Wounding

10.1 Jasmonic Acid – 116

10.2 Methyl Jasmonate – 116

10.3 Salicylic Acid – 117

10.4 Food Safety – 117

References – 118

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In nature, plants experience mechanical damage and biological injuries. As immobile organisms firmly set in substrate, they cannot move to avoid herbivore attacks. Therefore, plants have had to come up with alternative defence strategies:

- Physical barriers such as a cuticle, trichomes, thorns and other specialized organs
- Chemical defence substances such as phenolics and terpenoids (please see ► Chap. 3)
- Plant-plant communication via volatiles to 'warn' neighbouring plants
- Plant-insect interactions, e.g. extrafloral nectar secretion from wounds of bittersweet nightshade (*Solanum dulcamara*) to attract ants to defend the plant against herbivory by flea beetle larvae (Léon et al. 2001; Heil and Ton 2008; Bhattacharya et al. 2010; Steppuhn et al. 2016)

As our interest lies in improving the inner quality of crops, this chapter will focus on stimulating the wound-induced chemical defence of the plant in order to obtain substances beneficial to human health (Table 10.1). Responses to wounding can be local, systemic or both. Healing and repair are locally activated reactions, whereas herbivore deterrence can be locally and systematically activated. Wound-induced responses

Table 10.1 List of effects of jasmonic acid, methyl jasmonate and salicylic acid on selected crops

Treatment	Crop	Effects	Comment	Reference
JA	Madagascar periwinkle (*Catharanthus roseus*)	Stimulation of alkaloid biosynthesis		Van der Fits and Memelink (2000)
	Hemp (*Cannabis sativa*)	Increase of carotenoid, α-tocopherol and THC; decrease of CBD	10 µM JA (α-tocopherol), 5 µM JA (THC)	Salari and Mansori (2013)
MeJA	Norway spruce trees (*Picea abies*)	Increase of volatile terpenes	10 mM, foliar spray	Martin et al. (2003)
	Romaine lettuce (*Lactuca sativa*)	Increase of antioxidant activity and phenolics		Kim et al. (2007)
	Chinese bayberries (*Myrica rubra*)	Increase of antioxidant activity and phenolics		Wang et al. (2009)
	Red raspberries (*Rubus idaeus*)	Increase of flavonoids	0.01 mM, vapour	Flores and Ruiz del Castillo (2014)
	Peach (*Prunus persica*)	Increase of sucrose levels	10 µM, vapour	Yu et al. (2016)

Table 10.1 (continued)

Treatment	Crop	Effects	Comment	Reference
	Pomegranate (*Punica granatum*)	Increase of phenolics and anthocyanins	0.01–0.1 mM, vapour	Sayyari et al. (2011)
	Grapes (*Vitis vinifera*)	Increase of anthocyanins and phenols	1.78 mM, vapour	Flores et al. (2015)
	Blueberry (*Vaccinium* sect. Cyanococcus)	Increase of anthocyanins	0.01–0.1 mM, vapour	Huang et al. (2015)
	Blackberry (*Rubus* spp.)	Increase of anthocyanins and phenolic acid	0.1 mM, vapour	Wang et al. (2008)
	Strawberry (*Fragaria ananassa* Duch. cv. Allstar)	Increase of anthocyanins and phenolic acid	0.1 mM, vapour	Ayala-Zavala et al. (2005)
SA	Tomato (*Lycopersicon esculentum* cv. Baraka)	Increase of ascorbic acid, soluble solids, titratable acidity; decreased chilling injury	Foliar spray 3 weeks before harvest, + postharvest fruit dipping	Baninaiem et al. (2016)
		Increase of lycopene, carotenoids, phenolics and free amino acids	Dipping of mature green tomato fruit	Kant et al. (2016)
	Apple (*Malus domestica* Borkh. cv. Red Delicious)	Increase of phenolics, antioxidant activity and anthocyanins	Enhanced values only in early stages of cold storage	Hadian-Deljou et al. (2016)
	Banana (*Musa acuminata*)	Delayed ripening	During storage	Srivastava and Dwivedi (2000)

include changes in metabolic processes and in the expression of wound-inducible defence genes. Gene expression underlies the generation, perception, translocation and transduction of signals. Many structurally different molecules are involved in the regulation of wound signalling. Examples are:

- The oligopeptide systemin
- Oligosaccharides of the damaged cell wall

- Several phytohormones such as salicylic acid (SA) and jasmonic acid (JA), which have a central role in wound signalling (Bishop et al. 1981; Farmer and Ryan 1992; Pearce et al. 1991).

Deliberate injury to the entire plant stock to induce stress reactions would certainly not be practical in order to increase the concentration of desired metabolites. Thus, we have to come up with another strategy based on intra-plant communication and plant-to-plant communication. Instead of wounding the plant itself, we simply apply the wound signals themselves to stimulate physiological wound reactions.

10.1 Jasmonic Acid

Jasmonic acid (JA) is a well-recognized plant hormone known to activate many defence responses. JA is synthesized from its precursor alpha-linolenic acid. Farmer and Ryan (1992) noted that the application of linolenic acid (and of other JA precursors) to tomato leaves induced the expression of the same set of genes as JA itself. Van der Fits and Memelink (2000) found a transcription factor in Madagascar periwinkle (*Catharanthus roseus*) responding to exogenous JA by the expression of genes encoding alkaloid biosynthesis. This also indirectly affects alkaloid synthesis by the activation of primary metabolism pathways, which provide precursors for alkaloid formation. *Catharanthus roseus* is known to contain several anticancerous alkaloids such as vinblastine and vincristine (Arora et al. 2010). JA treatment of hemp (*Cannabis sativa)* results in increases of carotenoid, α-tocopherol and tetrahydrocannabinol (THC) (see also ► Chap. 3), whereas the cannabidiol (CBD) content decreases (Salari and Mansori 2013). Although the carotenoid increase and CBD decrease do not depend on the JA concentration, α-tocopherol shows an increase at 10 and 100 µM jasmonate, whereas THC levels are considerably enhanced at concentrations of 1 µM and 5 µM, with the 5 µM solution being more effective. However, despite both THC and CBD being the main secondary metabolites for medicinal uses, they have very distinct effects. Hence, JA application must be evaluated with regard to the sought medical treatment. Auxins have been demonstrated to have a negative effect on wound-induced gene expression, presumably to limit the extent and duration of the wound responses (Thornburg and Li 1991; Rojo et al. 1998). This should therefore also be considered when using phytohormones for quality improvement.

10.2 Methyl Jasmonate

Methyl jasmonate (MeJA) is another phytohormone produced after wounding. It is derived from JA by methylation through jasmonate-methyl-transferase and is a volatile form of jasmonate. MeJA is used for internal defence and as a communication signal between plants (Farmer and Ryan 1992). Exogenous MeJA stimulates volatile terpene biosynthesis in Norway spruce trees (*Picea abies*). Martin et al. (2003) detected a two-fold increase in terpene accumulation in needles of young saplings after MeJA treatment. The treatment involved the use of 150 ml of a 10 mM solution of 95% pure (w/w) MeJA in distilled water applied as a spray to saplings (40–50 cm) in a ventilated fume hood for 30 min. After being sprayed, the saplings were left under the fume hood for another 1–2 h until the needles were dry. Maximum values of volatile terpene levels were observed at 15 days after treatment, which declined within the next 5 days to control levels. An increase in antioxidant activity and phenolic compounds in romaine lettuce (*Lactuca sativa)* and Chinese bayberries (*Myrica rubra*) after MeJA application has also been noted (Kim et al. 2007; Wang et al. 2009). Flores and Ruiz del Castillo (2014) documented the promotion of phenylalanine ammonia lyase in red raspberries (*Rubus idaeus*) leading to an increase of health-promoting compounds including quercetin and myricetin. Yu et al. (2016) showed that MeJa treatment influences the quality of peaches (*Prunus persica*) even after harvest. During cold storage, the peach fruit increased their sucrose levels, which promoted a sweeter taste. Additionally, enhanced postharvest anthocyanin levels after MeJA application have been recorded for many crops including apple (*Malus pumila* Mill. var. *domestica* Schneid.) and pomegranate (*Punica granatum*) (Kondo et al. 2001; Sayyari et al. 2011). Aromatic compounds in grapevines (*Vitis vinifera*) and volatile organic compounds in strawberry (*Fragaria ananassa*) and mango (*Mangifera indica*) show increased values after MeJA exposure and thus an enhanced taste intensity in their fruits (Lalel et al. 2003; D'Onofrio et al. 2009; De la Peña et al. 2010). Notably, a preharvest application of MeJA is more effective than one postharvest because of the better reception of the fruit (Li et al. 2010).

10.3 Salicylic Acid

Another important wound signal for plant defence is salicylic acid (SA). SA is a phenolic compound and acts as an antioxidant defence system and as a plant growth regulator (Khan et al. 2003). Baninaiem et al. (2016) showed that foliar application of SA to tomato plants (*Lycopersicon esculentum* cv. Baraka) 3 weeks before harvest plus postharvest fruit dipping retains quality traits such as ascorbic acid content, total soluble solids and titratable acidity. It also has been demonstrated to delay ripening in several fruits including banana (*Musa acuminata*) during storage (Srivastava and Dwivedi 2000; Zhang et al. 2003). Furthermore, Kant et al. (2016) documented a delay in the biosynthesis of phytochemicals, e.g. lycopene, carotenoids, phenolics and free amino acids, after the dipping of mature green tomatoes in SA (*Solanum lycopersicon* L. cv. Pusa Rohini and Pusa Gaurav). These results show that the application of SA improves marketing quality indirectly by maintaining fruit quality during storage. 'Red Delicious' apples (*Malus domestica* Borkh. cv. Red Delicious) exhibit an increase in total phenolics and antioxidant activity in early stages of cold storage after SA treatment (2 mM) (Hadian-Deljou et al. 2016). Additionally, the anthocyanin content gradually increases until day 60 of storage and then immediately decreases.

10.4 Food Safety

With regard to safety concerns for human health, jasmonates are considered safe, and there are no restrictions for postharvest treatment. Experiments even indicate health-promoting effects. Jasmonates have been documented to possess selective cytotoxicity towards cancer cells (Fingrut and Flescher 2002; Kniazhanski et al. 2008). Thus, jasmonates inhibit the reproduction of cancer cells and induce apoptosis (cell death) in various cancer lines, e.g. breast, prostate and melanoma. Moreover, experiments by Umukoro et al. (2011) have suggested antidepressant effects of MeJA. Nevertheless, Wiesner et al. (2014) have recorded strongly (20-fold to control) mutagenic activity in juices from steamed pak choi (*Brassica rapa chinensis*) sprouts treated with MeJA. Therefore, the application of jasmonates must be evaluated and adjusted to the crop. SA is widely accepted as a health-promoting substance and extensively used because of its antipyretic and analgesic effects. Lethal doses are well-known but are negligible when plant fruit treatment is carried out correctly. Responses to JA and SA treatments depend on crop, phenological stage and dose.

Dedicated by J.J. Jones To my mother. To Lisa. To Oskar.

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