

2 The interactions between UV radiation, drought and selenium in different buckwheat species

Interakcije med UV sevanjem, sušo in selenom pri različnih vrstah ajde

Aleksandra Golob^a, Ana Kugovnik^a, Ivan Krefl^b, Alenka Gaberščik^a, Mateja Germ^{a*}

^aDepartment of Biology, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia

^bNutrition Institute, Tržaška cesta 40, SI-1000 Ljubljana, Slovenia

*correspondence: mateja.germ@bf.uni-lj.si

Abstract: Here we summarise the outcomes on biochemical response and growth of buckwheat with respect to UV radiation, drought and selenium, as well as their interactions. Buckweats are taxonomically and morphologically very diverse. They have been subjected to more or less intensive breeding, which results in higher susceptibility to environmental constraints including drought and also in different potential to cope and exploit UV radiation. The responses of different buckweats to UV, drought and their combination differed in different species. Selenium treatment may mitigate negative effects of environmental constraints on buckwheat. Regarding the production of UV absorbing compounds, buckweats mainly positively respond to UV dose. Ca druses in buckwheat seem to be important in affecting UV penetration.

Keywords: buckwheat, UV radiation, drought, selenium

Izvleček: V prispevku povzemamo biokemijske značilnosti in rast ajde glede na vplive UV sevanja, suše in selena ter njihovih interakcij. Ajda je taksonomsko in morfološko zelo raznolika. Ajda je bila podvržena bolj ali manj intenzivnemu žlahtnjenju, kar ima za posledico večjo dovzetnost za strese zaradi okoljskih omejitev, vključno s sušo in zaščito pred UV sevanjem. Rezultati so pokazali različne odzive različnih vrst ajd na UV sevanje, sušo in njihovo kombinacijo. Količina UV absorbirajočih snovi v ajdi se povečuje z odmerkom UV sevanja. Obravnavanje ajde s selenom lahko omili negativne učinke okoljskih omejitev na ajdo. Pri uravnavanju količine sevanja, ki prodira v tkiva, imajo pomembno vlogo tudi Ca kristali.

Ključne besede: ajda, UV sevanje, suša, selen

Introduction

Different plant species have different abilities to cope with environmental constraints. The success of agricultural crops therefore depends on climate, terrain, soil properties, water availability, and their adaptations to specific environments

(Nakabayashi et al. 2014). Agricultural plants are often grown in areas that differ significantly from their domestic environment and have been subjected to intensive breeding in order to increase yield, which in turn may compromise their potential to overcome unfavourable conditions in their environment.

The ozone layer that maintains favourable UV levels at the Earth surface, will presumably recover to the long-term mean that was recorded from 1964-1980 until 2050 (Chipperfield et al. 2015). This is important since enhanced UV radiation significantly affects plant properties and causes stress under elevated levels (Gaberščik et al. 2002). Plants have been subjected to UV radiation during their evolution, and they have evolved mechanisms to fully take advantage of their light environment including UV radiation. Many authors (Prado et al. 2012, Jansen et al. 2012, Björn 2015) even stated that ambient UV radiation presents an evolutionarily-important environmental factor for regulation of plant growth and development, and that ambient UV-B radiation might be more properly viewed as a photomorphogenic signal rather than a stressor for plants under field conditions. In many cases, UV induced plant properties increase the potential of plants to survive under different environmental constraints. UV affects biochemical, morphological, and anatomical plant characteristics, triggers activity of the phenyl-propanoid cycle, causes plant stunting, reductions in leaf area and total biomass, and causes alterations in patterns of biomass partitioning into various plant organs (Rozema et al. 2002). The intensity of UV effects on plants is species-specific and results in potential damage and consequently in activation of protective mechanisms (Gaberščik et al. 2001). Jin et al. (2017) reported about a negative effect of UV-B radiation on both survival and growth in a variety of species differing in their life history, trophic level, and habitat. Ambient UV radiation may cause reduction in biomass, photosynthesis, growth, and yield of many plant species. Nevertheless, these studies suggest that sensitivity to ambient UV radiation varies considerably both within and between plant species (Kataria and Guruprasad 2014). However, the exclusion or reduction of UV radiation during plant growth and development can significantly affect plant traits (Golob et al. 2017a).

Recent Earth's climate conditions observations indicate that the environmental changes today are faster and greater than in the past. Agricultural productivity all over the world is subjected to increasing environmental constraints, particularly to drought. In recent years, most European countries have been affected by drought (The European

Commission 2010; Vanwindekens et al. 2018). This is expected, since among several problems that crop plants face, water stress is the most critical one (Santhosh et al. 2017). A common adverse effect of water stress on crop plants is the reduction in fresh and dry biomass production (Farooq et al. 2009). From 1964 to 2007, national cereal production across the globe had been reduced by 9-10% due to drought and extreme heat (Lesk et al. 2016). In addition, drought and extreme heat are usually related to high radiation environment including UV radiation level. The worsening of the environmental conditions favours the use of crops which are able to survive in harsher environment. Under such conditions some crops can take advantage of high UV radiation, since UV may mitigate the vulnerability of crops to drought (Alexieva et al. 2001, Kakani et al. 2003, Zhang et al. 2011, Germ et al. 2013). Numerous studies revealed that exogenous application of selenium (Se) in small doses to crops increases their tolerance to different environmental conditions (Nawaz et al. 2015, Golob et al. 2017a). Selenium could play a protective role in crops during high UV radiation or water deficit by enhancing the antioxidant enzyme activity (Ekelund and Danilov 2001, Nawaz et al. 2015) and decreasing the content of reactive oxygen species (ROS). Supplemental Se improves growth and yield in wheat and buckwheat subjected to water deficit conditions and increased UV radiation respectively (Nawaz et al. 2015). Despite many positive effects of Se, the physiological mechanisms that underlie those effects have been poorly understood and needs to be elucidated (Hasanuzzaman et al. 2014).

Here we summarise the main research results on interactions between UV radiation, drought and Se in buckwheats. Buckwheat exhibits a lower sensitivity to various types of environmental constraints, due to less intensive breeding, compared to major cereals (Halbrecq et al. 2005). Buckwheat is also attracting attention because it possesses high potential for production of UV-absorbing substances (Kreft et al. 2002, Fabjan et al. 2003). Growing drought-tolerant crops with low nutrient requirement, or at least more resilient crops, is becoming more and more important in today's changing environment with prolonged hot and dry periods. In such manner, we would be able to compensate for the decrease in arable land

quality and thus ensure adequate food production for the ever-growing global population in a more sustainable way (Saha et al. 2016, Wang et al. 2016, Kumar et al. 2018). Drought tolerance and resilience of crops depends on a variety of factors like species origin and properties and environmental conditions including UV radiation and mineral nutrition. Special attention in this review will be therefore given to UV, water shortage and the effect of selenium treatment.

Buckwheat is a modest crop

Buckwheat can grow successfully in harsh environment since it has low demands for nutrients and can exhibit high phenotypic plasticity (Li and Zhang 2001, Kreft et al. 2002). In Tibet, it is found at altitudes of up to 4,500 m, therefore it can thrive at high altitudes with elevated UV radiation levels in comparison to lowlands (Bonafaccia et al. 2003). The increase in UV radiation along the altitudinal gradient ranges from between 6% and 8% (Caldwell et al. 1998) to 20% per each 1,000 m of elevation. Buckwheat produces a variety of phenolic compounds, which among others include flavonoids, whose synthesis is significantly enhanced by UV radiation, as shown in many studies (e.g. Gaberščik et al. 2002, Suzuki et al. 2005, Golob et al. 2018a). The most commonly used taxa of buckwheat around the world are common and Tartary buckwheat (Bonafaccia et al. 2003). Tartary buckwheat usually thrives at higher elevations in comparison to common buckwheat (Tsuji and Ohnishi 2001). In searching of possible ancestors of common and Tartary buckwheat it was shown that based on the distribution of their wild ancestors, common buckwheat originates in the northwestern corner of China's Yunnan Province, while Tartary buckwheat originates in the northwest part of Sichuan Province, as also confirmed by the variability of allozymes in the buckwheat (Ohnishi 1998). Wild and cultivated types of Tartary buckwheat exist in the same regions of northeastern Pakistan, Tibet, Yunnan, and Sichuan (Tsuji and Ohnishi 2001, Germ and Gaberščik 2016).

Protection of plants against high UV levels

Buckweats are C3 plants in which the photosynthetic photon flux density is saturated at about 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Larcher 2003), therefore their efficient protection against excessive radiation is of primary importance, especially if other constraints are present. The fate of the photons that hit the leaf surface depends primarily on the characteristics of the epidermis; namely, epidermal structures, the quantity and quality of phenolic substances (Grašič et al. 2019). Thick epidermal layer with well-developed cuticle is not only the protection against high level of solar radiation, but also presents important protection against water loss. The most important factor affecting the penetration of UV radiation is the production of UV-absorbing compounds like flavonoids and related phenyl-propanoids (Gaberščik et al. 2002). These are regarded as one of the key components of an overall acclimation response of plants to changing UV environments (Barnes et al. 2016). Their production is determined by UV dose, radiation quality, time of exposure and the presence of different environmental constraints including water shortage and the potential of plant species (Ren et al. 2007, Golob et al. 2017a, Golob et al. 2018a). The production of UV absorbing compounds is either inducible (dose dependent) or constitutive (not dose dependent). The latter is mainly characteristic in plants colonising high radiation environments. However, buckwheat mainly shows dose dependent response (Gaberščik et al. 2002). By triggering the secondary metabolic pathway, UV radiation also increases plant antioxidant activity (Sebastian et al. 2018). Indeed, Hideg and Strid (2017) reported that flavonoids have great potential to scavenge reactive oxygen species (ROS), which can be also produced during water shortage. The investigations of Tartary buckwheat showed significant positive correlations between phenolic compounds, the amounts of certain antioxidants and altitude of growing sites (Kishore et al. 2010). In comparison to other taxa, buckwheat exhibits high potential of production of UV-absorbing compounds. One of the most important and researched flavonoids in buckwheat is rutin (Fabjan et al. 2003, Kreft et al. 2006). Suzuki et al. (2015) reported that in buckwheat leaves, rutin and rutin-oxidase

are involved in enhancing the defence against UV radiation, low temperature, and desiccation. Regvar et al. (2012) studied the effects of elevated UV-B radiation on concentrations of rutin, catechin, and quercetin in both common and Tartary buckwheat, showing that in common buckwheat, they were induced by UV-B, while there were no differences in the concentrations in the Tartary buckwheat even though the latter contained more total flavonoids. Yao et al. (2006) who studied Tartary buckwheat grown under different UV-B levels showed that UV-B absorbing compounds and rutin concentrations increased under near ambient, but not under elevated UV-B. This may be related to the overall costs needed to prevent UV-B stress at highest radiation level (Suchar and Robberecht 2016). Suzuki et al. (2005) reported that Tartary buckwheat treated with UV light for 30 min showed increased rutin concentration by 122%. This potential is not only leaf specific since UV-B treatment of hairy roots of Tartary buckwheat seedlings also increased rutin and quercetin levels (Huang et al. 2016).

Jovanović et al. (2006) studied the mode of the enzymatic antioxidant defence system in common buckwheat leaves and seedlings subjected to short-term enhanced UV-B radiation showing a considerable increase in methanol-soluble flavonoids, which is in agreement with previously reported data (Gaberščik et al. 2002, Suzuki et al. 2005).

Plant biochemical protection can be also improved by improving plant nutrition. One of important elements benefiting plants is also Se (Golob et al. 2017a). The accumulation of secondary substances can be altered by biotic interactions. The effects of increased UV-B radiation on arbuscular mycorrhiza and secondary metabolite production in common and Tartary buckwheat revealed that root colonisation with arbuscular mycorrhizal fungi significantly reduced catechin concentrations in common buckwheat roots, and induced rutin concentrations in Tartary buckwheat (Regvar et al. 2012). Additional protection against UV-radiation in plants is the presence of calcium oxalate (CaOx) crystals (druses) in the leaf tissue that may contribute to uniform distribution of light within leaves (Kuo-Huang et al. 2007, Gal et al. 2012, Golob et al. 2018b). Their position varies with light intensity and at high intensity, crystals

are mainly formed at the top of the palisade cells (He et al. 2014). CaOx druses also reduce the transmission of UV-B through leaves as it was shown in the experiment with Tartary buckwheat where the density of CaOx druses positively correlated with the reflectance in the blue, green, yellow and UV-B regions of the spectrum (Golob et al. 2018b).

Adaptation to drought stress can increase tolerance to UV-B radiation

Vulnerability of crops to UV is affected by different environmental factors namely water regime, ambient levels of visible radiation, and nutrient status (Shen et al. 2015). Elevated UV radiation levels and drought usually occur at the same time under conditions of high solar irradiance and low precipitation rate, which are becoming more and more frequent and extreme (Comont et al. 2012). Clarification of the interaction between drought and UV-B will help us to understand their potential impact on plant adaptation to the changing environmental conditions that will enable efficient crop production (Alexieva et al. 2001, Rodríguez-Calzada et al. 2019). There is an evidence of both synergistic and antagonistic interactions between enhanced UV radiation and drought (Kakani et al. 2003).

Different studies showed that adaptation to drought stress contributes to increased tolerance to UV-B radiation (Hofmann et al. 2003). This is the consequence of specific morphological responses, like thicker cuticle, smaller leaves shorter internodes that are the same for both constraints (Larcher 2003, Jansen et al. 2012). During drought, some plants also enhance the synthesis of phenolic substances and waxes, which improves UV-B radiation screening and reflection and reduces UV-B damaging effects (Kulandaivelu et al. 1997). Alexieva et al. (2001) reported that drought induced activity of antioxidative enzymes that protect plants against oxidative damages caused by UV-B radiation. They also presumed that proline is the drought-induced substance, which plays an important protective role in response to UV-B. However, Caldwell et al. (1998) concluded that drought may cover up UV-B impacts on plants, since drought is a stronger plant stressor

than elevated UV-B radiation. However, there are also some opposite findings. Tian and Lei (2007) reported that simultaneous exposure to drought and UV-B caused even stronger damage to wheat seedlings than when these two stress factors were applied separately. This is possibly related to combine oxidative damage. Similarly, the earlier study of Runeckles and Krupa (1994) showed that enhanced UV-B radiation lowered tolerance of crops to drought. Common buckwheat and Tartary buckwheat exposed to different levels of UV-B radiation simulating 17% ozone depletion and water shortage, revealed significant negative effect of elevated UV-B on growth parameters in well-watered common buckwheat, that was less pronounced in drought affected group (Germ et al. 2013). In line with expectations, Tartary buckwheat showed less sensitivity to both stressors, presumably because it had been subjected to breeding to a lesser extent. Enhanced UV-B also significantly reduced total biomass accumulation and biomass allocation to root in well-watered *Fagopyrum dibotrys* plants, while UV-B mitigated the effect of water shortage on biomass accumulation (Zhang et al. 2011). Similarly, Alexieva et al. (2001) found out that UV-B and drought acted synergistically in pea and wheat, inducing protective mechanisms in a way that preapplication of either of the two stress factors lowered the damage, caused by subsequent exposure of plants to the other stressor. Authors evidenced that UV-B exerted a stronger negative effect than drought on the growth of seedlings in both species (Alexieva et al. 2001).

Ameliorative effects of the Se addition on UV-B and drought treatments

Selenium (Se) is regarded as a beneficial nutrient that can increase plant tolerance to different environmental constraints (Yao et al. 2013, Golob et al. 2017a). Ekelund and Danilov (2001) reported that plants, treated with Se, show enhanced tolerance to increased UV-B radiation, due to an antioxidative role of selenium that lowers oxidative damage in plants. It was indicated that addition of Se diminishes the negative influence induced by UV radiation and desiccation (Sieprawska et al. 2015). The addition of Se in appropriate doses can regulate oxidative stress via activation of antioxi-

dativ enzymes (Hartikainen et al. 2000) and/or by direct quenching of $O_2^{\cdot-}$ and OH^{\cdot} radicals. Se also upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites (Mimmo et al. 2017), such as flavonoids, which have UV absorbing as well as antioxidative role in plants.

The combined effects of UV-B irradiation and foliar treatment of common buckwheat and Tartary buckwheat with selenium 1 g Se m^{-3} showed that Se treatment mitigated the negative effect of UV-B radiation on plant height and on biomass production in common buckwheat and the effective quantum yield of photosystem II (PS II) in both buckwheat species (Breznik et al. 2005a). Se possibly promotes growth of UV-stressed plants, due to protection of chloroplast enzymes (Breznik et al. 2009). The interaction between Se addition and UV-B radiation in common buckwheat revealed the ameliorative effect of Se for the aboveground biomass, number of nodes, and number of seeds (Breznik et al. 2005b). Smrkolj et al. (2006) treated common buckwheat (*Fagopyrum esculentum* Moench cv. Darja) and Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) by spraying the leaves with Se solution, and exposed the plants to three levels of UV-B radiation. Selenium concentrations in flowers were higher under enhanced UV-B radiation compared to ambient and reduced UV-B radiation conditions in both species. This is in line with study from Ožbolt et al. (2008), where UV-B radiation increased Se content in common buckwheat plants, grown from seeds that were previously soaked in solutions with different Se concentrations.

Golob et al. (2018a) exposed hybrid buckwheat (*F. hybridum*) plants, grown under full and reduced ambient UV radiation to foliar Se treatment. Plants treated with 10 mg L^{-1} sodium selenate contained 20-fold more Se compared to Se-untreated plants, and ambient UV radiation partly reduced this response.

Golob et al. (2007b) studied the impact of Se addition and UV radiation on Tartary and hybrid buckwheat in an outdoor experiment. Tartary buckwheat had higher contents of anthocyanins, UV-B, and UV-A-absorbing substances compared to hybrid buckwheat. Higher contents of protective substances are possibly a consequence of adaptation to unfavourable environmental conditions, as

Tartary buckwheat originates from cooler areas at higher altitudes, often >1,500 m above the sea level.

Se mitigated negative effects of UV-B radiation in common and Tartary buckwheat, but not in hybrid buckwheat. Ameliorative effects of Se in UV-B treated plants were expected, since UV-B radiation causes the production of free radicals. Se upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites.

Summary

Agricultural plants are often subjected to environmental conditions that differ from their home environment so they have to overcome different environmental constraints. Increased UV radiation and drought are commonly present at the same time. The outcomes about joint action of increased UV radiation and drought in buckwheat are diverse. There are evidences of both synergistic and antagonistic interactions. Adaptation to drought stress contributes to increased tolerance to UV-B radiation, which is consequence of specific morphological, biochemical and physiological responses of buckwheat. The responses of buckwheats are different in different species, the UV dose and sites of origin of different cultivars. Some studies have shown that Tartary buckwheat is more tolerant to UV radiation compared to common buckwheat, while the others have shown the same sensitivity. The interactions of UV radiation with drought have also been demonstrated. In the experiments with *F. tataricum* and *F. dibotrys*, UV-B radiation mitigated negative effects of drought, however in *F. esculatum* the effect was less pronounced.

Se mitigated negative effects of UV-B radiation in common and Tartary buckwheat, but not in hybrid buckwheat. Se upregulates the phenyl-propanoid biosynthetic pathway, which results in the accumulation of specific metabolites. All these findings indicate that mineral nutrition of plants is of great importance for plant's protection against increased UV radiation and drought.

Biominingal Ca plays an important role in the genus *Fagopyrum*. CaOx druses in the leaf tissue of the buckwheat interact with the incoming UV light and affect optical properties of the leaves.

Povzetek

Kmetijske rastline so pogosto podvržene okoljskim razmeram, ki se razlikujejo od razmer v njihovem domačem okolju, zato morajo premagati različne okoljske omejitve. Rastline so mnogokrat izpostavljene povečanemu UV sevanju in suši hkrati. Izsledki o vplivih skupnega delovanja UV sevanja in suše so različni. Obstajajo dokazi o sinergističnih in antagonističnih interakcijah. Raziskave so pokazale, da prilagajanje na sušni stres prispeva k večji toleranci na UV-B sevanje, ki je posledica specifičnih morfoloških, biokemičnih in fizioloških odzivov rastlin. Odzivi ajde so različni pri različnih vrstah, odmerkih sevanja in krajih izvora različnih kultivarjev. Nekatere študije so pokazale, da je tatarska ajda bolj tolerantna na UV sevanje v primerjavi z navadno ajdo, druge pa so pokazale njeno precejšnjo občutljivost. Dokazane so bile tudi interakcije UV sevanja s sušo. Pri vrstah *F. tataricum* in *F. dibotrys* je UV-B sevanje omililo negativne učinke pomanjkanja vode, pri vrsti *F. esculatum* pa je bil omilitveni učinek manj izražen.

Se je ublažil negativne učinke UV-B sevanja pri navadni in tatarski ajdi, ni pa imel pozitivnih učinkov pri hibridni ajdi. Se lahko deluje kot antioksidant in niža raven prostih radikalov ter uravnava potek fenilno propanoidnega cikla, kar omogoča kopičenje specifičnih presnovnih produktov. Rezultati kažejo, da je mineralna prehrana rastlin zelo pomembna za varstvo rastlin pred povečanim UV sevanjem in sušo. Pri rodu *Fagopyrum* ima pomembno vlogo tudi biomineral Ca. CaOx kristali v listnem tkivu vplivajo na prehajanje UV svetlobe in na optične lastnosti listov.

Acknowledgements

This work was financed by the Slovenian Research Agency programmes and projects [grant numbers P1-0212, L4-7552, J7-9418, L4-9305].

References

- Alexieva, V., Mapelli, S.S., Karanov, E., 2001. The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. *Plant, Cell and Environment* 24, 1337-1344.
- Barnes, P.W., Tobler, M.A., Keefover-Ring, K., Flint, S.D., Barkley, A.E., Ryel, R.J., Lindroth, R.L., 2016. Rapid modulation of ultraviolet shielding in plants is influenced by solar ultraviolet radiation and linked to alterations in flavonoids. *Plant, Cell and Environment* 39, 222-230.
- Björn, L.O., 2015. On the history of phyto-photo UV science (not to be left in skoto toto and silence). *Plant Physiology and Biochemistry* 93, 3-8.
- Bonafaccia, G., Marocchini, M., Kreft, I., 2003. Composition and technological properties of the flour and bran from common and tartary buckwheat. *Food Chemistry* 80, 9-15.
- Breznik, B., Germ, M., Gaberščik, A., Kreft, I., 2005a. Combined effects of elevated UV-B radiation and the addition of selenium on common (*Fagopyrum esculentum* Moench) and tartary [*Fagopyrum tataricum* (L) Gaertn.] buckwheat. *Photosynthetica* 43, 583-589.
- Breznik, B., Gaberščik, A., Germ, M., Kreft, I., 2005b. The combined effects of enhanced UV-B radiation and selenium on common buckwheat (*Fagopyrum esculentum* Moench) habitus. *Fagopyrum: novosti o ajdi* 22, 83-87.
- Breznik, B., Germ, M., Kreft, I., Gaberščik, A., 2009. Crop responses to enhanced UV-B radiation. In: Singh, S.N. (ed.), *Climate change and crops*, (Environmental science and engineering). Springer, Berlin, pp. 269-281.
- Caldwell, M.M., Björn, L.O., Bornman, J.F., Flint, S.D., Kulandaivelu, G., Teramura, A.H., Tevini, M., 1998. Effects of increased solar ultraviolet radiation on terrestrial ecosystems. *Journal of Photochemistry and Photobiology B: Biology* 46, 40-52.
- Chipperfield, M.P., Dhomse, S.S., Feng, W., McKenzie, R.L., Velders, G.J.M., Pyle, J.A., 2015. Quantifying the ozone and ultraviolet benefits already achieved by the Montreal Protocol. *Nature Communications* 6, 7233.
- Comont, D., Winters, A., Gwynn-Jones, D., 2012. Acclimation and interaction between drought and elevated UV-B in *A. thaliana*: Differences in response over treatment, recovery and reproduction. *Ecology and Evolution* 2(11), 2695-2709.
- Ekelund, N.G.A., Danilov, R.A., 2001 The influence of selenium on photosynthesis and "light-enhanced dark respiration" (LED_R) in the flagellate *Euglena gracilis* after exposure to ultraviolet radiation. *Aquatic Science* 63, 457-465.
- The European Commission (2010) Water scarcity and drought in the European Union. The European Commission. http://ec.europa.eu/environment/pubs/pdf/factsheets/water_scarcity.pdf
- Farooq, M., Wahid, A., Kobayashi, N., Fujita, D., Basra, S.M.A., 2009. Plant drought stress: effects, mechanisms and management. *Agronomy Sustainable Development*. 29, 185-212.
- Fabjan, N., Rode, J., Košir, 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(22), 6452-6455.
- Gaberščik, A., Novak, M., Trošt, T., Mazej, Z., Germ, M., Björn, L.O., 2001. The influence of enhanced UV-B radiation on the spring geophyte *Pulmonaria officinalis*. *Plant Ecology* 154, 51-56.
- Gaberščik, A., Vončina, M., Trošt Sedej, T., Germ, M., Björn, L.O., 2002. Growth and production of buckwheat (*Fagopyrum esculentum*) treated with reduced, ambient, and enhanced UV-B radiation. *Journal of Photochemistry and Photobiology B: Biology* 66(1), 30-36.
- Gal, A., Brumfeld, V., Weiner, S., Addadi, L., Oron, D., 2012. Certain biominerals in leaves function as light scatterers. *Advanced Materials* 24, 77-83.
- 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 Communication* 41(1), 97-105.

- Germ, M., Gaberščik, A., 2016. The effect of environmental factors on buckwheat. In: Zhou, M., Kreft, I. (eds.). Molecular breeding and nutritional aspects of buckwheat. London [etc.]: Academic Press is an imprint of Elsevier. cop., pp. 273-282.
- Golob, A., Kavčič, J., Stibilj, V., Gaberščik, A., Vogel-Mikuš, K., Germ, M., 2017a. The effect of selenium and UV radiation on leaf traits and biomass production in *Triticum aestivum* L. *Ecotoxicology and Environmental Safety* 136, 142-149.
- Golob, A., Stibilj, V., Turk, J., Kreft, I., Germ, M., 2017b. Impact of UV radiation and selenium on two buckwheat species. *Acta biologica slovenica* 60(2), 29-39.
- Golob, A., Stibilj, V., Kreft, I., Vogel-Mikuš, K., Gaberščik, A., Germ, M., 2018a. Selenium treatment alters the effects of UV radiation on chemical and production parameters in hybrid buckwheat. *Acta Agriculturae Scandinavica B. S. P.* 68(1), 5-15.
- Golob, A., Stibilj, V., Nečemer, M., Kump, P., Kreft, I., Hočevár, A., Gaberščik, A., Germ, M., 2018b. Calcium oxalate druses affect leaf optical properties in selenium-treated *Fagopyrum tataricum*. *Journal of photochemistry and photobiology. B, Biology* 180, 51-55.
- Hasanuzzaman, M., Nahar, K., Fujita, M., 2014. Silicon and selenium: two vital trace elements that confer abiotic stress tolerance to plants. In: Ahmad, P. (ed.), *Emerging Technologies and Management of Crop Stress Tolerance* 1, pp. 377-422.
- Halbrech, B., Romedenne, P., Ledent, J.F., 2005. Evolution of flowering, ripening and seed set in buckwheat (*Fagopyrum esculentum* Moench): Quantitative analysis. *European Journal of Agronomy* 23, 209-224.
- Hartikainen, H., Xue, T., Piironen, V., 2000. Selenium as an antioxidant and pro-oxidant in ryegrass. *Plant and Soil* 225, 193-200.
- Hideg, É., Strid, Å., 2017. The effects of UV-B on the Biochemistry and Metabolism of plants. In: *UV-B Radiation and Plant Life: Molecular Biology to Ecology*. CABI Publishers, Wallingford, UK, pp. 90-110.
- Hofmann, R.W., Campbell, B.D., Bloor, S.J., Swinny, E.E., Markham, K.R., Ryan, K.G., Fountain, D.W., 2003. Responses to UV-B radiation in *Trifolium repens* L. - physiological links to plant productivity and water availability. *Plant, Cell & Environment* 26, 603-612.
- Jansen, M.A.K., Coffey, A.M., Prinsen, S., 2012. UV-B induced morphogenesis. Four players or a quartet? *Plant Signaling & Behavior* 7, 1185-1187.
- Huang, X., Yao, J., Zhao, Y., Xie, D., Jiang, X., Xu, Z., 2016. Efficient Rutin and Quercetin Biosynthesis through Flavonoids-Related Gene Expression in *Fagopyrum tataricum* Gaertn. Hairy Root Cultures with UV-B Irradiation. *Frontiers in Plant Science* 7, 63.
- He, H., Veneklaas, E.J., Kuo, J., Lambers, H., 2014. Physiological and ecological significance of biomineralization in plants. *Trends in Plant Science* 19, 166-174.
- Jin, P., Duarte, C.M., Agustí, S., 2017. Contrasting Responses of Marine and Freshwater Photosynthetic Organisms to UVB Radiation: A Meta-Analysis *Frontiers in Marine Science* 4, 45.
- Jovanović, Z.S., Milosević, J.D., Radović, S.R., 2006. Antioxidative Enzymes in the Response of Buckwheat (*Fagopyrum esculentum* Moench) to Ultraviolet B Radiation. *Journal of Agricultural and Food Chemistry* 54, 9472-9478.
- Kakani, V.G., Reddy, K.R., Zhao, D., Sailaja, K., 2003. Field crop responses to ultraviolet-B radiation: a review. *Agricultural and Forest Meteorology* 120, 191-218.
- Kataria, S., Guruprasad, K.N., 2014. Exclusion of solar UV components improves growth and performance of *Amaranthus tricolor* varieties. *Scientia Horticulture* 174, 36-45.
- Kishore, G., Ranjan, S., Pandey, A., Gupta, S., 2010. Influence of Altitudinal Variation on the Antioxidant Potential of Tartary Buckwheat of Western Himalaya. *Food Science and Biotechnology* 19, 1355-1363.
- Kreft, S., Štrukelj, B., Gaberščik, A., Kreft, I., 2002. Rutin in buckwheat herbs grown at different UV-B radiation level: comparison of two UV spectrophotometric and an HPLC method. *Journal of Experimental Botany* 53, 1801-1804.

- Kreft, I., Fabjan, N., Yasumoto, K., 2006. Rutin content in buckwheat (*Fagopyrum esculentum* Moench) food materials and products. *Food Chemistry* 98, 508-512.
- Kulandaivelu, G., Lingakumar, K., Premkumar, A., 1997. UV-B radiation. In: Prasad, M.N.V. (ed), *Plant Ecophysiology*, John Wiley & Sons, pp. 41-60.
- Kuo-Huang, L.L., Ku, M.S.B., Franceschi, V.R., 2007. Correlations between calcium oxalate crystals and photosynthetic activities in palisade cells of shade-adapted *Peperomia glabella*. *Botanical Studies* 48, 155-164.
- Larcher, W., 2003. *Physiological Plant Ecology: Ecophysiology and Stress Physiology of functional groups*. 4th Edition, Springer, New York, 513p.
- Lesk, C., Rowhani, P., Ramankutty, N., 2016. Influence of extreme weather disasters on global crop production. *Nature* 529, 84-87.
- Li, S., Zhang, H., 2001. Advances in the development of functional foods from buckwheat. *Critical Reviews in Food Science and Nutrition* 41, 451-464.
- Kumar, A., Tomer, V., Kaur, A., Kumar, V., Gupta, K., 2018. Millets: a solution to agrarian and nutritional challenges. *Agriculture and Food Security* 7, 31.
- Mimmo, T., Tiziani, R., Valentinuzzi, F., Lucini, L., Nicoletto, C., Sambo, P., Scampicchio, M., Pii, Y., Cesco, S., 2017. Selenium Biofortification in *Fragaria × ananassa*: Implications on Strawberry Fruits Quality, Content of Bioactive Health Beneficial Compounds and Metabolomic Profile. *Frontiers in Plant Science* 8, 1887.
- Nakabayashi, R., Yonekura-Sakakibara, K., Urano, K., Suzuki, M., Yamada, Y., Nishizawa, T., Matsuda, F., Kojima, M., Sakakibara, H., Shinozaki, K., Michael, A.J., Tohge, T., Yamazaki, M., Saito, K., 2014. Enhancement of oxidative and drought tolerance in *Arabidopsis* by over accumulation of antioxidant flavonoids. *The Plant Journal* 77, 367-379.
- Nawaz, F., Ashraf, M.Y., Ahmad, R., Waraich, E.A., Shabbir, R.N., Bukhari, M.A., 2015. Supplemental selenium improves wheat grain yield and quality through alternations in biochemical processes under normal and water deficit. *Food Chemistry* 175, 350-357.
- Ohnishi, O., 1998. Search for the wild ancestor of buckwheat. III. The wild ancestor or cultivated common buckwheat, and of Tartary buckwheat. *Economic Botany* 52(2), 123-133.
- Ožbolt, L., Kreft, S., Kreft, I., Germ, M., Stibilj, V., 2008. Distribution of selenium and phenolics in buckwheat plants grown from seeds soaked in Se solution and under different levels of UV-B radiation. *Food Chemistry* 110, 691-696.
- Prado, F.E., Rosa, M., Prado, C., Podazza, G., Interdonato, R., González, J.A., Hilal, M., 2012. UV-B Radiation, Its Effects and Defense Mechanisms in Terrestrial Plants. *Environmental Adaptations and Stress Tolerance of Plants in the Era of Climate Change* pp. 57-83.
- Regvar, M., Bukovnik, U., Likar, M., Kreft, I., 2012. UV-B radiation affects flavonoids and fungal colonisation in *Fagopyrum esculentum* and *F. tataricum*. *Central European Journal of Biology* 7(2), 275-283.
- Ren, J., Dai, W., Xuan, Z., Yao, Y., Korpelainen, H., Li, C., 2007. The effect of drought and enhanced UV-B radiation on the growth and physiological traits of two contrasting poplar species. *Forest Ecology and Management* 239(1), 112-119.
- Rodríguez-Calzada, T., Qian, M., Strid, Å., Neugart, S., Schreiner, M., Torres-Pacheco, I., Guevara-González, R.G., 2019. Effect of UV-B radiation on morphology, phenolic compound production, gene expression, and subsequent drought stress responses in chili pepper (*Capsicum annum* L.). *Plant Physiology and Biochemistry* 134, 94-102.
- Rozema, J., Bjorn, L.O., Bornman, J.F., Gaberščik, A., Hader, D.P., Trošt, T., Germ, M., Klisch, M., Groniger, A., Sinha, R.P., Lebert, M., He, Y.Y., Buffoni-Hall, R., de Bakker, N.V., van de Staaij, J., Meijkamp, B.B., 2002. The role of UV-B radiation in aquatic and terrestrial ecosystems – an experimental and functional analysis of the evolution of UV-absorbing compounds. *Journal of Photochemistry and Photobiology B: Biology* 66, 2-12.
- Runeckles, C.V., Krupa, V.S., 1994. The impact of UV-B radiation and ozone in terrestrial vegetation. *Environmental Pollution* 83, 191-213.

- Saha, D., Gowda, M.V.C., Arya, L., Verma, M., Bansal, K.C., 2016. Genetic and genomic resources of small millets. *Critical Reviews in Plant Sciences* 35, 56-79.
- Santhosh, B., Narender Reddy, S., Prayaga, L., 2017. Physiological attributes of sunflower (*Helianthus annuus* L.) as influenced by moisture regimes. *Green Farming* 3, 680-683.
- Sangtarash, M.H., Qaderi, M.M., Chinnappa, C.C., Reid, D.M., 2009. Differential responses of two *Stellaria longipes* ecotypes to ultraviolet-B radiation and drought stress. *Flora - Morphology, Distribution, Functional Ecology of Plants* 204, 593-603.
- Sebastian, A., Kumari, R., Kiran, B.R., Prasad, M.N., 2018. Ultraviolet B induced bioactive changes of enzymatic and non-enzymatic antioxidants and lipids in *Trigonella foenum-graecum* L. (Fenugreek). *The EuroBiotech Journal* 2(1), 64-71.
- Sieprawska, A., Kornaś, A., Filek, M., 2015. Involvement of selenium in protective mechanisms of plants under environmental stress conditions – Review. *Acta Biologica Cracoviensia Series Botanica* 57(1), 9-20.
- Shen, X., Dong, Z., Chen, Y., 2015. Drought and UV-B radiation effect on photosynthesis and antioxidant parameters in soybean and maize. *Acta Physiologiae Plantarum* 37, 25.
- Schirmer, M., Höchstötter, A., Jekle, M., Arendt, E., Becker, T., 2013. Physicochemical and morphological characterization of different starches with variable amylose/amylopectin ratio. *Food Hydrocolloids* 32, 52-63.
- 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.
- Smrkolj, P., Stibilj, V., Kreft, I., Germ, M., 2006. Selenium species in buckwheat cultivated with foliar addition of Se(VI) and various levels of UV-B radiation. *Food chemistry* 96, 675-681.
- Suchar, V.A., Robberecht, R., 2016. Integration and scaling of UV-B radiation effects on plants: from molecular interactions to whole plant responses. *Ecology and Evolution* 6(14), 4866-4884.
- Suzuki, T., Morishita, T., Kim, S.J., Park, S.U., Woo, S.H., Noda, T., Takigawa, S., 2015. Physiological Roles of Rutin in the Buckwheat. *Plant. Japan Agricultural Research Quarterly: JARQ* 49(1), 37-43.
- Tian, X.R., Lei, Y.B., 2007. Physiological responses of wheat seedlings to drought and UV-B radiation. Effect of exogenous sodium nitroprusside application. *Russian Journal of Plant Physiology* 54, 676-682.
- Tsuji, K., Ohnishi, O., 2001. Phylogenetic relationships among wild and cultivated Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) populations revealed by AFLP analyses. *Genes & Genetic Systems* 76(1), 47-52.
- Valkama, E., Kivimaenpää, M., Hartikainen, H., Wulff, A., 2003. The combined effects of enhanced UV-B radiation and selenium on growth, chlorophyll fluorescence and ultrastructure in strawberry (*Fragaria x ananassa*) and barley (*Hordeum vulgare*) treated in the field. *Agricultural and Forest Meteorology* 120, 267-278.
- Vanwindekens, F.M., Gobin, A., Curnel, Y., Planchon, V., 2018. New Approach for Mapping the Vulnerability of Agroecosystems Based on Expert Knowledge. *Mathematical Geosciences* 50, 679-696.
- Wang, R., Hunt, H.V., Qiao, Z., Wang, L., Han, Y., 2016. Diversity and cultivation of broomcorn millet (*Panicum miliaceum* L.) in China: a review. *Economic Botany* 70, 332-342.
- Zhang, Y., He, P., Zhang, C., 2011. Influences of enhanced UV-B radiation and drought stress on biomass accumulation and allocation of *Fagopyrum dibotrys*. *China journal of Chinese materia medica* 36(15), 2032-7.
- Yao, Y., Xuan, Z., Li, Y., He, Y., Korpelainen, H., Li, C., 2006. Effects of ultraviolet-B radiation on crop growth, development, yield and leaf pigment concentration of tartary buckwheat (*Fagopyrum tataricum*) under field conditions. *European Journal of Agronomy* 25, 215-222.
- Yao, X., Jianzhou, C., Xueli, H., Binbin, L., Jingmin, L., Zhaowei, Y., 2013. Effects of selenium on agronomical characters of winter wheat exposed to enhanced ultraviolet-B. *Ecotoxicology and Environmental Safety* 92, 320-326.