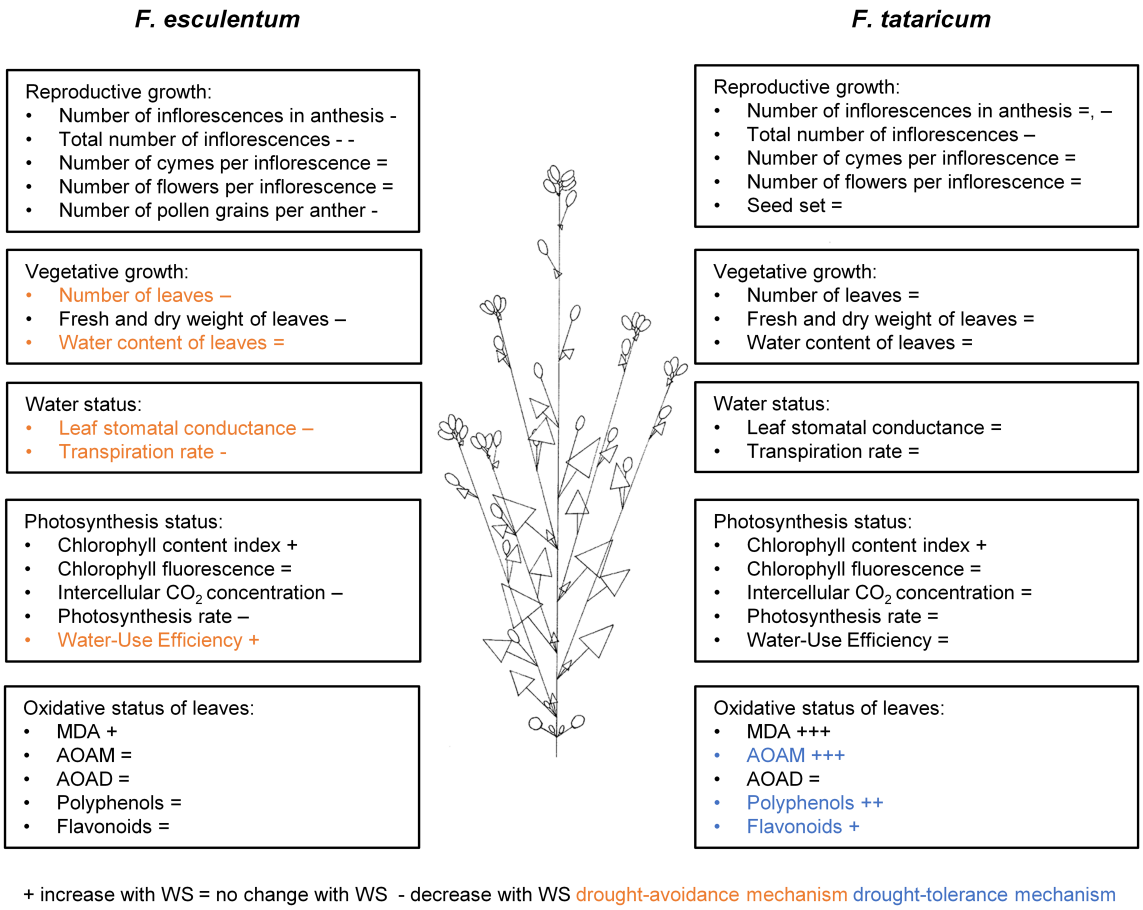

FIGURE 4 Summary of the effects of water stress on the reproductive growth, vegetative growth, water status, photosynthesis status, and oxidative status of two buckwheat species, *Fagopyrum esculentum* and *F. tataricum*. The plants were either well-watered or under water stress (WS) for 6 weeks. AOAD, hydrophobic antioxidants; AOAM, hydrophilic antioxidants; MDA, malondialdehyde

in *F. esculentum* but did not affect leaf water content, confirming that the plant limited water losses. When plants are facing water scarcity, cell division is limited as well as cell elongation, giving fewer leaves (Schuppler et al., 1998; Prasad et al., 2008; Gray and Brady, 2016). Another reason could be the reallocation of resources in favor of root development. Indeed, promoting root development improves water supply (Cornic and Massacci, 1996; Gray and Brady, 2016). However, root growth was not investigated in our study. In their work on *F. esculentum*, Tadina et al. (2007) did not observe any impact of water stress on root dry weight, but neither did they observe any effect on shoot dry weight, contrary to our results. Further investigations would be required to test this hypothesis. Limited resources to produce leaves could also be explained by a problem of photosynthesis (Farooq et al., 2009). Decreasing leaf production was reported as a strategy that allowed the plants to avoid transpiration and water loss (Cornic and Massacci, 1996). In response to drought, *F. esculentum* showed a reduction in the stomatal conductance and the transpiration rate in our study. This decrease in stomatal conductance translates a closure of the stomata, which is the first response to drought in many species (Schapendonk et al., 1989; Arnau et al., 1997; Delpérée et al., 2003; Nakayama et al., 2007; Tadina et al., 2007; Pszczółkowska et al., 2012). Indeed, this change allowed a reduction in transpiration which results in less water loss and the maintenance of the water status (Schapendonk et al., 1989; Cornic and Massacci, 1996; Nakayama et al., 2007), as observed in *F. esculentum*. However, the stomata closure resulted in a decrease of intercellular CO_2 concentration and net photosynthesis rate in *F. esculentum* as previously mentioned. Indeed, when the stomata are closed, less CO_2 can enter the leaves and be used for photosynthesis and carbohydrate production (Cornic and Massacci, 1996; Nakayama et al., 2007; Prasad et al., 2008; Pszczółkowska et al., 2012). This could explain the lower growth rate of *F. esculentum* in response to water stress. However, the WUE of *F. esculentum* increased with water stress. As defined by Prasad et al. (2008), the WUE is the assimilation of carbohydrates per unit of used water. As previously mentioned, in the face of water stress, plants limit the amount of transpired water but some of them continue to produce assimilates, hence increasing the WUE (Schapendonk et al., 1989; Prasad et al., 2008; Gray and Brady, 2016). Maintaining a high WUE under drought conditions has been reported as a mechanism of avoidant plants (Kooyers, 2015).

Regarding *F. tataricum*, except the impact on its chlorophyll content as discussed previously, there was no change in its water status, photosynthesis and vegetative growth in the face of water stress. This has also been observed in other species like *H. vulgare* and *Triticum aestivum* (Cornic and Massacci, 1996; Arnau et al., 1997; Shangguan et al., 1999). These plants were considered drought-tolerant thanks to

an osmotic adjustment (Arnau et al., 1997; Prasad et al., 2008). The accumulation of osmolytes like proline in the cells allowed these cells to remain at turgescence and to avoid impacts on their photosynthetic apparatus or changes in their water status (Cornic and Massacci, 1996; Arnau et al., 1997; Shangguan et al., 1999; Prasad et al., 2008). To validate this theory, it would be interesting to analyze the osmolytes concentrations in *F. tataricum*.

Another resistant strategy to cope with water stress is the production of antioxidants (Chaves et al., 2003). Buckwheat is known to produce high amount of antioxidants, particularly *F. tataricum* (Fabjan et al., 2003; Zhu, 2016). Antioxidants are involved in ROS scavenging and limit oxidative stress (Chaves et al., 2003; Farooq et al., 2009). Oxidative stress was observed in response to water stress in both buckwheat species and especially in *F. tataricum*, as indicated by the increase in MDA in the leaves. To cope with oxidative stress, antioxidant capacity, polyphenols, and flavonoids concentrations increased in response to water stress in *F. tataricum*. Our results suggest that antioxidant production was sufficient to avoid the negative effects of oxidative stress since neither plant growth nor the light phase of photosynthesis, which is generally the first site of oxidative stress (Farooq et al., 2009; Salehi-Lisar and Bakhshayeshan-Agdam, 2016), was affected in *F. tataricum*. Siracusa et al. (2017) highlighted the same increase in polyphenols and flavonoids compounds in *F. esculentum* in response to water stress. Suzuki et al. (2005) observed an increase in rutin, an important flavonoid present in buckwheat, in the leaves of *F. tataricum* facing desiccation. It was also observed in other species such as *Gossypium hirsutum*, *T. aestivum* and *Amaranthus tricolor* (Shah et al., 2011; Ma et al., 2014; Sarker and Oba, 2018). Polyphenols, and more precisely flavonoids, are the main antioxidants observed in buckwheat (Lee et al., 2016; Matsui and Walker, 2020). These molecules have often been highlighted for their antioxidant properties in many reviews (Heim et al., 2002; Shahidi and Ambigaipalan, 2015). They play an important role in the protection of plants against abiotic stresses (Treutter, 2006; Khlestkina, 2013; Sharma et al., 2019).

Although water stress affected differently the vegetative growth of *F. esculentum* and *F. tataricum*, it affected the reproductive growth in both species. In *F. esculentum*, the total number of inflorescences and the number of pollen grains per anther were reduced under water deficit. In *F. tataricum*, there was also a decrease in the total number of inflorescences under water deficit. Cawoy et al. (2006) also observed a decrease in the number of inflorescences and flowers in response to osmotic stress in *F. esculentum* var. La Harpe. A reduction in inflorescence number could be explained by lower assimilates production or by competition between organs for assimilates (Barnabás et al., 2008; Phillips et al., 2018). It is known that drought reduces the photosynthetic rate and so the amount of assimilates, leading to a reduction of inflorescences in species such as *Sorghum bicolor*, *Olea europaea*, or *Oryza sativa* (Craufurd and Peacock, 1993; Rapoport et al., 2012; Akram et al., 2013). We observed that the net photosynthesis rate was reduced in *F. esculentum*, it could thus result in lower assimilates production. However, such photosynthesis reduction was not observed in *F. tataricum*. Flower production is indeterminate and profuse in buckwheat and may represent a main sink organ (Quinet et al., 2004; Cawoy et al., 2007). Cawoy et al. (2007) demonstrated that, in response to defoliation and thus reduction of assimilates, *F. esculentum* var. La Harpe produced fewer inflorescences, thus validating this theory. Another reason could be the resources reallocation for roots at the cost of reproductive structures (Farooq et al., 2009). In other species, such as *Borago officinalis*, the reduction in the number of flowers in anthesis was explained by flower abortion (Descamps et al., 2018). Flower abortion could also be related to a shortage in assimilates. However, this parameter was not studied here.

In addition to flower number, flower fertility and seed set could also be affected by water stress (Barnabás et al., 2008; Farooq et al., 2009). *F. esculentum* is self-incompatible and pollen needs to be transferred between flowers by insects for seed production (Sharma, 1986; Campbell, 1997; Miljuš-Đukić et al., 2010). We observed that water stress reduced pollen production in this species. Cawoy et al. (2006) also observed a reduction of pollen grains per anther in response to osmotic stress in *F. esculentum*. A decrease in pollen grain number has also been observed in response to water stress in other species (Puteh et al., 2009; Waser and Price, 2016). Microsporogenesis is reported as one of the reproductive stages most sensitive to stress in several species (Saini, 1997; Cawoy et al., 2006). Indeed, the production of pollen requires a lot of energy and could thus also be limited due to low assimilates production or competition for assimilates (Borghi et al., 2019). However, due to the self-incompatibility, we did not investigate the consequence in terms of seed production in *F. esculentum*. In their study, Cawoy et al. (2006) showed that the seed production per inflorescence was reduced by osmotic stress but that it was more the consequence of a lower number of flowers than of a lower seed set. Unlike *F. esculentum*, *F. tataricum* is self-fertile (Sharma, 1986; Campbell, 1997). We observed that *F. tataricum* managed to maintain seed set under water stress. Usually, when plants are facing drought stress, they encounter a yield loss (Barnabás et al., 2008; Farooq et al., 2009). Other studies on the impacts of water stress on buckwheat showed no change in the seed production (Tadina et al., 2007; Germ et al., 2013).

5 | CONCLUSION

In response to water stress, *F. esculentum* and *F. tataricum* showed different resistance strategies. Water stress reduced vegetative growth, affected water status and photosynthesis in *F. esculentum* but not in *F. tataricum*, although oxidative stress was observed in both species. *F. tataricum* seems thus more tolerant to water stress than *F. esculentum*. Indeed, *F. esculentum* had more characteristics of drought avoidance and closed stomata to maintain its water status, while *F. tataricum* exhibited more traits of drought tolerance by the production of antioxidants. Water stress also affected the reproductive phase in both species by decreasing the inflorescence production, mainly in *F. esculentum*. It also reduced pollen production in the latter. Although seed set was maintained in *F. tataricum*, further studies are required to see the impact of water stress on seed production in both species.

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AUTHOR CONTRIBUTIONS

Lauranne Aubert contributed in investigation, formal analysis, writing—original draft, writing—review and editing. Daniela Konrádová contributed in investigation, writing—review and editing. Selma Barris contributed in investigation, formal analysis, writing—review and editing. Muriel Quinet contributed in conceptualization, investigation, writing—original draft, writing—review and editing, supervision.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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REFERENCES

Akram, H.M., Ali, A., Saeed-Ur-Rehman, H. & Bibi, A. (2013) Impact of water deficit stress on various physiological and agronomic traits of three basmati rice (*Oryza sativa* L.) cultivars. *Journal of Animal and Plant Science*, 23, 1415–1423.

Alexander, M.P. (1969) Differential staining of aborted and nonaborted pollen. *Biotechnic & Histochemistry*, 44, 117–122.

Alvarez-Jubete, L., Arendt, E.K. & Gallagher, E. (2010) Nutritive value of pseudocereals and their increasing use as functional gluten-free ingredients. *Trends in Food Science and Technology*, 21, 106–113.

Anithakumari, A.M., Nataraja, K.N., Visser, R.G.F. & van der Linden, C.G. (2012) Genetic dissection of drought tolerance and recovery potential by quantitative trait locus mapping of a diploid potato population. *Molecular Breeding*, 30, 1413–1429.

Arnau, G., Monneveux, P., This, D. & Alegre, L. (1997) Photosynthesis of six barley genotypes as affected by water stress. *Photosynthetica*, 34, 67–76.

Arunyanark, A., Jogloy, S., Akkasaeng, C., Vorasoot, N., Kesmala, T., Nageswara Rao, R.C., *et al.* (2008) Chlorophyll stability is an indicator of drought tolerance in peanut. *Journal of Agronomy and Crop Science*, 194, 113–125.

Aubert, L., Konrádová, D., Kebbas, S., Barris, S. & Quinet, M. (2020) Comparison of high temperature resistance in two buckwheat species *Fagopyrum esculentum* and *Fagopyrum tataricum*. *Journal of Plant Physiology*, 251, 153222.

Barnabás, B., Jäger, K. & Fehér, A. (2008) The effect of drought and heat stress on reproductive processes in cereals. *Plant, Cell and Environment*, 31, 11–38.

Borghi, M., Perez de Souza, L., Yoshida, T. & Fernie, A.R. (2019) Flowers and climate change: a metabolic perspective. *The New Phytologist*, 224, 1425–1441.

Campbell, C.G. (1997) *Buckwheat. Fagopyrum esculentum Moench. Promoting the conservation and use of underutilized and neglected crops. 19*. Rome, Italy: International Plant Genetic Resources Institute.

Cawoy, V., Lutts, S. & Kinet, J.M. (2006) Osmotic stress at seedling stage impairs reproductive development in buckwheat (*Fagopyrum esculentum*). *Physiologia Plantarum*, 128, 689–700.

Cawoy, V., Lutts, S., Ledent, J.F. & Kinet, J.M. (2007) Resource availability regulates reproductive meristem activity, development of reproductive structures and seed set in buckwheat (*Fagopyrum esculentum*). *Physiologia Plantarum*, 131, 341–353.

Chaves, M.M., Maroco, J.P. & Pereira, J.S. (2003) Understanding plant responses to drought - from genes to the whole plant. *Functional Plant Biology*, 30, 239–264.

Cornic, G. & Massacci, A. (1996) Leaf photosynthesis under drought stress. In: Baker, N.R. (Ed.) *Photosynthesis and the Environnement*. The Netherlands: Kluwer Academic Publishers, pp. 347–366.

Craufurd, P.Q. & Peacock, J.M. (1993) Effect of heat and drought stress on sorghum (*Sorghum bicolor*). II. Grain yield. *Experimental Agriculture*, 29, 77–86.

Delpérée, C., Kinet, J.M. & Lutts, S. (2003) Low irradiance modifies the effect of water stress on survival and growth-related parameters during the early developmental stages of buckwheat (*Fagopyrum esculentum*). *Physiologia Plantarum*, 119, 211–220.

Descamps, C., Quinet, M., Baijot, A. & Jacquemart, A.L. (2018) Temperature and water stress affect plant–pollinator interactions in *Borago officinalis* (Boraginaceae). *Ecology and Evolution*, 8, 3443–3456.

Fabjan, N., Rode, J., Kosĭr, I.J., Wang, Z., Zhang, Z. & Kreft, I. (2003) Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) as a source of dietary rutin and quercitrin. *Journal of Agricultural and Food Chemistry*, 51, 6452–6455.

FAOSTAT (2018) Crops. http://www.fao.org/faostat/en/#data/QC

Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S.M.A. & Plant, S.M. A.B. (2009) Plant drought stress: effects, mechanisms and management. *Agronomy for Sustainable Development*, 29, 185–212.

Germ, M., Breznik, B., Dolinar, N., Kreft, I. & Gaberščik, A. (2013) The combined effect of water limitation and UV-B radiation on common and tartary buckwheat. *Cereal Research Communications*, 41, 97–105.

Gray, S.B. & Brady, S.M. (2016) Plant developmental responses to climate change. *Developmental Biology*, 419, 64–77.

Heim, K.E., Tagliaferro, A.R. & Bobilya, D.J. (2002) Flavonoid antioxidants: chemistry, metabolism and structure-activity relationships. *The Journal of Nutritional Biochemistry*, 13, 572–584.

Hu, H. & Xiong, L. (2014) Genetic engineering and breeding of drought-resistant crops. *Annual Review of Plant Biology*, 65, 715–741.

IPCC. (2014) Climate Change 2014: Synthesis Report. In: R.K. Pachauri & L.A. Meyer (Eds.) *Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, (pp. 151). Geneva, Switzerland: IPCC.

Jacquemart, A.-L., Cawoy, V., Kinet, J.-M., Ledent, J.-F. & Quinet, M. (2012) Is buckwheat (*Fagopyrum esculentum* Moench) still a valuable crop today? *European Journal of Plant Science and Biotechnology*, 6, 1–10.

Khlestkina, E. (2013) The adaptive role of flavonoids: emphasis on cereals. *Cereal Research Communications*, 41, 185–198.

Kooyers, N.J. (2015) The evolution of drought escape and avoidance in natural herbaceous populations. *Plant Science*, 234, 155–162.

Kreft, M. (2016) Buckwheat phenolic metabolites in health and disease. *Nutrition Research Reviews*, 29, 30–39.

Lee, L.S., Choi, E.J., Kim, C.H., Sung, J.M., Kim, Y.B., Seo, D.H., *et al.* (2016) Contribution of flavonoids to the antioxidant properties of common and tartary buckwheat. *Journal of Cereal Science*, 68, 181–186.

Li, R.-H., Guo, P.-P., Baumz, M., Grando, S. & Ceccarelli, S. (2006) Evaluation of chlorophyll content and fluorescence parameters as indicators of drought tolerance in barley. *Agricultural Sciences in China*, 5, 751–757.

Ma, D., Sun, D., Wang, C., Li, Y. & Guo, T. (2014) Expression of flavonoid biosynthesis genes and accumulation of flavonoid in wheat leaves in response to drought stress. *Plant Physiology and Biochemistry*, 80, 60–66.

Matsui, K. & Walker, A.R. (2020) Biosynthesis and regulation of flavonoids in buckwheat. *Breeding Science*, 70, 74–84.

Miljuš-Đukić, J., Banović, B., Ninković, S. & Radović, S. (2010) The heteromorphic sporophytic self-incompatibility system of buckwheat

(*Fagopyrum esculentum* Moench). *European Journal of Plant Science and Biotechnology*, 4, 51–56.
Myers, R.L. & Meinke, L.J. (1994) Buckwheat: a multi-purpose, short-season alternative. *University of Missouri Extension*, g04306, 1–7.
Nakayama, N., Saneoka, H., Moghaieb, R.E.A., Premachandra, G.S. & Fujita, K. (2007) Response of growth, photosynthetic gas exchange, translocation of 13 C-labelled photosynthate and N accumulation in two soybean (*Glycine max* L. Merrill) cultivars to drought stress. *International Journal of Agriculture and Biology*, 9, 669–674.
Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J. M., *et al*. (2018) Drought reduces floral resources for pollinators. *Global Change Biology*, 24, 3226–3235.
Prasad, P.V.V., Staggenborg, S.A., Ristic, Z., Ahuja, L.R., Reddy, V.R., Saseendran, S.A., *et al*. (2008) Impacts of drought and/or heat stress on physiological, developmental, growth, and yield processes of crop plants. In: Ahuja, L.R., Reddy, V.R., Saseendran, S.A. & Qiang, Y. (Eds.) *Response of crops to limited water: understanding and modeling water stress eff ects on plant growth processes*. Madison, WI: American Society of Agronomy, Inc. Crop Science Society of America, Inc. Soil Science Society of America, Inc., pp. 301–355.
Pszczółkowska, A., Fordoński, G., Kulik, T., Olszewski, J., Płodzień, K. & Łojko, M. (2012) The effect of water stress on the gas exchange parameters, productivity and seed health of buckwheat (*Fagopyrum esculentum* Moench). *Acta Agrobotanica*, 63, 67–76.
Puteh, A.B., Jali, N., Ismail, J.M.R. & Samsudin, A.S. (2009) Pollen and seed yield components of water-stressed cultivated and weedy rice. *Pertanika Journal of Tropical Agricultural Science*, 32, 293–303.
Quinet, M., Cawoy, V., Lefèvre, I., Van Miegroet, F., Jacquemart, A.L. & Kinet, J.M. (2004) Inflorescence structure and control of flowering time and duration by light in buckwheat (*Fagopyrum esculentum* Moench). *Journal of Experimental Botany*, 55, 1509–1517.
Rapoport, H.F., Hammami, S.B.M., Martins, P., Pérez-Priego, O. & Orgaz, F. (2012) Influence of water deficits at different times during olive tree inflorescence and flower development. *Environmental and Experimental Botany*, 77, 227–233.
Saini, H.S. (1997) Effects of water stress on male gametophyte development in plants. *Sexual Plant Reproduction*, 10, 67–73.
Salehi-Lisar, S.Y. & Bakhshayeshan-Agdam, H. (2016) Drought stress in plants: causes, consequences & tolerance. In: Hossain, M.A., Wani, S. H., Bhattacharjee, S., Burritt, D.J. & Tran, L.-S.P. (Eds.) *Drought stress tolerance in plants, volume I Physiology & Biochemistry*, (pp. 1–16). Switzerland: Springer International Publishing.
Sarker, U. & Oba, S. (2018) Drought stress enhances nutritional and bioactive compounds, phenolic acids and antioxidant capacity of Amaranthus leafy vegetable. *BMC Plant Biology*, 18, 1–15.
Schapendonk, A.H.C.M., Spitters, C.J.T. & Groot, P.J. (1989) Effects of water stress on photosynthesis and chlorophyll fluorescence of five potato cultivars. *Potato Research*, 32, 17–32.
Schuppler, U., He, P.-H., John, P.C.L. & Munns, R. (1998) Effect of water stress on cell division and cell-division-cycle 2-like cell-cycle kinase activity in wheat leaves. *Plant Physiology*, 117, 667–678.
Shah, A.R., Khan, T.M., Sadaqat, H.A. & Chatha, A.A. (2011) Alterations in leaf pigments in cotton (*Gossypium hirsutum*) genotypes subjected to drought stress conditions. *International Journal of Agriculture and Biology*, 13, 902–908.
Shahidi, F. & Ambigaipalan, P. (2015) Phenolics and polyphenolics in foods, beverages and spices: antioxidant activity and health effects - a review. *Journal of Functional Foods*, 18, 820–897.
Shangguan, Z., Shao, M. & Duckmans, J. (1999) Interaction of osmotic adjustment and photosynthesis in winter wheat under soil drought. *Journal of Plant Physiology*, 154, 753–758.
Sharma, A., Shahzad, B., Rehman, A., Bhardwaj, R., Landi, M. & Zheng, B. (2019) Response of phenylpropanoid pathway and the role of polyphenols in plants under abiotic stress. *Molecules*, 24, 1–22.
Sharma, M.P. (1986) The biology of Canadian weeds. 74. *Fagopyrum tataricum* (L.) Gaertn. *Canadian Journal of Plant Science*, 66, 381–393.
Siracusa, L., Gresta, F., Sperlinga, E. & Ruberto, G. (2017) Effect of sowing time and soil water content on grain yield and phenolic profile of four buckwheat (*Fagopyrum esculentum* Moench.) varieties in a Mediterranean environment. *Journal of Food Composition and Analysis*, 62, 1–7.
Słomka, A., Michno, K., Dubert, F., Dziurka, M., Kopeć, P. & Płazek, A. (2017) Embryological background of low seed set in distylous common buckwheat (*Fagopyrum esculentum* Moench) with biased morph ratios, and biostimulant-induced improvement of it. *Crop & Pasture Science*, 68, 680–690.
Small, E. (2017) Buckwheat–the world's most biodiversity-friendly crop? *Biodiversity*, 18, 108–123.
Suzuki, T., Honda, Y. & Mukasa, Y. (2005) Effects of UV-B radiation, cold and desiccation stress on rutin concentration and rutin glucosidase activity in tartary buckwheat (*Fagopyrum tataricum*) leaves. *Plant Science*, 168, 1303–1307.
Tadina, N., Germ, M., Kreft, I., Breznik, B. & Gaberščik, A. (2007) Effects of water deficit and selenium on common buckwheat (*Fagopyrum esculentum* Moench.) plants. *Photosynthetica*, 45, 472–476.
Talebi, R. (2011) Evaluation of chlorophyll content and canopy temperature as indicators for drought tolerance in durum wheat (*Triticum durum* Desf.). *Australian Journal of Basic and Applied Sciences*, 5, 1457–1462.
Treutter, D. (2006) Significance of flavonoids in plant resistance: a review. *Environmental Chemistry Letters*, 4, 147–157.
van der Mescht, A., de Ronde, J.A. & Rossouw, F.T. (1999) Chlorophyll fluorescence and hlorophyll content as measure of drought tolerance in potato. *South African Journal of Science*, 95, 407–412.
Waser, N.M. & Price, M.V. (2016) Drought, pollen and nectar availability, and pollination success. *Ecology*, 97, 1400–1409.
Zhu, F. (2016) Chemical composition and health effects of Tartary buckwheat. *Food Chemistry*, 203, 231–245.

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