

Exploring the potential of priming agents towards enhanced performance of *Rubus* species

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Abstract

The concept of the application of priming agents (PAs) to enhance yield performance and quality attributes of fruit crops is relatively novel. The process of priming involves prior exposure to biotic or abiotic stress factors rendering a plant more resistant/tolerant to future exposure. There is a wide range of compounds that are considered to have a priming effect and can be classified into the following categories: i) chemicals (i.e., hormones, reactive oxygen nitrogen and sulphur species (RONSS), and small organic molecules), ii) microorganisms (i.e., arbuscular mycorrhizal fungi (AMF) and plant growth-promoting bacteria (PGPR)), and iii) nanomaterials (i.e., organic and inorganic nanoparticles, as well as polymers). Soft fruits, also referred to as small fruits or berries, represent a wide and very diverse group of crops that have high nutritional value but are very perishable with limited shelf-life potential. These crops are also greatly affected by stress conditions. To our knowledge, the concept of priming in soft fruits is relatively new with scarce information available. The aim of the current report is dual. Initially, this report provides information regarding the prospects of priming agents as a novel agricultural and technological approach to improve stress tolerance for a range of *Rubus* species, namely red raspberry, blackberry, boysenberry, cloudberry, loganberry and black raspberry. Additionally, it describes the challenges and constraints of raspberry production within a global context, providing examples and case studies from the United States and Europe, two industries with striking differences in their production models.

Keywords: soft fruits, berries, *Rubus idaeus*, agricultural biostimulants, stress conditions, melatonin, putrescine, sodium alginate, raspberry production model

INTRODUCTION

Small (or soft) fruits are an excellent natural source of biologically active components that provide significant health-promoting benefits and this has led to an exponential growth in their production, including *Rubus* species (Pantelidis et al., 2007; Manganaris et al., 2014; Fotirić Akšić et al., 2019; Milosavljević et al., 2020). Most *Rubus* species used for commercial production are native to Europe and belong to the subgenus *Idaeobatus* within the genus *Rubus*, which contains approximately 740 species (Hummer, 2010). Given the global distribution and scale of production of *Rubus* species, they are used both commercially and in niche markets.

Red raspberry (*Rubus idaeus* L.) has a predominant position among *Rubus* species with a diversity and richness in the content of phenolic compounds, such as anthocyanins, flavonoids, and phenolic acids. Raspberry fruits have been reported as an important source of antioxidants with differences noted between tested florican- and primocane-fruiting cultivars (Dragišić Maksimović et al., 2013; Milivojević et al., 2011). Besides genotypic (cultivar) effects, other factors such as the environment, ripening stage, cultivation techniques, postharvest treatments and storage conditions may affect their content (Di Vittori et al., 2018).

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However, soft fruits severely suffer from exogenous stress conditions, such as drought or heat stress. The application of priming agents can minimize the effects of biotic and abiotic stress, resulting in increased productivity and improved fruit physicochemical characteristics. Priming can be achieved by applying natural or synthetic compounds which act as signaling transducers, 'activating' the plant's defence system. Exposure to a stimulus allows a plant to respond in a more rapid and effective way to a later stimulus (the same or equivalent) compared with a non-primed plant. However, the effects of priming agents have been poorly characterized in *Rubus* species.

The current report provides information on the prospects of applying priming agents as a novel agricultural and technological approach from a range of perspectives in raspberries and, moreover, in the other *Rubus* species about which little information is available. It additionally provides an up-to-date overview of the current challenges and perspectives of raspberry production by examining main producing areas: the United States in the Americas and the Republic of Serbia in Europe, two industries that apply different production models.

DESCRIPTION OF PRIMING AGENTS FOR POTENTIAL USE ON SOFT FRUITS

Plants suffer from abiotic (salinity, drought, heavy metals, etc.) and biotic (pathogenic microorganisms and pests) stress conditions. Reception of multiple environmental stimuli causes several metabolic pathways to become 'switched on' in response to accumulation of signaling molecules. The process of priming involves prior exposure to biotic or abiotic stress factors making a plant more resistant/tolerant to future exposure. A first encounter with a particular stress factor can trigger the establishment of a molecular memory that primes or acclimates the plant (Savvides et al., 2016; Sherin et al., 2022). Priming agents applied in agriculture simulate this process.

Priming agents can be classified into the following classes: 1) chemicals (including natural and synthetic molecules) such as i) hormones (i.e., salicylic acid, jasmonic acid, strigolactones), ii) reactive oxygen nitrogen and sulphur species (RONSS: NO, H₂S, H₂O₂) and iii) small organic molecules (i.e., melatonin, putrescine); 2) microorganisms such as i) arbuscular mycorrhizal fungi (AMF, including *Funneliformis mosseae* and *Rhizophagus irregularis*), and ii) plant growth-promoting bacteria (PGPR, soil bacteria living in the rhizosphere that are involved in promoting plant growth and development); and 3) nanomaterials, which can include organic nanoparticles, inorganic nanoparticles and polymers (Savvides et al., 2016; Ioannou et al., 2020; Sherin et al., 2022). This work focuses on the effect of polyamines (with special reference to putrescine), melatonin and sodium alginate as potential agents that can be successfully used in *Rubus* crop production to increase yield performance and improve plant adaptability to stress conditions.

Polyamines

These compounds play a pivotal role in shaping the intricate web of physiological processes within plants that impact the quality, yield, and nutritional properties of fruits. As essential regulators of growth and development, these organic compounds are synthesized through the intricate pathways of amino acid metabolism. In addition to the well-known polyamines (putrescine, spermidine, and spermine), other variations are found in different plant species, which may contribute to the diversity of functions of these compounds (Minocha et al., 2014). One of the primary functions of polyamines lies in their influence on cell division and differentiation. During plant development, the controlled and precise division of cells is crucial for the formation of tissues and organs. Polyamines act as crucial modulators in this process, ensuring the proper organization and differentiation of various cell types (Chen et al., 2019). Moreover, they participate in the regulation of the cell cycle, ensuring that cell division occurs at the right time and in the appropriate context. As plants progress through their life cycle, they eventually undergo senescence, a natural ageing process. Polyamines are intricately involved in this phase, orchestrating the breakdown of cellular components and facilitating nutrient remobilization, which is vital for the overall health and resource utilization of the plant (Alcázar et al., 2010, 2020).

The impact that polyamines have on plant growth, development, and stress response

has led to the exploration of their potential application in agriculture, particularly in enhancing pre- and postharvest fruit quality (Chen et al., 2019). As priming agents, polyamines have demonstrated their ability to prepare fruits to better withstand various stresses they may encounter during growth and storage, thereby enhancing overall fruit quality and plant resilience (Gao et al., 2021). Preharvest treatments involve the application of polyamines to plants before fruit maturation and harvest. This treatment has been found to positively influence the fruit development and the ripening processes. By regulating gene expression and protein synthesis, polyamines can impact the production of ripening-related enzymes and signalling molecules, leading to improved fruit flavour, colour, and texture. Moreover, preharvest polyamine treatment has been shown to increase fruit yield by promoting cell division and differentiation in the growing fruits. This effect translates into larger and more abundant fruits, contributing to higher overall crop productivity (Fortes and Agudelo-Romero, 2018; Gao et al., 2021).

As a postharvest treatment, polyamines have proven valuable in extending the shelf life of fresh fruit. Postharvest stressors, such as temperature fluctuations, humidity changes, and mechanical damage during handling and transportation, can cause fruit deterioration. Polyamines, with their role in maintaining cell membrane stability and protecting against oxidative stress, help delay the onset of senescence and maintain the quality of harvested fruits for a longer duration (Aghdam and Bodbodak, 2014; Zhang et al., 2020). In addition to their direct effects on fruit quality, the role of polyamines as priming agents enhances the ability of fruits to cope with stressors during postharvest storage. By pre-conditioning the fruits with polyamines, their defence mechanisms are activated and primed, allowing them to respond more effectively to stress factors encountered after harvest. This includes better resistance to pathogens, reduced fruit decay, and a higher capacity to withstand physiological disorders (Gao et al., 2021).

In addition to improving pre- and postharvest fruit quality, polyamines can also improve yield components and the nutritional value of fruits by enhancing antioxidant capacity and essential nutrients. Putrescine is the most widely studied polyamine that impacts some of these variables. For example, several studies have demonstrated that putrescine treatment can significantly impact fruit size and weight in various crops. This effect is attributed to its ability to stimulate cell division and elongation (Khan and Singh, 2010; Shanbehpour et al., 2020). By promoting these crucial growth processes, putrescine contributes to the development of larger fruits, resulting in enhanced market appeal and overall crop yields (Gao et al., 2021). Furthermore, putrescine application exhibits a remarkable influence on fruit colour development. Through its role in stimulating the synthesis of pigments, such as anthocyanins and carotenoids, putrescine contributes to vibrant and attractive fruit hues. This enhancement in colour not only adds visual appeal to the fruits but also signifies potential health-promoting benefits associated with these pigments. Application of putrescine leads to a notable increase in the antioxidant capacity of fruits. Torrigiani et al. (2004) and Singh et al. (2022) have highlighted its positive effect on enhancing the activity of antioxidant enzymes and maintaining elevated levels of phytochemical compounds. This heightened antioxidant defence system provides fruits with enhanced protection against oxidative stress, which is crucial for extending postharvest shelf life and ensuring better fruit quality during storage and transportation. In addition to the impact on size, colour, and antioxidant capacity, putrescine application also positively influences the nutritional composition of fruit. Notably, it has been associated with higher levels of essential nutrients, including vitamins, minerals, and phenolic compounds (Mirdehghan and Rahimi, 2016; Singh et al., 2021). This nutritional enrichment further augments the value of the fruits, offering consumers with more nutrient-dense and health-promoting options. As research in this field continues, further insights into the molecular mechanisms behind polyamine action and their applications to food production will undoubtedly open new avenues for agricultural innovation (Valero et al., 2002; Fortes and Agudelo-Romero, 2018).

Melatonin

Melatonin, a natural plant hormone, acts as a potent antioxidant and free radical



scavenger, providing protection against oxidative stress induced by environmental factors like high temperature extremes, drought, and UV radiation. This protective effect contributes to the overall health and vigour of horticultural crops. Furthermore, melatonin has a pivotal role on various physiological processes in fruit trees, such as photosynthetic enhancement, circadian rhythm regulation, and hormone balance promotion, leading to improved nutrient assimilation and allocation, and ultimately resulting in better fruit development and quality (Agathokleous et al., 2021; Nawaz et al., 2016; Zeng et al., 2022; Zhang et al., 2020).

Postharvest application of melatonin involves treating harvested fruits with melatonin solutions or coatings to enhance their quality, extend shelf life, and reduce postharvest losses. Melatonin applied postharvest has been reported to delay ripening, preserve antioxidant capacity and reduce the intensity and severity of postharvest diseases (Ze et al., 2021; Zhang et al., 2020). Melatonin can also be incorporated into edible coatings or films applied to fruit surfaces. These coatings provide a protective barrier against moisture loss, gas exchange, and microbial contamination. Melatonin-infused coatings subsequently help to maintain fruit quality and prolong shelf life (Arnao and Hernández-Ruiz, 2020; Xu et al., 2019; Ze et al., 2021). A recent meta-analysis provides an overview of the effect of melatonin on postharvest performance and antioxidant properties of fresh fruits (Madebo et al., 2022)

The mode of action of melatonin is through activation of i) enzymatic (SOD, APX, CAT) and non-enzymatic antioxidant systems (ascorbate and glutathione, total phenols, anthocyanins, flavonoids), ii) the GABA-shunt pathway, iii) endogenous melatonin, as well as causing a decrease in lipid peroxidation (MDA) and hydrogen peroxide. It has been also reported to reduce tissue softening and enhance resistance to fruit fungal decay. Recent studies have shown that melatonin-primed raspberry plants exhibit increased resilience against diseases and pests, bolstering the plant's defence mechanisms and reducing pathogen infestations which leads into higher fruit yields (Arnao and Hernández-Ruiz., 2020; Zhang et al., 2020).

Sodium alginate

It is a biodegradable polymer that can be broken down and metabolized by microorganisms or degrades naturally in the environment when disposed of properly. This in turn reduces its impact on the ecosystem compared to non-biodegradable materials that persist in the environment. This inherent eco-friendly property makes it an attractive solution for a wide range of applications (Shit and Shah, 2014). Chemically, sodium alginate is a linear polysaccharide composed of repeating units of two monosaccharides: β -D-mannuronic acid (M) and α -L-guluronic acid (G). These monosaccharide units are linked together by 1,4-glycosidic linkages. The arrangement and composition of M and G units within the polymer chain play a crucial role in determining the physicochemical properties of sodium alginate. In its chemical structure, the M and G units alternate along the polymer chain, creating distinct patterns of M-G and G-M sequences (Yerramathi et al., 2021). The distribution and ratio of these units can vary, resulting in different alginate variants with diverse properties such as solubility, gelation capacity, and viscosity. This versatility allows sodium alginate to be tailored for specific applications, making it an ideal choice for a wide range of industrial and biomedical uses (Yerramathi et al., 2021; Karim et al., 2022). Overall, the viscosity of sodium alginate solutions can be fine-tuned by controlling the distribution and composition of M and G units, making it valuable for thickening and stabilizing applications in various industries (Yerramathi et al., 2021; Karim et al., 2022).

Sodium alginate can be applied via nano smart delivery systems in the following ways: i) encapsulation of active ingredients: it can be used to encapsulate active ingredients within alginate-based nanostructures; the encapsulation helps protect the active ingredient, control its release, and enhance its stability; ii) nanoparticle formulation: it can be utilized to form nanoparticles, either alone or in combination with other materials for targeted delivery; iii) hydrogel systems: it can form hydrogels when crosslinked with divalent cations like calcium ions. Alginate-based hydrogels have been used as smart delivery systems for the controlled release of growth factors or other bioactive agents; iv) bioactive scaffold material for tissue engineering applications (Nair et al., 2020; Yerramathi et al., 2021; Karim et al., 2022).

RASPBERRY FRUIT PRODUCTION: CHALLENGES AND CONSTRAINTS WITHIN A GLOBAL CONTEXT

The case of the United States (US)

The US ranked as the 5th largest global producer of raspberries in 2021 with a production area covering 6,578 ha (FAOSTAT, 2023). Within the US, Washington and California lead processed and fresh market production, respectively, with the value of utilized production in 2021 estimated at \$ 531.3 million US dollars (United Department of Agriculture, National Agricultural Statistics Service, 2022). Washington primarily grows floricanne-fruiting raspberry that is machine harvested with the average yield at 8687 kg ha⁻¹. In contrast, California hand harvests primocane-fruiting plants with average yields at 21296 kg ha⁻¹. 'Meeker' along with 'WakeField' and 'WakeHaven' are the most widely planted cultivars in Washington, while California growers often use private genetics from companies such as Driscoll's. Other states cultivate raspberry and the crop is used within local and regional foodsheds.

The US raspberry industry works cooperatively with public and private research and outreach programs to address prioritized production issues. Development of new and adapted cultivars with high yield potential, superior fruit quality, and tolerance or resistance to key pests and diseases is an important breeding aim addressed by public and private breeding programs. Management of pests such as spotted wing drosophila (*Drosophila suzukii*) and mites as well as pathogens and plant-parasitic nematodes are also high priority production constraints. Diseases of most concern include botrytis fruit rot, Phytophthora root rot, yellow rust, and cane blight, while root lesion nematode (*Pratylenchus penetrans*) and virus-transmitting nematodes are also of concern. Labour is yet another key constraint as the cost of labour continues to increase, while the availability of an agricultural workforce diminishes. Recently, adaptation to heat has emerged as a new challenge. High temperatures have been especially challenging in the Pacific Northwest region with some growers suffering complete or partial crop loss due to recent extremes in heat. California growers often use poly-tunnels, which can provide some protection from heat and UV damage depending on implementation, but this practice is not widely used in raspberry production in Washington and the greater Pacific Northwest region. Release of new cultivars with improved tolerance or resistance to key biotic and abiotic stressors will be important in helping the raspberry industry adapt to production challenges, but breeding is a slow process and needs to be complemented with other horticultural tactics. Priming agents are one potential avenue that can be rapidly employed to enhance or sustain production of this economically important crop. However, research is needed to inform the utilization of priming agents and needs to be paired with economic analyses to understand the implications of this new practice on profitability.

The case of Serbia

According to FAOSTAT (2023), the total cultivated area is 20,807 ha with an annual production of 110,589 t in 2021 that results on a relative low yield per hectare. The area of each farm is 0.25 ha and cultivation costs are estimated at 1.7 € kg⁻¹ of produced fruit with labour costs representing the largest share. More than 90% of raspberries produced are frozen in cold stores. The selling price varies significantly from 4.5 € kg⁻¹ (2022) to 1.7 € kg⁻¹ (2023) with the vast majority of fruits destined for freezing/processing (>90%) and exported to foreign markets as various frozen products (rollend, gris and block). The export of fresh raspberries is insignificant.

The predominant cultivar is 'Willamette' (90%), followed by 'Meeker' (3%) and 'Fertödi Zamos' (2%), while 'Tulameen' and 'Glen Ample', which are mainly used for fresh consumption, are rarely present due to domestic consumption of this fruit being very small and the export of fresh raspberries from Serbia quite limited (Nikolić and Tanović, 2012). The vertical trellis system and careful balancing of the vegetative and generative growth of biennial raspberries by removing the first series of primocanes have been employed towards enhanced crop efficiency (Milivojević et al., 2017). However, removing young canes is a very labour-intensive and expensive management practice in commercial raspberry plantations;

therefore, previous studies have highlighted the need to apply growth retardants (i.e., prohexadione-calcium, ProCa), which block the last steps of gibberellin biosynthesis and thus prevent the formation of active forms of gibberellins. In 'Willamette', ProCa treatment was effective at reducing vegetative growth, increasing the number of inflorescences cane⁻¹ and promoting the yield and nutritional fruit quality (Dragišić Maksimović et al., 2017).

Over the last decade, the production volume of primocane fruiting cultivars was slightly increased. Older cultivars such as 'Polka', 'Polana', 'Autumn Bliss', 'Himbo Top' and 'Heritage' are the most common in commercial plantations, which are mainly cultivated in a hedgerow system with additional trellises. In open-field production, all canes are mowed down after fruiting in early spring and the crop is only produced on newly developed primocanes from mid-July to fall. More recently, two newly-introduced cultivars ('Enrosadira' and 'Kwanza') have been extended into protected environments to meet the growing needs of producers and consumers. These cultivars continually set fruit on the current season's canes from mid-July to fall, and some of the previous season's canes are retained to produce early fruit from late May to late June in the following year, thus extending the harvest season and providing higher total yields for bearing twice a year. The introduction of new cultivars that are more productive and resistant or tolerant to pathogens and stress conditions is essential for the raspberry industry to overcome production constraints. The main constraints in the Serbian raspberry industry are: adverse effects of climatic factors; poor quality of planting material (mainly propagated in commercial plantations); use of inappropriate soils and sites for establishment of new plantations; lack of labour for harvesting; inability to use the same cultivar(s) for fresh and processed markets, and the stock of unsold frozen raspberries from the previous year depressing prices. As labour costs have increased, basic cultural practices should be mechanized. In Serbia, the daily harvest rate per worker is between 40 and 60 kg, which accounts for up to 70-80% of production costs, while mechanization of harvesting can reduce this value by 10-12 times and reduce direct operating costs by 50-70% (Kazakov et al., 2009).

New directions for the Serbian raspberry industry include machine harvesting of raspberries destined for freezing and processing, cultivation of raspberries in protected environments (anti-hail nets, rain shelters, and greenhouses) to prevent adverse effects of extreme climatic factors and the promotion of new, superior primocane fruiting raspberry cultivars. For example, 'Enrosadira' (Sant Orsola, Italy) and 'Kwanza' (Advanced Berry Breeding, The Netherlands, etc.) have been reported to yield more than 30 t ha⁻¹ and have very large fruit size with good flavor and excellent shelf life. The development of new cultivation techniques, such as use of long canes and soilless culture, are also new directions to produce year-round raspberries for fresh consumption. The ability to produce year-round raspberries for fresh consumption through a combination of superior cultivars and new production techniques with a gap during July and August is a realistic scenario under Mediterranean conditions (Evangelos Tsormpatsidis, pers. commun.). The application of priming agents may have an important role as a new production technique that expands the resiliency and viability of this evolving raspberry industry in Europe.

CONCLUSIONS

The following conclusions can be drawn from this report:

- Expanding global production of soft fruits, including *Rubus* species, is challenged by biotic and abiotic stress factors. Climate change and extremes in weather necessitate new tools that can rapidly and economically reduce crop loss due to abiotic stress and should complement other breeding and horticultural research efforts;
- In the context of the high demand for fresh and processed raspberries in the world market, there is a great need to increase the profitability of cultivation through the use of innovative, low-cost technologies, such as the application of priming agents;
- Research and use of priming agents should be prioritized, particularly considering the adverse stress conditions experienced due to climate change. It is also important to understand and apply the potential benefit from the postharvest use of priming agents towards enhanced cold chain management from field to consumer;

- The utilization of priming agents offers a promising strategy to improve raspberry plant health, enhance productivity, and elevate fruit quality amid changing global climactic conditions. By countering the detrimental effects of biotic and abiotic stresses, priming agents empower raspberry plants to thrive in challenging environments;
- As ongoing research continues to unravel the specific mechanisms behind these priming agents' effects on raspberry physiology and fruit quality, the potential for optimizing raspberry production and providing consumers with high-quality, nutritious berries becomes increasingly evident.

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Literature cited

- Agathokleous, E., Zhou, B., Xu, J., Ioannou, A., Feng, Z., Saitanis, C.J., Frei, M., Calabrese, E.J., and Fotopoulos, V. (2021). Exogenous application of melatonin to plants, algae, and harvested products to sustain agricultural productivity and enhance nutritional and nutraceutical value: a meta-analysis. *Environ Res* 200, 111746 <https://doi.org/10.1016/j.envres.2021.111746>. PubMed
- Aghdam, M.S., and Bodbodak, S. (2014). Postharvest heat treatment for mitigation of chilling injury in fruits and vegetables. *Food Bioprocess Technol.* 7 (1), 37–53 <https://doi.org/10.1007/s11947-013-1207-4>.
- Alcázar, R., Altabella, T., Marco, F., Bortolotti, C., Reymond, M., Koncz, C., Carrasco, P., and Tiburcio, A.F. (2010). Polyamines: molecules with regulatory functions in plant abiotic stress tolerance. *Planta* 231 (6), 1237–1249 <https://doi.org/10.1007/s00425-010-1130-0>. PubMed
- Alcázar, R., Bueno, M., and Tiburcio, A.F. (2020). Polyamines: small amines with large effects on plant abiotic stress tolerance. *Cells* 9 (11), 2373 <https://doi.org/10.3390/cells9112373>. PubMed
- Arnao, M.B., and Hernández-Ruiz, J. (2020). Melatonin in flowering, fruit set and fruit ripening. *Plant Reprod* 33 (2), 77–87 <https://doi.org/10.1007/s00497-020-00388-8>. PubMed
- Chen, D., Shao, Q., Yin, L., Younis, A., and Zheng, B. (2019). Polyamine function in plants: metabolism, regulation on development, and roles in abiotic stress responses. *Front Plant Sci* 9, 1945 <https://doi.org/10.3389/fpls.2018.01945>. PubMed
- Di Vittori, L., Mazzoni, L., Battino, M., and Mezzetti, B. (2018). Pre-harvest factors influencing the quality of berries. *Sci. Hortic. (Amsterdam)* 233, 310–322 <https://doi.org/10.1016/j.scienta.2018.01.058>.
- Dragišić Maksimović, J.J., Milivojević, J.M., Poledica, M.M., Nikolić, M.D., and Maksimović, V.M. (2013). Profiling antioxidant activity of two primocane fruiting red raspberry cultivars (Autumn Bliss and Polka). *J. Food Compos. Anal.* 31 (2), 173–179 <https://doi.org/10.1016/j.jfca.2013.05.008>.
- Dragišić Maksimović, J.J., Poledica, M.M., Radivojević, D.D., and Milivojević, J.M. (2017). Enzymatic profile of 'Willamette raspberry leaf and fruit affected by prohexadione-Ca and young canes removal treatments. *J Agric Food Chem* 65 (24), 5034–5040 <https://doi.org/10.1021/acs.jafc.7b00638>. PubMed
- Food and Agriculture Organization STAT. (2023) <https://www.fao.org/faostat/en/#home>.
- Fortes, A.M., and Agudelo-Romero, P. (2018). Polyamine metabolism in climacteric and non-climacteric fruit ripening. In *Polyamines. Methods in Molecular Biology*, Vol. 1694, R. Alcázar, and A. Tiburcio, eds. (New York, NY: Humana Press), https://doi.org/10.1007/978-1-4939-7398-9_36.
- Fotirić Akšić, M., Dabić Zagorac, D., Sredojević, M., Milivojević, J., Gašić, U., Meland, M., and Natić, M. (2019). Chemometric characterization of strawberries and blueberries according to their phenolic profile: combined effect of cultivar and cultivation system. *Molecules* 24 (23), 4310 <https://doi.org/10.3390/molecules24234310>. PubMed
- Gao, F., Mei, X., Li, Y., Guo, J., and Shen, Y. (2021). Update on the roles of polyamines in fleshy fruit ripening, senescence, and quality. *Front Plant Sci* 12, 610313 <https://doi.org/10.3389/fpls.2021.610313>. PubMed
- Hummer, K.E. (2010). *Rubus* pharmacology: antiquity to the present. *HortScience* 45 (11), 1587–1591 <https://doi.org/10.21273/HORTSCI.45.11.1587>.
- Ioannou, A., Gohari, G., Papaphilippou, P., Panahirad, S., Akbari, A., Dadpour, M.R., Krasia-Christoforou, T., and Fotopoulos, V. (2020). Advanced nanomaterials in agriculture under a changing climate: the way to the future?

- Environ. Exp. Bot. 176, 104048 <https://doi.org/10.1016/j.envexpbot.2020.104048>.
- Karim, A., Rehman, A., Feng, J., Noreen, A., Assadpour, E., Kharazmi, M.S., Lianfu, Z., and Jafari, S.M. (2022). Alginate-based nanocarriers for the delivery and controlled-release of bioactive compounds. *Adv Colloid Interface Sci* 307, 102744 <https://doi.org/10.1016/j.cis.2022.102744>. PubMed
- Kazakov, I.V., Evdokimenko, S.N., and Kulagina, V.L. (2009). Selective potential to create the everbearing raspberry varieties for machine harvesting. *Agric. Biol.* 1, 28–33.
- Khan, A.S., and Singh, Z. (2010). Pre-harvest application of putrescine influences Japanese plum fruit ripening and quality. *Food Sci Technol Int* 16 (1), 53–64 <https://doi.org/10.1177/1082013209353242>. PubMed
- Madebo, M.P., Zheng, Y., and Jin, P. (2022). Melatonin-mediated postharvest quality and antioxidant properties of fresh fruits: a comprehensive meta-analysis. *Compr Rev Food Sci Food Saf* 21 (4), 3205–3226 <https://doi.org/10.1111/1541-4337.12961>. PubMed
- Manganaris, G.A., Goulas, V., Vicente, A.R., and Terry, L.A. (2014). Berry antioxidants: small fruits providing large benefits. *J Sci Food Agric* 94 (5), 825–833 <https://doi.org/10.1002/jsfa.6432>. PubMed
- Milivojević, J., Maksimović, V., Nikolić, M., Bogdanović, J., Maletić, R., and Milatović, D. (2011). Chemical and antioxidant properties of cultivated and wild *Fragaria* and *Rubus* berries. *J. Food Qual.* 34 (1), 1–9 <https://doi.org/10.1111/j.1745-4557.2010.00360.x>.
- Milivojević, J., Radivojevic, D., Dragišić Maksimović, J., Veberic, R., and Mikulic-Petkovsek, M. (2017). Does plant growth and yield affected by Prohexadione Ca cause changes in chemical fruit composition of 'Loch Ness' and 'Triple Crown' blackberries? *Eur. J. Hortic. Sci.* 82 (4), 190–197 <https://doi.org/10.17660/eJHS.2017/82.4.4>.
- Milosavljević, D.M., Mutavdžić, D.R., Radotić, K., Milivojević, J.M., Maksimović, V.M., and Dragišić Maksimović, J.J. (2020). Phenolic profiling of 12 strawberry cultivars using different spectroscopic methods. *J Agric Food Chem* 68 (15), 4346–4354 <https://doi.org/10.1021/acs.jafc.9b07331>. PubMed
- Minocha, R., Majumdar, R., and Minocha, S.C. (2014). Polyamines and abiotic stress in plants: a complex relationship. *Front Plant Sci* 5, 175 <https://doi.org/10.3389/fpls.2014.00175>. PubMed
- Mirdehghan, S.H., and Rahimi, S. (2016). Pre-harvest application of polyamines enhances antioxidants and table grape (*Vitis vinifera* L.) quality during postharvest period. *Food Chem* 196, 1040–1047 <https://doi.org/10.1016/j.foodchem.2015.10.038>. PubMed
- Nair, M.S., Tomar, M., Punia, S., Kukula-Koch, W., and Kumar, M. (2020). Enhancing the functionality of chitosan- and alginate-based active edible coatings/films for the preservation of fruits and vegetables: a review. *Int J Biol Macromol* 164, 304–320 <https://doi.org/10.1016/j.ijbiomac.2020.07.083>. PubMed
- Nawaz, M.A., Huang, Y., Bie, Z., Ahmed, W., Reiter, R.J., Niu, M., and Hameed, S. (2016). Melatonin: current status and future perspectives in plant science. *Front Plant Sci* 6, 1230 <https://doi.org/10.3389/fpls.2015.01230>. PubMed
- Nikolić, M., and Tanović, B. (2012). *Rubus* and *Ribes* industry in Serbia: a production model for developing countries. *Acta Hort.* 946, 405–412 <https://doi.org/10.17660/ActaHortic.2012.946.67>.
- Pantelidis, G.E., Vasilakakis, M., Manganaris, G.A., and Diamantidis, G. (2007). Antioxidant capacity, phenol, anthocyanin and ascorbic acid content in raspberries, blackberries, red currants, gooseberries and cornelian cherries. *Food Chem.* 102 (3), 777–783 <https://doi.org/10.1016/j.foodchem.2006.06.021>.
- Savvides, A., Ali, S., Tester, M., and Fotopoulos, V. (2016). Chemical priming of plants against multiple abiotic stresses: mission possible? *Trends Plant Sci* 21 (4), 329–340 <https://doi.org/10.1016/j.tplants.2015.11.003>. PubMed
- Shanbehpour, F., Rastegar, S., and Ghasemi, M. (2020). Effect of preharvest application of calcium chloride, putrescine, and salicylic acid on antioxidant system and biochemical changes of two Indian jujube genotypes. *J Food Biochem* 44 (11), e13474 <https://doi.org/10.1111/jfbc.13474>. PubMed
- Sherin, G., Aswathi, K.R., and Puthur, J.T. (2022). Photosynthetic functions in plants subjected to stresses are positively influenced by priming. *Plant Stress* 4, 100079 <https://doi.org/10.1016/j.stress.2022.100079>.
- Shit, S.C., and Shah, P.M. (2014). Edible polymers: challenges and opportunities. *J. Polym.* 2014, 1–13 <https://doi.org/10.1155/2014/427259>.
- Singh, V., Jawandha, S.K., and Gill, P.P.S. (2021). Effect of exogenous putrescine treatment on internal browning and colour retention of pear fruit. *J. Food Meas. Charact.* 15 (1), 905–913 <https://doi.org/10.1007/s11694-020-00696-7>.
- Singh, V., Jawandha, S.K., Gill, P.P.S., and Singh, D. (2022). Preharvest putrescine application extends the shelf life and maintains the pear fruit quality. *Int. J. Fruit Sci.* 22 (1), 514–524 <https://doi.org/10.1080/15538362.2022.2068733>.
- Torrigiani, P., Bregoli, A.M., Ziosi, V., Scaramagli, S., Ciriacci, T., Rasori, A., Biondi, S., and Costa, G. (2004). Pre-harvest

polyamine and aminoethoxyvinylglycine (AVG) applications modulate fruit ripening in Stark Red Gold nectarines (*Prunus persica* L Batsch). *Postharvest Biol. Technol.* 33 (3), 293–308 <https://doi.org/10.1016/j.postharvbio.2004.03.008>.

United Department of Agriculture, National Agricultural Statistics Service. (2022). Noncitrus Fruits and Nuts 2021 Summary. https://www.nass.usda.gov/Publications/Todays_Reports/reports/ncit0522.pdf.

Valero, D., Martínez-Romero, D., and Serrano, M. (2002). The role of polyamines in the improvement of the shelf life of fruit. *Trends Food Sci. Technol.* 13 (6-7), 228–234 [https://doi.org/10.1016/S0924-2244\(02\)00134-6](https://doi.org/10.1016/S0924-2244(02)00134-6).

Xu, T., Chen, Y., and Kang, H. (2019). Melatonin is a potential target for improving post-harvest preservation of fruits and vegetables. *Front Plant Sci* 10, 1388 <https://doi.org/10.3389/fpls.2019.01388>. PubMed

Yerramathi, B.B., Kola, M., Muniraj, B.A., Aluru, R., Thirumanyam, M., and Zyryanov, G.V. (2021). Structural studies and bioactivity of sodium alginate edible films fabricated through ferulic acid crosslinking mechanism. *J. Food Eng.* 301, 110566 <https://doi.org/10.1016/j.jfoodeng.2021.110566>.

Ze, Y., Gao, H., Li, T., Yang, B., and Jiang, Y. (2021). Insights into the roles of melatonin in maintaining quality and extending shelf life of postharvest fruits. *Trends Food Sci. Technol.* 109, 569–578 <https://doi.org/10.1016/j.tifs.2021.01.051>.

Zeng, W., Mostafa, S., Lu, Z., and Jin, B. (2022). Melatonin-mediated abiotic stress tolerance in plants. *Front Plant Sci* 13, 847175 <https://doi.org/10.3389/fpls.2022.847175>. PubMed

Zhang, W., Cao, J., Fan, X., and Jiang, W. (2020). Applications of nitric oxide and melatonin in improving postharvest fruit quality and the separate and crosstalk biochemical mechanisms. *Trends Food Sci. Technol.* 99, 531–541 <https://doi.org/10.1016/j.tifs.2020.03.024>.

