HORMONAL CONTROL OF GUMMOSIS IN *Rosaceae*

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A B S T R A C T

Gums are induced by infection, insect attack, mechanical and chemical injury, water stress, and other environmental stressors in some plant species. All of these factors are believed to act *via* ethylene produced in plant tissues. Ethylene is believed to be the main factor responsible for the induction of gummosis. Ethylene or ethylene-releasing compounds such as ethephon (2-chloroethyl-phosphonic acid) substantially stimulate gum formation in stone-fruit trees and their fruits of the *Rosaceae* family, such as cherries, ornamental Japanese cherries, plums, apricots, peaches and almonds. Gums consist mostly of polysaccharides, although they contain several other substances as well.

Biotic and abiotic stressors cause a rapid increase in the level of endogenous jasmonates, mainly jasmonic acid (JA). Jasmonates are a new group of plant hormones. Infection, insect attack, mechanical wounding and other stresses induce ethylene production in plant tissues. Jasmonates exogenously applied to plant tissues also stimulate ethylene production. Jasmonates substantially induces gummosis in cherries, plums, peaches and apricots. In this review, the ways in which ethylene and jasmonates act and the pathways of gum biosynthesis are discussed.

Key words: ethylene, jasmonates, gummosis, *Rosaceae,* plum, cherry, peach, almond, apricot

Environmental stress factors, ethylene and gummosis

Gummosis is widely encountered throughout the plant kingdom. Gum formation in plants is induced by environmental stressors such as infection, insect attack, flooding, and mechanical or chemical injury. All of the factors which stimulate gum exudation also promote ethylene production in plant tissues (Boothby, 1983). Ethylene or ethylene-releasing compounds such as ethephon (2-chloroethylphosphonic acid) stimulate gum formation in trees and fruits of stone-fruit species of the *Rosaceae* family, such as:

- apricots (*Prunus armeniaca* L.) (Bradley et al., 1969);
- Japanese apricots (*Prunus mume* Sieb. et Zucc.) (Li et al., 1995);
- cherries (*Prunus cerasus* L.) (Olien and Bukovac, 1982ab);
- ornamental Japanese cherries (*Prunus yedoensis*) (Ueda et al., 2003);
- peaches (*Prunus persica* Batsch.) (Buchanan and Biggs, 1969; Li et al., 1995);
- plums (*Prunus domestica* L.) (Bukovac et al., 1969); and
- almonds (*Prunus amygdalus* Batsch.) (Ryugo and Labavitch, 1978).

Based on these studies, ethylene is believed to be the main factor responsible for the induction of gummosis.

In peaches and Japanese apricots, gummosis can be caused by *Botryosphaeria dothidea* and *Lasiodiplodia theobromae* (syn. *Botryodiplodia theobromae*) (Li et al., 1995; Beckman, 2003; Okie and Reilly, 1983). In apricot shoots, gum formation can be caused by the *Monilia laxa*, *M. fructigena*, *Cytospora cincta*, or by larvae of *Grapholita molesta* (Rosik et al., 1971, 1975). In plum and cherry trees, gummosis can be caused by the bacterium *Pseudomonas syringae* or the fungus *Stereum purpureum* (Boothby, 1983). When a solution of naphthalene acetic acid (NAA) is applied to peach trees, it inhibits sprout formation well, but causes severe gummosis around the treated areas (Couvillon et al., 1977).

The rate of ethylene production in vegetative tissue is correlated with the internal level of the free auxin. Regulation of auxin-induced ethylene biosynthesis has been found in mungbean and pea seedlings. Indole-3-acetic acid (IAA) stimulates ethylene production by inducing synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC) from S-adenosylmethionine (SAM) (Yang and Hoffman, 1984). Gummosis induced by NAA in peach trunks is probably associated with ethylene production. IAA and NAA substantially stimulate ethylene production in tulip stems (Saniewski et al., 2003 b).

Gums are complexes of different substances, mostly polysaccharides of diverse structure. The composition of gum polysaccharides varies from species to species and from cultivar to cultivar (Boothby, 1983; Saniewski et al., 2002, 2004ab).

Gummosis of fungal origin significantly reduces tree growth and fruit yield in susceptible peach cultivars (Beckman, 2003). This kind of gummosis is difficult to control with fungicides (Beckman, 2003; Li et al., 1995). Breeding cultivars resistant to pathogens and insects may be the only effective way to limit or eliminate gummosis.

Gum duct formation

Gum ducts have been found in both woody tissues and fruits in all cultivated *Prunus* species. Gum ducts form naturally in healthy fruit trees. However, gum production intensifies after treatment with ethylene or ethylene releasing compounds, infection, insect attack, mechanical damage, and environmental stress (Morrison and Polito, 1985).

Gum duct formation is one of the processes involved in cell wall decomposition. This means that it is associated with living tissue. In cherry shoots, the beginning of gum duct formation can usually be seen in the non-lignified tissue formed by the cambium during lateral growth. The cells from which form the gum ducts are called the initial cells. They can be identified by their dense cytoplasm and by the more intense staining of their cell walls with the periodic acid-Schiff's (PAS) reaction for carbohydrates. The dissolution of cells starts in the center of the initial cells. Gum ducts of different sizes finally form in the wood. After the gum ducts form, the cambium remains active, and the ducts finally become enclosed in the wood (Stösser, 1979).

In almond fruits, the first sign of gum duct initiation is the differentiation of densely cytoplasmic secretory cells of the mesocarpal vascular parenchyma (Morrison and Polito, 1985). These secretory cells contain abundant dictyosomes, dictyosomal vesicles, mitochondria, and rough endoplasmic reticulum. Duct formation starts with the schizogenous separation of parallel rows of secretory cells. Later, the cytoplasm of the secretory cells degenerates as gum accumulates in the space between the plasmalemma and the cell wall. Finally, the cell walls and remaining cytoplasm disintegrate. Gum is primarily a secretory product of specialized secretory cells, but decomposed cell walls also appear to be incorporated into the gum during the lysigenous stage of duct development (Morrison and Polito, 1985). In intact almond fruits, there was a transient increase in ethylene production during gum duct initiation. Treatment with ethylene promoted gum duct formation (Morrison et al., 1987a).

In almonds, cell wall-degrading enzymes extracted from the free space of the cell wall are active during gum duct formation (Morrison et al., 1987b). Polygalacturonase and 1,3-β-glucanase activity rapidly increased during or right before the early schizogenous stage of duct initiation. α-galactosidase, β-galactosidase, α-arabinosidase and α-mannosidase were active during later lysigenous stage of duct formation.

Jasmonates and gummosis

Jasmonic acid (JA), methyl jasmonate (JA-Me) and related compounds are widely distributed throughout the plant kingdom. They show various biological activities in regulating plant growth and development. These compounds are called jasmonates, a new group of plant hormones (Ueda and Kato, 1980; Saniewski, 1995; Creelman and Mullet, 1997; Koiwa et al., 1997; Murofushi et al., 1999).

Jasmonates promote gum production in tulip bulbs and stone-fruit trees and their fruits (Saniewski et al., 2000). JA-Me induced gum formation in plum shoots and fruits, peach shoots, cherry shoots and apricot shoots (Saniewski et al., 1998; 2003a; 2004ab). Endogenous jasmonates rapidly increase in plant tissues in response to infection, insect attack, mechanical damage, osmotic stress and other abiotic stressors (Saniewski, 1997). Stress induces ethylene production in plants. Jasmonates increase ethylene biosynthesis in intact plants and their organs by stimulating ACC synthase and ACC oxidase activity (Saniewski, 1995; 1997; Saniewski et al., 1995). Exogenously applied JA-Me substantially increases ethylene production in pre-climacteric apples and in tomatoes at different stages of ripening (Saniewski, 1995).

How jasmonates control ethylene biosynthesis in stressed tissues is not yet fully understood. In the plants described above, JA-Me seems work by the same mechanism as ethephon (Saniewski et al., 2004ab).

Interaction of ethylene and jasmonates in induction of gummosis

Applying JA-Me and ethephon at the same time enhances gum production in cherry, plum, apricot and peach shoots far more than applying either JA-Me or ethephon alone. Endogenous jasmonates and exogenously applied ethylene act synergistically in gum formation. The reverse situation is also possible. The level of endogenous ethylene may be high enough to induce gum formation with exogenously applied JA-Me. Another possibility is that ethylene was able to induce gum formation without an increase in ethylene concentration because the process had already been triggered by JA-Me.

When ethylene binds to its receptor on the plasma membrane, it might sensitize JA-Me membrane receptors (Xu et al., 1994). In this case, ethylene and JA-Me may co-regulate osmotin gene expression. JA-Me and ethylene synergistically caused the breakdown of cell membranes and cell disintegration (Emery and Reid, 1996). This might be the reason for the induction of gum formation. Ethylene interacts with jasmonates in gummosis and other physiological processes (Saniewski et al., 1999). When JA-Me alone is applied ornamental Japanese cherry shoots, it does not induce gum formation. This is probably because the level of endogenous ethylene is too low to induce gummosis (Ueda et al., 2003). When inhibitors of cell wall polysaccharides biosynthesis such as monensin and 2,6-dichlorobenzonitrile are applied together with ethephon or JA-Me, they do not inhibit gum production (Saniewski et al., 2004b). Gummosis is therefore probably independent of the sugar metabolism involved in the biosynthesis of cell wall polysaccharides. When ethephon is applied together with inhibitors of jasmonates biosynthesis such as diethyldithiocarbamate, salicylic acid, acetylsalicylic acid, indomethacin, ibuprofen, phenidone, or monophenylbutazone, it inhibits gum production in plum fruits.

On the other hand, when inhibitors of ethylene biosynthesis such as salicylic acid, acetylsalicylic acid, aminooxyacetic acid and $CoCl_2$ are applied together with JA-Me, they do not limit gum formation. This is difficult to explain, though it is possible that these inhibitors are only partially effective in inhibiting ethylene production.

The gums induced by ethephon, JA-Me, or both together have a similar polysaccharide composition. Ethephon and JA-Me therefore probably induce gummosis by the same or a very similar mechanism (Saniewski et al., 2002, 2004ab). The induction and production of gums is regulated by a signal network of jasmonates and ethylene, especially by cross-signals between them. Further research is needed to elucidate the physiological roles of ethylene and jasmonates in gum induction and formation.

The physiological role of gums in plants is not yet clearly understood. Gums may play a role in inhibiting the spread of bacterial and fungal pathogens within infected tissues and from infected tissues to healthy ones. Gummosis in stone-fruit trees and their fruits is strictly connected with plant defense system against infection and insect attack. Gummosis reduces tree growth and fruit yield, especially in susceptible cultivars of stone-fruit species. Breeding cultivars resistant to pathogens and insects may be the only effective way to limit or eliminate gummosis.

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HORMONALNA REGULACJA GUMOZY W *Rosaceae*

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STRESZCZENIE

Gumy są indukowane w niektórych gatunkach roślin przez środowiskowe czynniki stresowe, takie jak infekcja patogenów, inwazja owadów, mechaniczne i chemiczne uszkodzenia, stres wodny i inne. Wszystkie wymienione czynniki wpływają na rośliny przez produkcję etylenu w tkankach. Etylen jest uważany za główny czynnik odpowiedzialny za indukcję procesu gumozy. Etylen i związki wydzielające etylen (jak np. etefon: kwas 2-chloroetylofosfonowy) zasadniczo stymulują tworzenie się gum w pestkowych drzewach owocowych i ich owocach z rodziny *Rosaceae*, tj. u śliwy, wiśni, ozdobnej wiśni japońskiej, moreli, brzoskwini i migdałów. Polisacharydy są głównymi składnikami gum, ale zawierają one także wiele innych związków.

W ostatnich latach wykazano, że jasmoniany, nowa grupa hormonów roślinnych, indukują gumozę u wiśni, śliwy, brzoskwini i moreli. Stres w roślinach powoduje szybkie zwiększanie poziomu endogennych jasmonianów, głównie kwasu jasmonowego. Z kolei infekcja patogenów, żerowanie owadów, mechaniczne uszkodzenie i inne środowiskowe czynniki stymulują produkcję etylenu w tkankach roślin. Egzogenne zastosowanie jasmonianów także stymuluje w tkankach roślin tworzenie się etylenu. W pracy omawiane są możliwe sposoby działania, etylenu i jasmonianów oraz mechanizmy biosyntezy gum.

Słowa kluczowe: gumoza, etylen, jasmoniany, *Rosaceae*, wiśnia, śliwa, brzoskwinia, morela, migdały