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Selenium-Ethylene Interplay in Postharvest Life of Cut Flowers

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Selenium (Se) is considered a beneficial element in higher plants when provided at low concentrations. Recently, studies have unveiled the interactions between Se and ethylene metabolism throughout plant growth and development. However, despite the evidence that Se may provide longer shelf life in ethylene-sensitive flowers, its primary action on ethylene biosynthesis and cause-effect responses are still understated. In the present review, we discuss the likely action of Se on ethylene biosynthesis and its consequence on postharvest physiology of cut flowers. By combining Se chemical properties with a dissection of ethylene metabolism, we further highlighted both the potential use of Se solutions and their downstream responses. We believe that this report will provide the foundation for the hypothesis that Se plays a key role in the postharvest longevity of ethylene-sensitive flowers.

Keywords: ethylene inhibitors, vase life, flower quality, preservative solutions, Se metabolism

INTRODUCTION

Selenium (Se) is an essential nutrient for humans, bacteria, and most of the chlorophyte species (Lobanov et al., 2009; Nancharaiah and Lens, 2015). In higher plants, the beneficial effect of Se occurs in a concentration-dependent manner (Hawrylak-Nowak et al., 2014; Saidi et al., 2014; Boldrin et al., 2016; Sattar et al., 2019). At low concentrations, ranging from 0.1 to 1.0 mg L^{-1}, Se stimulates plant growth and activates components of the reactive oxygen species (ROS) scavenge system, thereby protecting against multiple abiotic and biotic stresses (Feng et al., 2013; Ahmad et al., 2016; Lapaz et al., 2019). On the other hand, Se can be also toxic at concentrations ranging from 1 to 5 mg L^{-1}, but the degree of tolerance varies among species (Freeman et al., 2010; Feng et al., 2013). Biological functions of Se occur primarily through selenoproteins which contain this element as part of the amino acids, selenocysteine (SeCys) and selenomethionine (SeMet) (Daniels, 1996), but also as a component of antioxidants, co-enzymes, specialized metabolites, and lipids (Khan M.I.R. et al., 2014; Khan N.A. et al., 2014). Therefore, the multiple presence of Se in plant metabolites evidences the unlimited possibilities of its action on plant metabolism, which has not been entirely explored.

Ethylene is a plant hormone mainly known for its role in affecting leaf and flower senescence, and fruit ripening. However, this simple gaseous molecule is also involved with other elemental processes throughout the plant's life cycle, including seed germination (Corbineau et al., 2014;

Miransari and Smith, 2014; Wilson et al., 2014), root initiation and development (Ivanchenko et al., 2008; Lima et al., 2009; Huang et al., 2013), floral development (O'Neill, 1997; Wuriyanghan et al., 2009), sexual determination (Iwahori et al., 1970; Yamasaki et al., 2001; Salman-Minkov et al., 2008), fruit ripening (Giovannoni, 2001; Barry and Giovannoni, 2007; Lim et al., 2007; De Martinis et al., 2015), plant senescence (Kim et al., 2014; De Martinis et al., 2015; Ueda and Kusaba, 2015), and response to biotic and abiotic stresses (Morgan and Drew, 1997; Wang et al., 2007; Lin et al., 2013; Steffens, 2014). Recently, several studies have uncovered evidence of a relationship between Se and ethylene metabolism in plants (Malorgio et al., 2009; Iqbal et al., 2015; Zhu et al., 2017; Hajiboland et al., 2019; Malheiros et al., 2019). In this vein, Malheiros et al. (2019) demonstrated that Se partially inhibits ethylene biosynthesis in roots of rice seedlings. Likewise, Iqbal et al. (2015) evidenced that Se inhibits 1-aminocyclopropane-1-carboxylate synthase (ACS) activity in wheat, the main limiting step of ethylene production in higher plants.

The production of flowers is one of the most important segments of horticulture in the field of agroindustry in many countries. The increased demand for high-quality products, however, requires postharvest technologies to improve floral vase life longevity. In recent years, the biological importance of ethylene on ornamental plant production and development of methods to alleviate its deleterious consequences in the overall ornamental value have been well explored. Nevertheless, many chemicals currently used to lessen ethylene responses present raised environmental and public health concerns. Thus, the development of methods that are environmentally friendly has become crucial (Scariot et al., 2014). Selenium presents suitable proprieties to be an eco-friendly (Cochran et al., 2018) and inexpensive (Haug et al., 2008) alternative to composing ethylene-sensitive flower preservative solutions. Recently, it was demonstrated that Se (6 mg L^{-1}) increases the vase life of Easter Lily (*Lilium longiflorum*) by alleviating cell damage via the ROS scavenging system and osmotic adjustment (Lu et al., 2020). However, it seems that Se may have additional functions affecting the postharvest life of cut flowers that have yet to be investigated. Based on the current literature, herein we propose a novel model of interaction between Se metabolism and ethylene biosynthesis, which likely underlies positive consequences on postharvest life of cut flowers.

AN OVERVIEW OF Se CHEMICAL CHARACTERISTICS AND METABOLISM

As part of the chalcogen group of chemical elements, Se is normally found in soils at concentrations from 0.01 to 2.0 mg kg^{-1} (Fordyce, 2005). This element exists in different oxidative states in soil conditions, such as elemental selenium (Se^0), selenide (Se^{2-}), thioselenate ($Se_2O_3{}^{2-}$), selenite ($SeO_3{}^{2-}$), and selenate ($SeO_4{}^2$) (Neal et al., 1987; White et al., 2004). Among the different forms of Se, selenate is the most soluble and bioavailable for plants; additionally, it is the most predominant form of transport through the xylem, as compared to selenite (Asher et al., 1977; Gupta and Gupta, 2017). The essentiality of Se in plants has not been proven, but it seems to affect several aspects of plant metabolism. Discovered in 1817, this trace element is actively absorbed by root cells through the sulfur (S) transporters SULTR1;2 and SULTR1; however SULTR1;2 seems to be the preferential transporter for the uptake of Se (Gupta and Gupta, 2017). Once absorbed, all synthesized organoselenium compounds are derived from pathways associated with S metabolism (Terry et al., 2000) and accumulate in roots (Galeas et al., 2007), leaves, stems (Liang et al., 2019), flowers (Quinn et al., 2011), and seeds (Liang et al., 2019).

The metabolism of Se is partially dependent on chloroplast metabolic machinery, where the reduction of selenate to selenite occurs under the sequential action of two enzymes that incorporate Se into amino acids (Terry et al., 2000). The accumulation of selenoamino acids allows non-specific incorporation of SeCys or SeMet in plant proteins since SeCys insertion machinery has allegedly been lost through evolution (Lobanov et al., 2009; Pilon-Smits and Quinn, 2010). Moreover, selenoamino acids can be converted to volatile compounds or Se^0 from the action of enzymes, such as methionine *S*-methyltransferase (Tagmount et al., 2002; Gupta and Gupta, 2017), SeCys methyltransferase (SMT) (Neuhierl and Boeck, 1996; Brummell et al., 2011; Chen et al., 2019) and SeCys lyase (SCL) (Pilon-Smits and Quinn, 2010). Because of this, most plants prevent excessive selenoamino acid accumulation to avoid metabolic impairments, especially those that may affect structural integrity and protein functions (Burnell, 1981; Brown and Shrift, 1982). The presence of Se in excess causes serious disruption at the metabolic level, including major changes in energy metabolism and ATP production, starch mobilization, and cell wall extension, which explains how Se causes a plant growth reduction (Ribeiro et al., 2016).

Selenoamino acids appear to be beneficial to growth in some conditions with an underlying influence on the oxidative protection networks in plants (Pilon-Smits and Quinn, 2010; Feng et al., 2013; Ahmad et al., 2016). Different strategies have been adopted to evaluate the role of Se in response to stress, including the application of Se as a seed priming treatment (Hasanuzzaman and Fujita, 2011; Nawaz et al., 2013; Hussain et al., 2016), soil fertilizer (Kumar et al., 2014; Khan et al., 2015; Atarodi et al., 2018), and foliar drench (Iqbal et al., 2015; Shahverdi et al., 2020). Treatment with Se at low concentrations is known to alleviate several stresses in plants, including those ones caused by drought (Hasanuzzaman and Fujita, 2011; Nawaz et al., 2013), heat (Iqbal et al., 2015), arsenic (Kumar et al., 2014), cadmium (Khan et al., 2015), low phosphorus (Jia et al., 2018), salinity (Shahverdi et al., 2020), as well as lead and aluminum (Feng et al., 2013). In addition to positive results in responding to several stresses, low concentrations of Se can also induce plant growth (Lehotai et al., 2012; Boldrin et al., 2016), via an effect on mitochondrial metabolism (Dimkovikj and Van Hoewyk, 2014) and molecular switches (Lehotai et al., 2012; Khan et al., 2015; Jia et al., 2018).

Concerning specific organs, several studies have demonstrated that this element delays fruit ripening (Zhu et al., 2017; Choudhary and Jain, 2018) and senescence

(Pezzarossa et al., 2012, 2014), leading to reductions in postharvest losses. Its ability to alter these processes is related to increased glutathione peroxidase (GSH-Px) activity (Rayman, 2002; Hasanuzzaman et al., 2010; Feng et al., 2013), neutralization of oxidative stress through the inhibition of lipid peroxidation (Cartes et al., 2005), and ethylene biosynthesis downregulation (Pezzarossa et al., 2014). However, despite some studies had examined the effect of Se on postharvest vase life in cut flowers (Tognon et al., 2016; Lu et al., 2020), none of them investigated yet the relationship between Se and ethylene biosynthesis directly.

ETHYLENE METABOLISM AND ITS INHIBITORS

As a simple gaseous hormone, ethylene acts in many fundamental processes in the plant's life cycle, including regulation of leaf and root development, senescence, fruit ripening, and germination. Ethylene also acts in response to several abiotic stresses such as heat (Savada et al., 2017), heavy metals damage (Thao et al., 2015), salinity (Zhang et al., 2016; Silva et al., 2018), low soil pH (Brito et al., 2018; Ribeiro et al., 2018), and water deficiency (Dubois et al., 2017), triggering adaptive responses (Wang et al., 2002).

The complete elucidation of the ethylene biosynthetic pathway by Yang and Hoffman (1984) was a notable episode for the progress of studies of this hormone in higher plants. Ethylene is synthesized from carbons C3 and C4 of methionine (Met) through three key enzymatic reactions: (i) conversion of Met into *S*-adenosyl-L-methionine (SAM) by the enzyme SAM synthetase (SAMS); (ii) conversion of SAM to 1-aminocyclopropane-1-carboxylic acid (ACC) by the enzyme ACC synthase (ACS); and (iii) conversion of ACC to ethylene by the enzyme ACC oxidase (ACO). The 2nd step in this process, i.e., the formation of ACC from SAM is considered the rate-limiting step, since the formation of ethylene is strongly controlled by the ACS enzyme (Yang and Hoffman, 1984; Alonso and Ecker, 2001; Pattyn et al., 2020). The final conversion of ACC to ethylene is oxygen-dependent (Kende, 1993) and yields CO_2 and cyanide as by-products. Once it is synthesized and perceived, the ethylene signaling pathway involves both positive and negative regulators, with the initial steps of signal transduction occurring at the endoplasmic reticulum membrane. The signal transduction involves ethylene receptors and transcription factors, with negative regulators inhibiting downstream responses via protein phosphorylation under the absence of ethylene (Azhar et al., 2019; Binder, 2020).

Ethylene biosynthesis/action inhibitors and ethylene removal technologies can mitigate premature senescence and abscission caused by exposure to exogenous or endogenous ethylene (Martínez-Romero et al., 2007). Interference in ethylene biosynthesis in ornamental plants can be achieved by blocking components of the ethylene synthesis pathway. Inhibition of the conversion of SAM to ACC by the compounds 1-aminoethoxyvinylglicine (AVG) and aminooxy acetic acid (AOA) effectively blocks the increase in ethylene production that accompanies senescence in a variety of ethylene sensitive flowers (Broun and Mayak, 1981; Serek and Andersen, 1993).

The inhibition of ethylene action is achieved by the use of antagonist molecules that bind to ethylene receptors, thus preventing downstream signaling. Among them, 2,5-norbornadiene (2,5-NBD) (Wang and Woodson, 1989), diazocyclopentadiene (DACP) (Blankenship and Sisler, 1993; Sisler et al., 1993; Serek et al., 1994), silver thiosulphate (Veen, 1979; Celikel and Reid, 2002), and 1-methyl cyclopropane (1-MCP) (Serek et al., 1995, 2006a; Sisler et al., 1999) are the most commonly studied and exploited. 1-MCP is the most commonly-used compound to control ethylene action during postharvest handling of fruits, flowers and vegetables commercially (Sisler and Serek, 1997). Its inhibitory mechanism is a result of competitive interaction with the ethylene receptors, since the ligand-binding site affinity is higher for 1-MCP than that of the gaseous hormone itself (Blankenship and Dole, 2006; Serek et al., 2006a). Nevertheless, it is thought that the development of new receptors recovers tissue sensitivity to ethylene in some plant materials, which can be treated with multiple applications of 1-MCP (Feng et al., 2004; Blankenship and Dole, 2006; In et al., 2013). On the other hand, 2,5-NBD also competes with ethylene for binding to ethylene receptors; however, high concentrations of ethylene can overcome the inhibitory effect of 2,5-NBD (Sisler and Yang, 1984). Moreover, 2,5-NBD is limitedly useful commercially as an ethylene inhibitor since it requires continuous exposure to be effective, and presents a strong and disagreeable odor (Sisler et al., 1990). Similarly, DACP is unlikely to be used commercially due to its instability and hazardous characteristics (Serek et al., 2006b). Finally, silver ions (Ag^+) may also block ethylene action, perhaps by replacing the metal component in the receptor. However, commercial use of silver is limited due to its heavy metal toxicity (Atta-Aly et al., 1987). Furthermore, the use of solutions containing silver íon by florists has raised environmental concerns, mostly regarding disposal issues (Sisler and Serek, 1997).

MODEL FOR Se-INDUCED DOWNREGULATION OF ETHYLENE BIOSYNTHESIS IN CUT FLOWER

Recently, a direct interaction between Se and ethylene was elegantly demonstrated in experiments involving cadmium stress alleviation in wheat (Iqbal et al., 2015), tomato fruit ripening (Zhu et al., 2017), and control of primary root growth in the rice system (Malheiros et al., 2019). These independent but complementary studies generated shreds of evidence that such responses were a consequence of an ethylene biosynthesis downregulation induced by Se. In close agreement with this, Se was also reported to improve minimally processed vegetable life span through ethylene depletion (Malorgio et al., 2009).

In this review, we propose the action of Se on ethylene biosynthesis in a cut flower model system through selenate (**Figure 1**) – the main form of Se to be transported in the xylem (Asher et al., 1977; Terry et al., 2000). The first

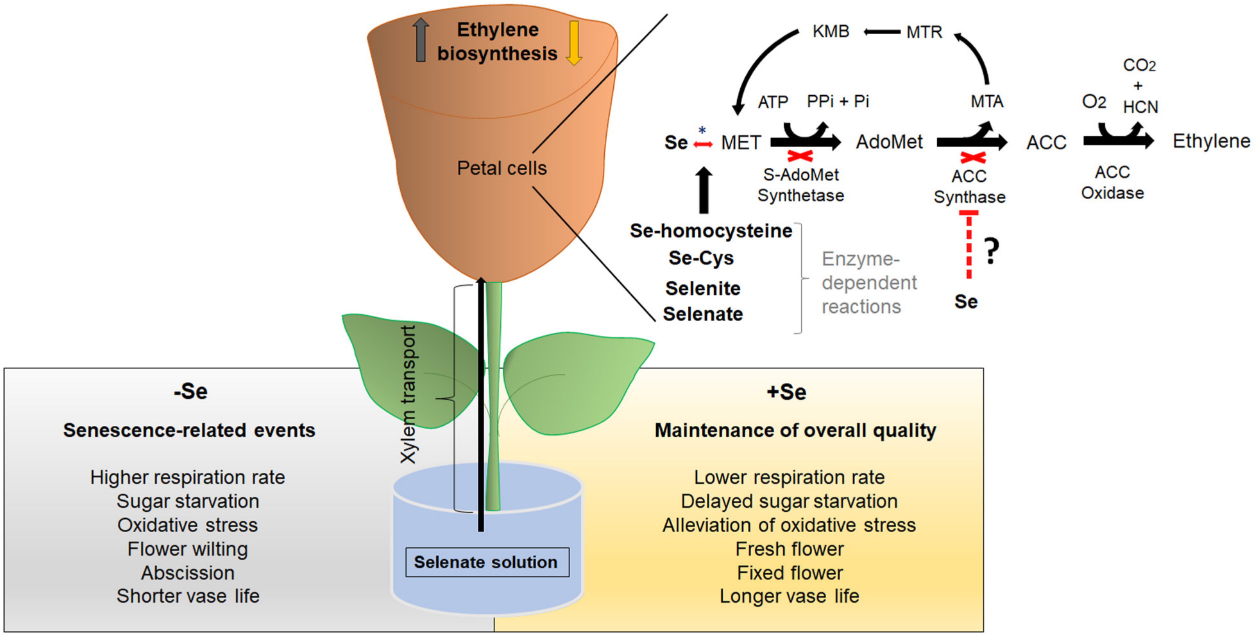

FIGURE 1 | Model for Se-induced ethylene biosynthesis downregulation in a cut flower system. Firstly, Se is provided as selenate – the main transported form in the xylem. In petal cells, selenate is converted to selenite and subsequently to Se-homocysteine by a series of enzymatic reactions. In a third stage, Se-homocysteine forms SeMet, reducing free Met levels toward to biosynthesis ethylene pathway. This event affects subsequently SAMS and ACS activities by reducing substrate (Met) availability to sustain ethylene biosynthesis pathway. Finally, the decreased ethylene biosynthesis may lead to the maintenance of overall quality on the postharvest life of cut flowers. Ethylene biosynthesis pathway: ACC, 1-aminocyclopropane-1-carboxylate; ACS, ACC synthase; MTR, *S*-methyl-5-thio-D-ribose; MTA, *S*-methyl-5′-this adenosine; KMB, 2-keto-4-methylthiobutyrate; Se, Selenium; SAM, *S*-adenosylmethionine; SAM synthetase, SAMS; HCN, Hydrogen cyanide; CO_2, Carbon dioxide; O_2, Oxygen; Met, Methionine; Pi, inorganic phosphate; and PPi, inorganic pyrophosphate. Se metabolism: Se, Selenium; SeCys, selenocysteine; SeMet, selenomethionine. *Enzymatic reaction.

step of Se metabolism in the cells involves the reduction of selenate to selenite under the sequential action of two enzymes, ATP sulfurylase (ATPS) and APS reductase (APR) (Shaw and Anderson, 1972; Sors et al., 2005; Pilon-Smits and Quinn, 2010; Quinn et al., 2011; Gupta and Gupta, 2017). ATPS catalyzes the hydrolysis of ATP, coupling ATP to selenate to form adenosine phosphoselenate (APSe), being subsequently reduced to selenite by APR (Sors et al., 2005; Pilon-Smits and Quinn, 2010). Both enzymes are present in the cytosol and plastids, but this process occurs primarily in the plastids, as observed in S metabolism (Kolosova et al., 2001). The reduction from selenite to selenide is also carried out in an enzyme-independent way by reduced glutathione (GSH) (Terry et al., 2000; Wallenberg et al., 2010). In the presence of the cysteine synthase (CS) enzyme, selenide can be converted into SeCys by coupling with *O*-acetylserine (OAS) (Ng and Anderson, 1978).

Selenocysteine may be incorporated into proteins, thereby impairing their activities (Burnell, 1981; Brown and Shrift, 1982; Terry et al., 2000). On the other hand, SeCys can be also transferred to Met, forming MeSeCys by selenocysteine methyltransferase (SMT) (Sors et al., 2005; Gupta and Gupta, 2017). In this case, a critical point arises since Met is shared with the ethylene biosynthesis pathway (**Figure 1**). For such convergences, it has been suggested that SeMet reduces free Met, which in turn diminishes internal ethylene levels by limiting the substrate for SAMS and ACS activities (Konze and Kende, 1979; Malorgio et al., 2009; Iqbal et al., 2013, 2015). The improvement of cut flowers vase life by manipulating ethylene biosynthesis has been addressed in several previous studies (Baker et al., 1977; Wang et al., 1977; Reid and Wu, 1992; Zeng et al., 2012). Kosugi et al. (2002), for instance, demonstrated that the suppression of ethylene biosynthesis in the *ACO* antisense line prolonged the vase life of carnation by 1.6-fold, as compared to its counterpart. In our proposed model (**Figure 1**), we hypothesize that Se diminishes ethylene levels in cut flowers by reducing the presence of free precursor Met to sustain ethylene biosynthesis, leading to extended postharvest life in ethylene-sensitive species.

DOWNSTREAM RESPONSES ASSOCIATED WITH Se USE IN VASE SOLUTION

Senescence is a complex, critical, and coordinated event that determines the longevity of cut flowers (Wu et al., 2017; Aalifar et al., 2020). The final phase of flower vase life, for instance, is characterized by time-dependent petal wilting, flower withering (Su et al., 2019), and flower or petal abscission (Van Doorn, 2001). Some flowers usually show symptoms of color change and desiccation of petals before abscission (Ma et al., 2005; Shibuya et al., 2016).

Ethylene is one of the most important hormones involved in the regulation of flower senescence (Ma et al., 2018; Wang et al., 2020) and elicits responses at concentrations as low as 0.1 μL L^{-1} in highly sensitive flowers (Macnish et al., 2011). Sensitivity to ethylene differs between species and cultivars (Macnish et al., 2010; Costa and Finger, 2016; Wu et al., 2017). In ethylene-sensitive species, ethylene induces endogenous and autocatalytic ethylene biosynthesis that triggers petal and flower senescence. Ethylene causes petal and flower wilting during senescence by inhibiting cell expansion through the regulation of aquaporins (Ma et al., 2008), proteins that promote water transport through biological membranes (Xue et al., 2020). This causes subsequently a negative water balance, a key limiting event in the vase life of cut flowers (Van Meeteren and Aliniaeifard, 2016).

High rates of respiration are also one of the main causes of short vase life in cut flowers (Jones et al., 2009). Ethylene is known to induce respiratory activity, thereby depleting carbohydrates levels (Gonzalez-Candelas et al., 2010; John-Karuppiah and Burns, 2010). On the other hand, ethylene is also involved with flower abscission by triggering abscission zone formation (Van Doorn, 2002) and by oxidative stress promoted by ROS, including the overproduction of superoxide anion ($O_2{}^{-}$) and hydrogen peroxide (H_2O_2) (Rogers and Munné-Bosch, 2016; Ren et al., 2017; Jędrzejuk et al., 2018; Bayanati et al., 2019).

Therefore, we suggest that Se increases vase life directly by downregulating ethylene synthesis and indirectly by reducing flower senescence-related events, such as respiration rate, sugar starvation, petal and flower wilting and abscission, and oxidative stress (**Figure 1**).

CONCLUSION AND BROADER PERSPECTIVES

Herein, we have proposed a new model of interaction between Se metabolism and ethylene biosynthesis, and pointed out the positive effects of this event on the postharvest life of cut flowers. We believe the use of Se can provide a commercially viable and environmentally friendly alternative to current methods applied to ethylene-sensitive cut flowers. Practical aspects such as doses and standard use methods should be further investigated for each species under study.

AUTHOR CONTRIBUTIONS

LC, LL, and VN conceptualized and organized all this manuscript. LC, LL, VN, and MS contributed in survey and writing for selenium metabolism. VN, FA, CF, and TS performed a survey and writing for ethylene metabolism and postharvest quality of flowers. KF and FF supervised all the surveys and writing. All authors equally contributed to the development of the article's theoretical framework and approved the submitted version.

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