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Plant Protection by Tannins Depends on Defence-Related Phytohormones

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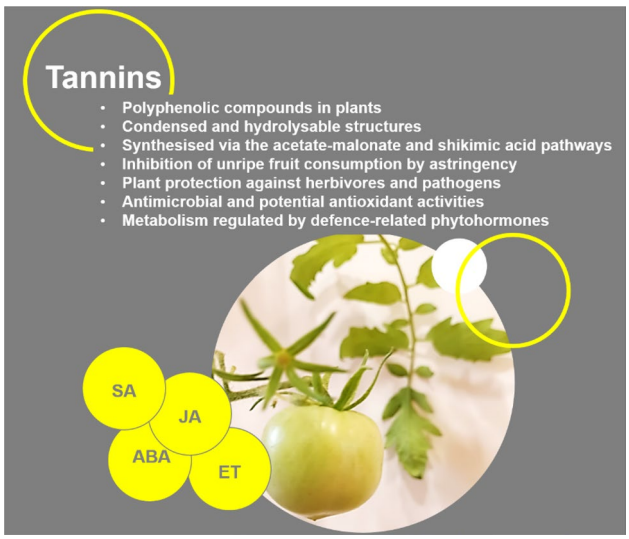
Abstract

Plants produce a wide variety of secondary metabolites to sustain and protect themselves against a wide range of stresses. Among these metabolites, tannins are one of the most abundant polyphenolic compounds, accounting for 25% of the dry weight of leaves, roots and bark of woody plants, but are also abundant in flowering and seed-producing plants. The presence of tannins in these organs serves to protect plants against herbivorous and pathogenic attack through their antidigestive and antimicrobial properties. In addition, tannins play a role in regulating plant growth and development by inhibiting the consumption of unripe fruits due to their astringency. In addition, several studies have also revealed various roles of them under environmental stresses. Tannins can be classified into condensed tannins (CTs), hydrolysable tannins (HTs) and phlorotannins. They are synthesised in plants via the acetate–malonate and shikimic acid pathways. Their accumulation is regulated by several transcription factors during normal development and under different stress conditions. Despite their multiple roles in plant life, information on the regulation of tannin metabolism by defence-related phytohormones is very limited. To cope with biotic and abiotic stresses, plant responses are regulated by defence-related phytohormones such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA), which act as regulators of tannin production under adverse conditions. This review focuses on tannin production, moreover its occurrence, defence potential and regulation by phytohormones under different environmental and biotic stresses, based on the most recent and relevant data.

Graphical Abstract



Keywords Abscisic acid · Ethylene · Jasmonic acid · Salicylic acid · Tannin

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Introduction

Plants are constantly exposed to harmful environmental conditions such as high light, UV-B radiation, drought, heat waves, infections, etc. at all developmental stages throughout their lives. The fluctuating environmental conditions are severely affecting crop production worldwide, resulting in reduced crop yields and food insecurity for the rapidly growing population (Samota et al. 2017; Saijo and Loo 2020). Thus, various abiotic and biotic stresses due to climate change cause severe damage to agricultural plants (Zhou et al. 2020; de Bang et al. 2021; Chauhan et al. 2022). These stresses, with their devastating effects on crop production are driving scientists to find solutions for sustainable agriculture. Enhancing plant resistance by endogenous or exogenous agents and inducing the production of secondary metabolites under stress conditions are also considered as suitable approaches to reduce the negative effects of different stressors (Dresselhaus and Hückelhoven 2018). Therefore, it is essential to pay attention to plant–stress interactions and to provide relevant scientific knowledge on the molecular-biochemical mechanisms involved in these defence responses.

Stress stimuli trigger an increase in intracellular calcium levels as well as the production of reactive oxygen species (ROS) and nitric oxide (NO) in plant cells, which affect the biosynthesis and signalling of various defence-related phytohormones such as salicylic acid (SA), jasmonic acid (JA), ethylene (ET) and abscisic acid (ABA) to induce multiple functions, including defence responses, to enhance plant resistance/acclimatisation and to regulate plant growth and development (Pieterse et al. 2012; Edel and Kudla 2016; Checker et al. 2018; Ku et al. 2018). These phytohormones can orchestrate long-term plant defence responses by regulating the synthesis of secondary metabolites, such as tannins, locally or systemically. At the same time, their differential effects have not been analysed systemically.

In plants, several secondary metabolites such as phenolics, flavonoids, terpenoids and tannins are accumulated in response to adverse stressors (Dehghanian et al. 2022). Among these, tannins play a crucial role in regulating plant's life during plant–environment interactions (Ucar et al. 2013). Among others, tannins as polyphenolic compounds play an important role in inhibiting various diseases due to their antimicrobial effects, moreover by limiting oxidative stress, inhibiting herbivore feeding as antidigestive compounds, and preventing gene mutations (Sommerauer et al. 2019; Champagne et al. 2020; Tong et al. 2022). Tannins impart a bitter taste to various plant parts to repel herbivores, e.g., to protect leaves and unripe fruits, but can also prevent bacterial infections (War et al. 2012; Kubalt 2016). On the other hand, tannins' consumption can result in serious consequences for invertebrates, including liver or kidney damage (Champagne et al. 2020; Sharma et al. 2021). Due to their diverse functions in living organisms, tannins play a crucial role in mitigating the negative effects of various stressors, thus enhancing plant defence, in particular the protection of plant organs in terms of survival and reproduction. Despite their multiple roles in plants, information on the regulation of tannin metabolism by defence-related phytohormones is very limited. The following review provides a current overview of the relevant literature, highlighting the function of tannins and regulation by the key defence-related phytohormones. Other functions of tannins in relation to various stress stimuli are also discussed.

Basic Properties of Tannins

Tannins are high molecular weight (500–3000 Da) and water soluble molecules at 20–35 °C, except for some complex high molecular weight structures (Serrano et al. 2009; Hassanpour et al. 2011; Marsh et al. 2020). Tannins can be defined as polyphenolic compounds that bind to proteins to form tannin-protein complexes. In addition, tannins can also bind to saponins, nucleic acids, alkaloids and polysaccharides such as cellulose, hemicellulose and pectin (Chaichi Semsari et al. 2011). They are localised in plant vacuoles preventing their inhibitory effect on cellular metabolism (Mir et al. 2015). Moreover, it is known that tannins have antimicrobial activity and inhibit the growth of a wide range of microbes in vitro at inhibitory concentrations of 0.5–20.0 g L^{-1} for bacteria and at 0.012 g L^{-1} for pathogenic fungi (Njokuocha 2020). However, the antimicrobial capacity of tannins depends mainly on the specific tannin and the microbial strain under consideration (Anderson et al. 2012).

Tannins can be classified into condensed tannins (CTs), hydrolysable tannins (HTs) and phlorotannins in plants (Fig. 1) (Shirmohammadli et al. 2018; Dehghanian et al. 2022). Among these, phlorotannins are the simplest tannins and are commonly found in aquatic species such as brown algae (Mannino and Micheli 2020). A single phlorotannin consists of two phloroglucinols with C–C or C–O–C bonds, while two single phlorotannins with four phloroglucinols form a tetrameric phlorotannin. The structural changes in these molecules may be due to an increased number of –OH groups or increased bonding in the monomers. Similarly, two or more monomer units combine to form concentrated tannins known as procyanidins (Smeriglio et al. 2017). HTs are considered to be plant secondary metabolites in combination with phenolic compounds such as caric acid, which have various biological functions (Das et al. 2020). Furthermore, HTs can be classified according to their structure into

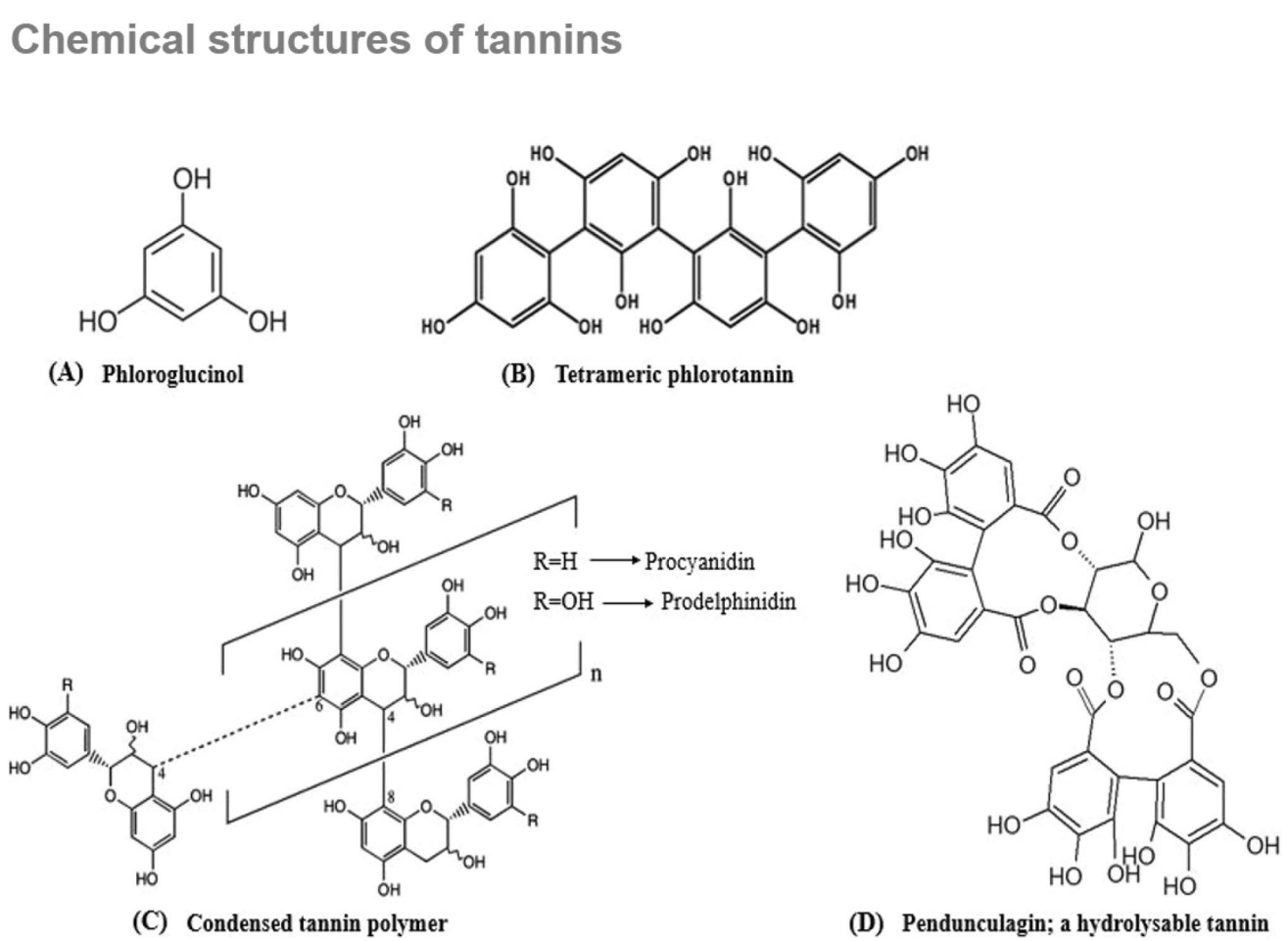

Fig. 1 The chemical structures of **A** phloroglucinol, **B** tetrameric phlorotannin, **C** condensed tannin, and **D** hydrolysable tannin (Dehghanian et al. 2022)

ellagitannins, gallic acid and gallotannins. Interestingly, the hydrolysis of gallotannins and ellagitannins yields gallic acid and ellagic acid, respectively, which are potent antioxidants and maintain cellular redox homeostasis (Barbehenn and Constabel 2011; Anstett et al. 2019). In contrast to HTs, CTs contain monomers of prodelphinidins and procyanidins, whose accumulation plays role e.g., in the protection of plant cells under insect or herbivore attack (Abdalla et al., 2014; Kumar et al. 2020; Rubert-Nason and Lindroth 2021).

Biosynthesis of Tannins in Plants

The synthesis of basic polyphenols in plants is achieved by the acetate–malonate and shikimic acid pathways (Dehghanian et al. 2022) (Fig. 2). Briefly, carbon dioxide is fixed to glyceraldehyde-3-phosphate via the Calvin cycle, which is further degraded to phosphoenolpyruvate or pyruvate if required, or to erythrose-4-phosphate via the oxidative pentose phosphate pathway (Salminen and Karonen 2011). Both pyruvate and erythrose-4-phosphate are substrates of the acetate/malonate and the shikimate pathway, respectively, enabling the synthesis of the respective CTs and HTs downstream (Takos et al. 2006). However, brown algae only require the acetate/malonate pathway for the synthesis of phlorotannins, whereas plants can produce tannins using both pathways (Salminen and Karonen 2011). It was reported that this step of tannin biosynthesis (the synthesis of phloroglucinol monomers from malonyl-CoA) in the brown alga *Ectocarpus siliculosus* is catalysed by the type III polyketide synthase, PKS1 (Meslet-Cladière et al. 2013).

In higher plants, the precursor of shikimic acid, 3-dehydroshikimic acid, is the primary building block of gallic acid for the synthesis of HTs regulated by shikimate dehydrogenase (SDH; Mora et al. 2022). The pentgalloyl glucose of the HT pathway yields gallotannins and ellagitannins, while the *p*-coumaroyl CoA of the phenylpropanoid precursors combines with the malonyl-CoA of the acetate pathway (Mora et al. 2022).

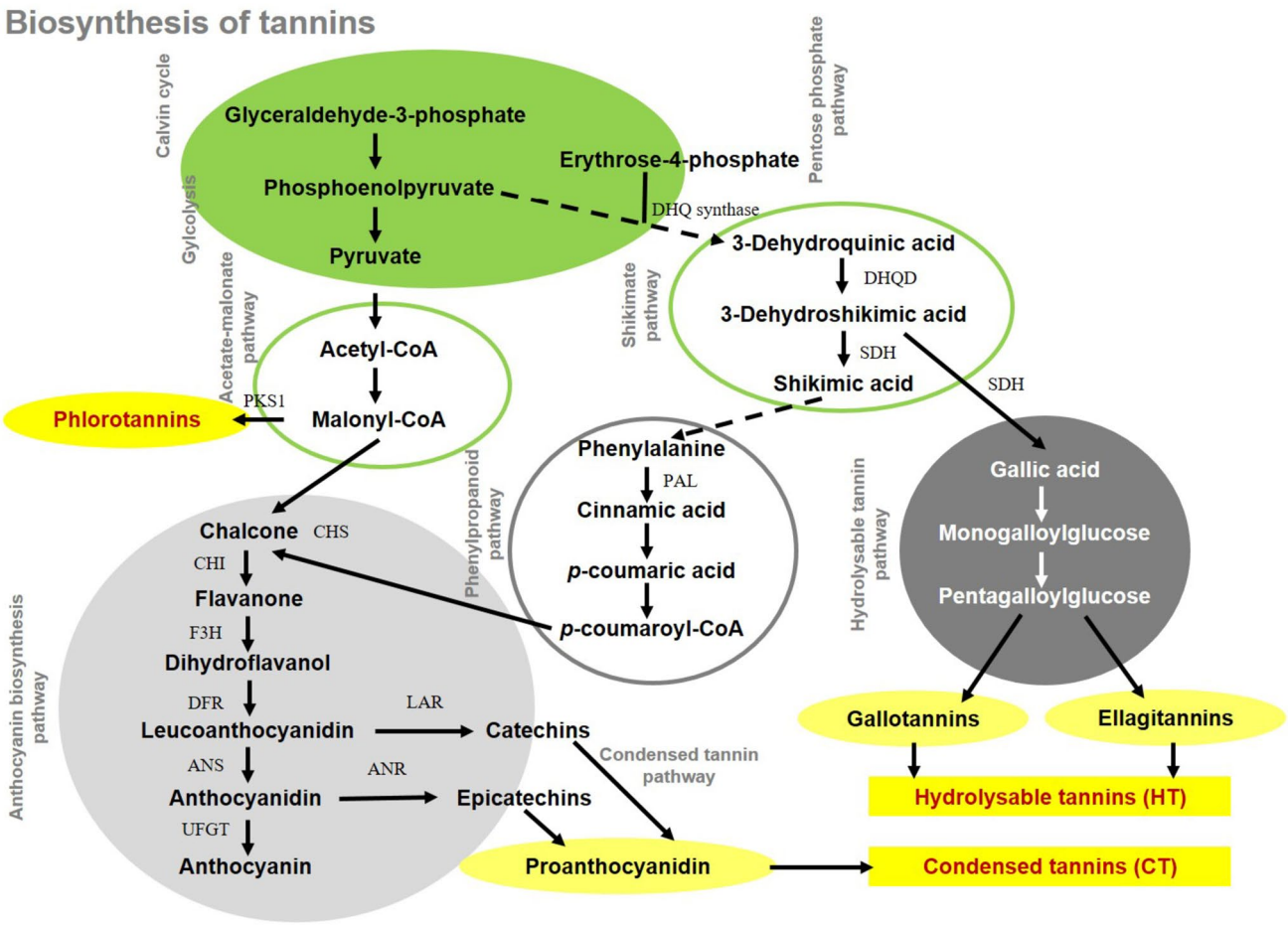

Fig. 2 The biosynthetic pathways of tannins in plants (Takos et al. 2006; Salminen and Karonen 2011; Mora et al. 2022)

The acetate/malonate CoA initiates the CT pathway by forming chalcone in the presence of chalcone synthase (CHS), which is then converted to flavanone by chalcone isomerase (CHI), followed by the production of dihydroflavanol due to the activity of flavanone-3β-hydroxylase (F3H) (Anwar et al. 2021). In the next step, dihydroflavanol is converted to leucoanthocyanidin by dihydroflavonol-4-reductase (DFR) and then to anthocyanidin by anthocyanidin synthase (ANS). The enzyme UDP-glucose: flavonoid-3-*O*-glycosyltransferase (UFGT) is involved in the synthesis of anthocyanin from anthocyanidin (Takos et al. 2006). During this CT synthesis pathway, two enzymes, leucoanthocyanidin reductase (LAR) and anthocyanidin reductase (ANR) convert leucoanthocyanidin and anthocyanidins to catechins and epicatechins, respectively, which are the initial constructing units of CTs (Anwar et al. 2021). The essential compounds for the biosynthesis of CTs are flavan-3 and flavan-3, 4-diol (Hassanpour et al. 2011). The synthesis of CTs in plants can be influenced by various factors such as plant species, soil fertility, plant organ/part and developmental season (Bharathidhasan 2018; Kumar et al. 2020; Roca-Fernandez et al. 2020). For example, structural differences have been reported in polymers isolated from leaves and roots of the same plant, suggesting different regulation of tannin synthesis in both plant tissues. In *Lotus pedunculatus* two distinct mechanisms of tannin biosynthesis was revealed; the first was light quality-mediated and found in the apical meristem, while the second was nutrient supply based such as nitrogen and found in the root zone (Hassanpour et al. 2011). Moreover, other studies documented the synthesis of tannins in fruits of e.g., wine grapes, pomegranate, persimmon and seeds of sorghum (Hassanpour et al. 2011; Bernjak and Kristl 2020), as well as in leaves of woody plants such as acacia, poplar, oak, especially under infection or wounding (Gourlay and Constabel 2019, Gourlay et al. 2020; Rubert-Nason and Lindroth 2021). These findings also suggest that phytohormone-mediated regulation of tannin synthesis is required in the different parts of plants, as well as in the case of different environmental stimuli.

Role of Phytohormones in Tannin Production

Plants have evolved different defence mechanisms against different environmental stressors or at different stages of pathogen or herbivore attacks. For example, at the pre-invasion stage in the case of biotic stress, cell wall modification followed by thickening by callose and lignin deposition prevents pathogen invasion and provides a more stable cell wall structure against cell wall-degrading enzymes secreted by phytopathogens (Das et al. 2016). At the next stage, programmed cell death (PCD) can limit further spread of pathogenic infection, followed by induction of defence-related gene expressions and synthesis of metabolites with antimicrobial and antioxidant properties (Jahangir et al. 2009). Various phytohormones such as SA, JA, ET and ABA are involved in the regulation of defence responses of plants against abiotic and biotic stressors such as microbial pathogens and herbivores (Pieterse et al. 2012; Belkadhi et al. 2014; Murcia et al. 2016; Iqbal et al. 2023a). As part of the signalling mechanisms induced by biotic stressors, pathogen-derived proteins are recognised by specific receptors which induces the activation, production and transport of hormones to their target sites (Spoel and Dong 2012). The hormonal responses under biotic stress, especially under bacterial and fungal infection, depend on the nature of the pathogens such as biotrophs, hemibiotrophs and necrotrophs. In general, SA induces plant defence responses against biotrophic pathogens, whereas JA and ET are involved in the induction of plant resistance against necrotrophs and herbivores (Das et al. 2016). At the same time, all of these phytohormones regulate the defence responses of plants against abiotic stressors, respectively, such as ABA mediates rapid stomatal closure to prevent plants from water loss under drought stress, as well as regulates cold- or salt stress tolerance (Lim et al. 2015). It is also known that phytohormones regulate the allocation of plant resources to prevent energy starvation and provide a balance between plant growth and defence (Huot et al. 2014). Several studies have examined the exogenous application of these hormones, while a few have focused on their endogenous roles in plant defence responses using transgenic and mutant plants (Shao et al. 2016; Machado et al. 2017). Hormonal crosstalk has also been studied under different conditions, such as herbivory, and changes in plant primary and secondary metabolism have been analysed (Liu et al. 2019).

Among the secondary metabolites, tannins are well-known for their diverse roles in inducing plant defence responses and protecting plants from stress, particularly biotic stress, as increasing tannin levels in various plant organs provides astringency and bitter taste (Dehghanian et al. 2022; Mora et al. 2022). Despite the importance of tannins in plant defence responses, there is a significant scientific gap in the hormonal regulation of their metabolism. This may be due to the fact that tannin production in some woody or food plants has been the focus of most scientific attention, particularly during ripening. This may also explain the lack of in-depth scientific studies in model plants such as *Arabidopsis*, tomato, rice or other crops.

In the next subchapters, the effects of key defence-related phytohormones on various plant species and organs are summarised for the first time to gain a better understanding of hormone-regulated changes in tannin metabolism at the physiological, biochemical, and molecular levels under diverse environmental conditions (Table 1). This knowledge can provide new scientific questions and research perspectives, as well as help to improve our ability to improve stress resistance in crops, facing future challenges in a changing environment.

Salicylic Acid (SA)

SA is involved in many plant defence responses to biotic and abiotic stresses through various defence mechanisms, including morphological, physiological and biochemical, to enhance plant growth and development (Kobayashi et al. 2020; Zhong et al. 2021). SA plays a crucial role in the hypersensitive reaction (HR) upon infection by generating high production of ROS and local cell death but it also plays role in the systemic responses of distal parts of infected plants, respectively (Klessig et al. 2018; Kachroo et al. 2020; Vlot et al. 2021).

The concentration of tannins also depends on the proximity to the infection sites, similar to SA. Higher levels of tannins were found in turtle grass (*Thalassia testudinum* L.) against marine protists (*Labyrinthula* sp.), but the concentration of CTs gradually increased with distance from the lesions. At the same time, the levels of other phenolic compounds also increased with infection (Steele et al. 2005). A similar study reported higher levels of CTs in the root and rhizome of turtle grass when sea urchins grazed on the leaves, suggesting a systemic induction of tannin biosynthesis which could be used as an indicator of infection or grazer attack (Arnold et al. 2008).

The eight-toothed spruce bark beetle (*Ips typographus* L.) is one of the most important pests of Norway spruce [*Picea abies* (L.) H. Karst] in Europe (Felicijan et al. 2016). Tannins in the bark provide chemical resistance to bark penetration and act as antifeedant and antifungal chemicals (Beckman 2000; Franceschi et al. 2005). Since, there is a crosstalk between SA and polyphenols (Liao et al. 2021), Norway spruce trees were treated with exogenous SA (Felicijan et al. 2016). It was found that SA increased the accumulation of CTs as a function of time, alleviated phenolic responses and inhibited bark beetle colonisation (Felicijan et al. 2016).

Table 1 The role of defence-related phytohormones in the regulation of tannin metabolism in different parts of various plant species

Plant species	Plant part/organ	Concentration of applied hormone	Duration of treatment	Results after hormonal treatment or production	References
Bean (*Phaseolus vulgaris* L.)	Seedlings	1 mM SA	6 days	Enhanced superoxide dismutase (SOD), guaiacol peroxidase (GPOX), catalase (CAT), ascorbate peroxidase (APX) activities and increased tannins, phenolics, flavonoids, nitric oxide (NO), hydrogen sulphide (H_2S) contents by SA	Hediji et al. (2021)
Cherimoya (*Annona cherimola* Mill.)	Fruits	100 mL min^{-1} CO_2	1, 2, 3, 4, and 5 days	Significantly increased non-tannin polyphenolic content, improved fruit colour, and prevented reduction in tannins' content by CO_2	Assis et al. (2001)
Chestnut (*Castanea dentata* L.)	Galls and leaves	1.5 mM JA	73 days	Pronounced levels of tannins and increased gall resistance against gall wasp by JA	Cooper and Rieske (2011)
Chestnut (*Castanea dentata* L.)	Leaves and stems	1.5 mM JA	96 h	JA treatment enhanced the content of proanthocyanidins in stem and hydrolysable tannins in leaves and stem of American chestnut and reduced moth growth	Cooper and Rieske (2008)
Cocoa (*Theobroma cacao* L.)	Cell cultures	0.01 and 0.1 mg L^{-1} SA	60 days	SA-treated plants showed higher contents of alkaloids, tannins, phenols, flavonoids, free amino acids than the control	Rosabal et al. (2022)
Cocoa (*Theobroma cacao* L.)	Shoots and buds	ET induced by *Crinipellis perniciosa* (1.7×10^6 spores mL^{-1}) fungal infection	3, 4, 7, 14, 21. 35, 61, and 132 days	Higher tannin levels were observed and then decreased as the fungal infection progressed, depending on ET	Scarpari et al. (2005)
Dahurian larch (*Larix gmelinii* L.)	Needles	Different levels of irradiance were applied by shading: 100% natural sunlight without shading, 52% and 26%. inducing SA accumulation	30, 60, and 90 days	100% Irradiance level resulted in the highest condensed tannin accumulation followed by higher production of SA under 52% irradiance	Yan et al. (2014)
Groundnut (*Arachis hypogaea* L.)	Leaves	1 mM JA, 1 mM SA	24 h	Both JA and SA-induced resistance against insects and increased the level of tannin-, phenolic-, and flavonoid compounds	War et al. (2015)

Table 1 (continued)

Plant species	Plant part/organ	Concentration of applied hormone	Duration of treatment	Results after hormonal treatment or production	References
Hybrid poplar (*Populus nigra* L.×*P. deltoides* W.)	Leaves	5 mM JA	24 and 48 h	Enhanced carbohydrate import and invertase activity in younger branches and leaves along with higher condensed tannin levels upon JA	Appel et al. (2012)
Hybrid poplar (*Populus nigra* L.×*P. deltoides* W.)	Leaves	2 mM JA	13 days	JA-induced tannins' production in younger leaves and condensed tannins' level was significantly higher in apical leaves	Arnold et al. (2004)
Muscadine grape (*Vitis rotundifolia* L.)	Fruits	300 ppm ABA	8, 10, and 13 days	Increased total phenolic content and antioxidant capacity, as well as flavonol and anthocyanin contents, and ellagic acid production after ABA treatments	Sandhu et al. (2011)
Norway spruce (*Picea abies* L.)	Barks	100 mM SA	90 days	Increased accumulation of condensed tannins was observed with SA application against bark beetles by inhibiting beetle colonisation	Felicijan et al. (2016)
Paradise-tree (*Simarouba glauca* DC.)	Leaves	10 ppm ABA, 50 ppm SA	4, 8, 12, and 16 days	Higher levels of tannins, flavonoids, alkanoids, and polyphenols were found after the hormonal treatments	Awate and Gaikwad (2014)
Pea (*Pisum sativum* L.)	Shoots and roots	250 µM SA	20 days	The results showed that artificial magnetism along the SA significantly increased tannin in pea plants	Naseer et al. (2023)
Persimmon (*Diospyros kaki* L.)	Fruits	95% CO_2, 1 µL L^{-1} 1-MCP, 100 µL L^{-1} ET, 300 mg L^{-1} ABA	1 day	ABA and ET affect tannin degradation during fruit ripening, and the RNA binding protein RBM24 is a common regulator of both phytohormones	Wu et al. (2022)
Persimmon (*Diospyros kaki* L.)	Fruits	100 µg kg^{-1} ET	6 days	ET decreased the level of soluble tannins, astringency, and accelerated fruit ripening	Tilahun et al. (2017)
Persimmon (*Diospyros kaki* L.)	Fruit	50 µL L^{-1} ET, 10 µL L^{-1} 1-MCP	18 h	ET promoted fruit ripening and induced ET signalling pathway genes and ripening-related genes such as *PDC1* and *PDC2*	Kou et al. (2020)

Table 1 (continued)

Plant species	Plant part/organ	Concentration of applied hormone	Duration of treatment	Results after hormonal treatment or production	References
Persimmon (*Diospyros kaki* L.)	Fruits	100 µL L^{-1} ET, 95% CO_2	1, 2, 3 days	ET eliminates fruit astringency, reduces soluble tannins' content, ERF-ADH/PDC cascade-induced deastringency under ET treatments	Min et al. (2012)
Persimmon (*Diospyros kaki* L.)	Fruits	100 µL L^{-1} ET, 95% CO_2	1, 2, 3, 5, 7 days	Induced deastringency, reduced soluble tannin content after ET exposure	Yin et al. (2012)
Persimmon (*Diospyros kaki* L.)	Fruits	1 and 2 mM SA	10 min	SA reduced disease symptoms in the fruit but did not suppress ET production. SA prolonged the shelf life of the fruit	Khademi et al. (2012)
Pomegranate (*Punica granatum* L.)	Leaves	100–250 µM JA	2, 3, 6, 12, 24, 30, 36, 48, and 72 h	JA regulated transcription factors of hydrolysable tannins, phytooxylipin, and flavonoids	Chang et al. (2021)
Rice (*Oryza sativa* L.)	Cell cultures	50–200 mg L^{-1} SA	28 days	SA increased biomass, fresh weight, dry weight, and the level of total flavonoids, anthocyanins, tannins and total phenolics	El-Beltagi et al. (2022)
Rose (*Rosa rugosa* L.)	Leaves	1 mmol L^{-1} JA, 1 mmol L^{-1} MeJA, 1 mmol L^{-1} Z-jasmone	1, 3, and 5 d	Jasmonates increased tannin and total phenolic contents in the leaves while the feeding area of insects was reduced	Yan et al. (2021)
Turtle grass (*Thalassia testudinum* L.)	Leaves	5 mM SA	15 min	Levels of phenolic compounds increased at the infection site where SA concentration was high, while tannins gradually increased with distance from the infection site	Steele et al. (2005)
Walnut (*Juglans regia* L.)	Fruits	3000 ppm Ethephon	4 days	ET-induced higher cellulase activity and increased tannin, flavonoid and phenolic contents	Farooq et al. (2023)

Table 1 (continued)

Plant species	Plant part/organ	Concentration of applied hormone	Duration of treatment	Results after hormonal treatment or production	References
Wine grapes (*Vitis vinifera* L.)	Fruits	53 mg L^{-1} ABA	24, 34, 45, 59, 61, 63, 67, 83, and 110 days	ABA decreased and then increased tannin levels in green grapes during berry ripening. It decreased the enzymatic activities of leucoanthocyanin reductase (LAR) and anthocyanin reductase (ANR) by decreasing the expression of their respective genes in the grape skin	Lacampagne et al. 2010
Wine grapes (*Vitis vinifera* L.)	Leaves	5% ABA	70 days	ABA elevated sugar and tannin contents, and enzymatic activities of the phenolpropanoid pathway	Villalobos-González et al. (2016)
Wine grapes (*Vitis vinifera* L.)	Seeds	1000 ppm ABA	4 days	ABA increased the number of seeds per berry and tannins' content at an early stage of development	Mallea (2010)

These results also indicated the time-dependent effects of SA in plants.

Not only time-dependent but also concentration-dependent effects of SA have been investigated. Using Hassawi rice (*Oryza sativa* L.) cell suspension culture, 50 and 100 mg L^{-1} SA significantly increased the biomass-packing cell volume, fresh weight, dry weight, antioxidant activity, as well as total flavonoids, anthocyanins, tannins and total phenolics content (El-Beltagi et al. 2022). At the same time, 200 mg L^{-1} SA did not alter CT content in cells (El-Beltagi et al. 2022), confirming its concentration-dependent effects on tannin biosynthesis.

The organ-specific effects of SA on tannin levels have also been described. The role of SA was investigated in bean (*Phaseolus vulgaris* L.) seedlings under cadmium (Cd) toxicity in a 6-day-long experiment. SA application (1 mM) significantly reversed Cd-induced negative effects by promoting plant growth and improving germination rate (Hediji et al. 2021). SA treatment generally increased CT content in cotyledons but decreased it in embryonic axes of bean seedlings (Hediji et al. 2021). The effects of exogenous SA application on different parts of *Theobroma cacao* plants and calli from its stamen and petals were also demonstrated, and it was found that 0.1 mg L^{-1} SA concentration significantly increased the content of tannins, alkaloids, phenols, flavonoids, reducing carbohydrates and free amino acids as compared to the control, while SA-induced reducing power was also observed to be elevated in cells obtained from petals (Rosabal et al. 2022).

The genotype-dependent effects of SA were investigated in groundnut (*Arachis hypogaea* L.) leaves (War et al. 2015). In this experiment, different resistant genotypes, including ICG1697, ICGV86699, ICG2271 and ICGV86031, and the insect-susceptible genotype JL24, were used to determine the effects of SA and JA application against an insect (*Helicoverpa armigera*). It was found that SA and JA increased the levels of tannins, phenolic and flavonoid compounds, and antioxidant activities in a genotype-dependent manner, more significantly in the resistant genotypes than in the susceptible genotype (War et al. 2015). At the same time, JA showed a greater potential to induce resistance than SA by reducing plant growth and larval survival and increasing CT levels in resistant genotypes (War et al. 2015).

The application of exogenous SA as a postharvest method and changes in tannin content were investigated for the first time by Khademi et al. (2012). Postharvest softening and disease development are among the major problems during storage of Karaj persimmon fruit. Therefore, SA treatments were carried out to improve disease resistance and prolong the storage period of this fruit. It was found that SA application at 2 mM concentration significantly reduced disease symptoms in fruits, but SA at 1 mM concentration failed to prevent disease incidence (Khademi et al. 2012). On the

contrary, SA did not affect soluble tannin or total soluble solids content and fruit firmness. The authors explained these changes based on the ineffectiveness of SA on ET production in Karaj persimmon fruit (Khademi et al. 2012).

Secondary metabolites are the main components of the defence responses of plants whose content are highly dependent on environmental stimuli such as light (Landi et al. 2020). Moreover, SA levels and their effects are also dependent on the light quality and quantity (Poór et al. 2019). The effect of different irradiances of sunlight (100, 52 and 26%) on the production of phenolic compounds such as SA and condensed tannins in the needles of *Larix gmelinii* seedlings was investigated (Yan et al. 2014). Interestingly, needles under full irradiance had the highest CT content, but phenolic acid content was the highest under the lowest irradiance (Yan et al. 2014). These negative changes suggested the key role of abiotic factors in the regulation of defence-related phytohormones and tannin biosynthesis. At the same time, foliar application of SA under water deficit ameliorated the stress effects and significantly increased the levels of secondary metabolites such as tannins, flavonoids, alkaloids and polyphenols in *Simarouba glauca* leaves (Awate and Gaikwad 2014). Curiously, the effect of artificial magnetism on tannin content was also investigated recently in the presence and absence of SA in shoots and roots of pea (*Pisum sativum* L.) plants (Naseer et al. 2023). However, the results showed that artificial magnetism along with foliar application of SA did not alter or reduce the tannin content in these organs of pea plants (Naseer et al. 2023).

It can be concluded that different abiotic and biotic stresses can result in significant increment in the levels of tannins and other phenolic compounds in an SA-dependent manner. Moreover, the effects of SA on tannin levels may depend on environmental stimuli (e.g., light), plant species and genotypes, as well as on organs (e.g., leaves, fruits, bark) and time (e.g., within hours or days). At the same time, more detailed studies are needed to describe the effects of SA on tannin metabolism at the transcriptional and metabolomic level.

Jasmonic Acid (JA)

Due to its involvement in various biological processes, the regulatory role of JA has been studied in different plant species to regulate stress conditions and induce plant defence responses against both biotic and abiotic factors (Lu et al. 2015; Machado et al. 2017). JA can limit plant growth by reducing the accumulation of carbohydrates, including starch and sugars, and enhancing plant defence responses, such as the accumulation of defensins or proteinase inhibitors (Goossens et al. 2016; Costarelli et al. 2020; Li and Ahammed 2023). It was found that exogenous JA treatment can increase the resistance of tomato (*Solanum lycopersicum* L.) plants against herbivory, whereas JA-deficient mutants showed susceptibility to herbivores (Lu et al. 2015). Upon herbivore attack, chemicals present in herbivore oral secretions induce herbivore-induced molecular patterns (HAMPs) in plants, similar to microbe-associated molecular patterns (MAMPs), leading to higher Ca^{2+} and ROS production, followed by a rapid increase in the levels of plant hormones such as JA (Gandhi et al. 2020). For example, ROS accumulation in plants resulted in resistance to oral secretion from a caterpillar (*Manduca sexta*) and similarly, oral secretion from pests such as *Spodoptera litura* and *H. armigera* due to rapidly increased JA levels in cotton plants (Si et al. 2020). Interestingly, phenolic compounds such as tannins, coumarins, lignins and flavonoids are synthesised in plants under pathogen attack and are involved in plant defence responses regulated by JA (Jaiswal et al. 2012; Gantner et al. 2019). In addition, tannin compounds reduce nutritional quality following pathogen infection. It was found that tannin complexes can reduce nitrogen content and protect plants from plant-feeding insects by inhibiting enzymatic activities in their digestive tract. However, some insects possess specific proteins in their saliva that can mitigate the negative effects of tannins (Kariñho-Betancourt 2018; Perkovich and Ward 2022).

Exogenous JA application was tested by Cooper and Riske (2008) to analyse the JA-dependence of defensive responses of two chestnut species, an American (*Castanea dentate* Borkh.) and a Chinese (*Castanea mollissima* Blume), against gypsy moths (*Lymantria dispar*) (Cooper and Rieske 2008). Soluble tannins and proanthocyanidins were quantified in the leaves and stems of both chestnut species as a result of which higher levels of proanthocyanidins were observed in the leaves and stems of American chestnut, whereas Chinese chestnut had higher levels of soluble tannins in the leaves. These results confirm the genotype-dependent differences in tannin content. At the same time, neither of the chestnuts showed difference under moth attack (Cooper and Rieske 2008). JA treatment significantly increased the level of proanthocyanidins in the stem and hydrolysable tannins in the stem and leaves of American chestnut, with organ-specific changes. On the contrary, JA application did not affect the tannin concentrations in the examined plant tissues of Chinese chestnut. The effect of JA treatment significantly reduced the growth of caterpillars (gypsy moth) in American chestnut, which remained unaffected in case of Chinese chestnut. It can be concluded that this study was the first to demonstrate JA-induced tannin production and defensive responses against herbivory depending on plant species and organs (Cooper and Rieske 2008). The effects of JA on changes in tannin levels were further confirmed using a JA inhibitor (diethyldithiocarbamic acid; DIECA) in different chestnut species (Cooper and Rieske 2011). The authors demonstrated the

effects of JA and DIECA on American and Chinese chestnut on gall development and their interaction with the gall wasp (*Dryocosmus kuriphilus*). They found that JA-treated leaves of both chestnuts showed reduced empty chambers and pronounced levels of tannins, while DIECA application resulted in opposite results with higher fungal lesion development, indicating the role of JA in the regulation of gall development and nutrient partitioning (Cooper and Rieske 2011).

The age-dependent accumulation of tannins induced by JA was first described in poplar by Arnold et al. (2004). In their experiments, leaves of hybrid poplar seedlings were treated with JA to check its effects on source-to-sink carbohydrate and secondary metabolite production. Carbohydrate import directly and positively influenced phenylpropanoid metabolism in induced sink leaves and uninfluenced leaves as well (Arnold et al. 2004). JA-induced tannin production was detected in younger leaves, but no change was observed in mature leaves. The concentration of CTs was found to be three times higher in apical and basal sink leaves, but JA-induced CT production was only correlated with this in apical sink leaves (Arnold et al. 2004). Similarly, JA treatment increased carbohydrate import and invertase activity in younger branches and leaves of poplar. Conversely, JA did not affect nitrogen import in girdling and branching. Nevertheless, girdling significantly increased CTs' production in poplar seedlings after 48 h (Appel et al. 2012).

Genotype-dependent effects were also found in groundnut plants treated with JA and SA. Both phytohormones increased the levels of tannins, phenolic and flavonoid compounds, especially in the leaves of resistant peanut compared to the susceptible genotype (War et al. 2015). In addition, JA-induced changes were more significant, primarily in increasing CT levels and reducing *H. armigera* larval growth in resistant groundnut genotypes (War et al. 2015).

The effects of different types of jasmonates on tannin levels have also been described as a function of time (Yan et al. 2021). The effects of JA, methyl jasmonate (MeJA) and Z-jasmone were investigated in *Rosa rugosa* leaves in response to the insect *Monolepta hieroglyphica* and it was found that JA and MeJA increased the tannin content of the leaves more than Z-jasmone after 1 day. The highest tannin levels were found after 5 days of jasmonate treatment. In parallel, the feeding area on the leaves was significantly reduced after 1 day (Yan et al. 2021). Interestingly, the activity of detoxification enzymes such as glutathione *S*-transferase (GST), alkaline phosphatase (AKP) and acid phosphatase (ACP) was reduced in adult insects feeding on jasmonate-treated leaves compared to controls. These results firstly show a strong positive correlation between the reduced feeding area of insects with higher tannin and phenol content induced by jasmonates and the negative correlation with insect detoxification enzymes (Yan et al. 2021).

Another recent study elucidated the positive effect of exogenous MeJA on the production of HTs, flavonoids and phyto-oxylipin in pomegranate (*Punica granatum* L.) leaves and showed that MeJA is involved in the regulation of expression of genes and transcription factors involved in the biosynthesis of HTs, phyto-oxylipin and flavonoids (Chang et al. 2021). JA induced the expression of lipoxygenase-encoding genes responsible for the oxidation of polyunsaturated fatty acids, while non-jasmonate phyto-oxylipin was produced in cellular compartments. MeJA treatment increased HTs' levels in leaves by promoting the expression of 3-dehydroquinate dehydratase/shikimate dehydrogenase (*DHQ/SDH*) and two glycosyltransferase genes (*PgUGT84A23*, *PgUGT84A24*) within 6 h, indicating the key role of MeJA in tannin production (Chang et al. 2021).

In conclusion, besides SA, JA is the other phytohormone whose role in the regulation of the metabolism of tannins has been more extensively studied, e.g., at the gene expression level. Tannins not only play a role in plant defence responses to herbivory, but also against insects and control the feeding range regulated by JA. At the same time, there are different effects of different jasmonates, which depend on time, concentration, plant species, genotype and organ from the aspect of influencing tannin levels.

Ethylene (ET)

ET regulates several physiochemical processes in plants, including fruit ripening, senescence, seed germination, and plant defence responses to biotic and abiotic stresses by regulating ROS levels and influencing cell death and plant survival (Khan et al. 2017; Iqbal et al. 2022, 2023b). ET plays an important role in fruit ripening in climacteric plants, which produce fruits that continue to ripen after harvest due to ET production, whereas non-climacteric fruits only ripen until they are attached to their parent plants (Alferez et al. 2021; Wang et al. 2022). Ethephone, the ET-releasing compound can enhance fruit ripening depending on its concentration, application rate, the fruit ripening stage, temperature and environmental conditions, but excessive use of ET can lead to the accumulation of harmful ROS and cell death (Huang et al. 2021).

Due to the key role of ET in fruit ripening and the influence of tannins on fruit consumption, most of the scientific results have come from food and post-harvest science. One of the first studies described the effects of elevated CO_2 concentration (20%) on the inhibition of ET biosynthesis in cherimoya (*Annona cherimola* Mill.) fruit (Assis et al. 2001). High CO_2 level significantly increased the content of non-tannin polyphenols and improved fruit colour, prevented the reduction of tannin content and simultaneously increased ET production after 3 days (Assis et al. 2001). At the same time, lignin deposition and phenylalanine ammonia

lyase (PAL) activity were not affected by CO_2 treatment during the 5 days studied (Assis et al. 2001). These results showed that inhibition of ET synthesis could lead to a delay in the reduction of tannin content in ripening fruit. Later, the effects of ET on tannin content were studied most thoroughly in persimmon (*Diospyros kaki* L.) fruit (Akagi et al. 2009). First, it was found that the reduction of soluble tannins was significantly accelerated in ET treatments, which further accelerated the deastringency process, but CO_2 also promoted these changes, already after 1 day (Min et al. 2012). Later, the involvement of ET-responsive genes in the ripening process of Mopan (astringent) and Yangfeng (non-astringent) persimmon fruits was investigated by treating the fruits with ET and CO_2, and it was found that both chemicals promoted deastringency by reducing the content of soluble tannins (Yin et al. 2012). In addition, the role of ET in the ripening of Bansi persimmon fruits was investigated using 1-methylcyclopropene (1-MCP), a gaseous inhibitor of ET action, moreover its effects on fruit quality and expression levels of ET response genes were also observed (Park et al. 2017). The results showed that 1-MCP treatment slightly softened the fruit as compared to control fruit, which showed a rapid decrease in firmness. Control fruits showed reduced tannin levels after harvest, while 1-MCP-treated fruits did not show difference in tannin levels during ripening. Expression levels of ET signalling-related genes such as *ERF1*, *ERF3* and *ERF8* were significantly decreased under 1-MCP exposure compared to control fruits (Park et al. 2017). This study clearly indicates that the appropriate application of ET at a specific stage of plant development and in a specific plant species can not only decrease tannin production, but also improve fruit ripening, deastringency and fruit development. Furthermore, ET-related genes such as *ERF8*, *ETR2* and *ERS1* significantly increased the ripening process and fruit softening, while *ERF4*, *ERF5* and *ETR2* genes showed an association with decreased tannin content in the case of Mopan persimmon, suggesting the key role of these genes in astringency removal. In contrast, *ERF1* and *ERF6* can induce deastringency in persimmon fruit under CO_2 treatment (Yin et al. 2012). Another scientific report revealed the role of ET in ripening Daebong persimmon fruit at 15 and 25 °C by reducing the content of soluble tannins and astringency as well as increasing the expression of *EIL*, *ERF2*, *ERF5* and *ERF8* genes at 25 °C compared to 15 °C, which justifies the rapid ripening of the fruit. These results indicate that ET can reduce fruit firmness in a temperature-dependent manner by reducing the content of soluble tannins (Tilahun et al. 2017). Furthermore, the negative effect of ET on the production of tannins was further confirmed using its inhibitor 1-MCP. The results showed that ET promoted fruit ripening, while 1-MCP had the opposite effect. During fruit storage, the tannin content remained almost the same in case of both treatments and controls, but the total soluble tannin content decreased steadily as the fruit ripened (Kou et al. 2020). The levels of total soluble solids were relatively higher upon 1-MCP treatment, while the ET treatment reduced their levels but increased the respiration rate. In addition, ET treatments significantly enhanced the expression of ET signalling pathway genes such as *ETR1*, *ETR2, CTR1* and *EIL1*, while 1-MCP had an inhibitory effect on the expression of these genes. ET treatment also increased the transcript levels of ET transcription factors such as *ERF19* and *ERF22* as compared to control and other treatments (Kou et al. 2020). In addition, ET treatment also increased the expression of deastringency genes such as two pyruvate decarboxylase-related genes, *PDC1* and *PDC2*, which are involved in the conversion of acetaldehyde from pyruvate. Exogenous ET treatment also increased the expression of genes encoding cell wall hydrolases, including *β-GAL1* (galactokinase 1), *PG1* (polygalacturonase 1), *PME1* (phosphatase methylesterase 1) and *XTH2* (xyloglucan endotransglucosylase/hydrolase 2), while 1-MCP inhibited their expression (Kou et al. 2020). Recently, the interaction of ET and ABA was described in persimmon fruits, which was triggered by high CO_2 concentration and inhibited by 1-MCP (Wu et al. 2022). The authors found that both hormones influence tannin degradation during fruit ripening and that the RNA binding protein RBM24 is a common regulator of both phytohormones in persimmon fruit (Wu et al. 2022). More recently, the effects of different hulling methods such as heaping, steeping and spraying were tested on walnut (*Juglans regia* L.) fruit and it was found that spray hulling significantly increased tannins', flavonoids' and phenolics' content more than other methods. In addition, ethephone application accelerated cellulase activity to break down cellulose in the cell wall to improve the ripening process of green walnut (Farooq et al. 2023).

The connection between ET production and tannins content as a function of time under biotic stress was also investigated. Cocoa (*T. cacao* L.) seedlings were infected with the causal agent of witches' broom, *Crinipellis perniciosa*. ET production and tannin content were increased during infection and then significantly reduced after the development of disease symptoms leading to cell death at the infection site (Scarpari et al. 2005). Interestingly, procyanidin (CT) has the potential to inhibit basidiomycetes' spores and alter germ tube morphology during their biotrophic phase, whereas this compound has no effect during the necrotrophic phase. This finding suggests that a higher concentrations of tannins may be involved in inhibiting fungal growth during the early phase of infection (Scarpari et al. 2005).

Finally, a specific effect of ET has also been reported in the case of forage. Interestingly, forage also contains high concentrations of tannins whose stability and water solubility depend on various factors such as climatic conditions, plant growth stage and specific parts of the plant used for browsing (Seresinhe and Pathirana 2003). However,

during browsing, ET induces tannin production in different but unaffected parts of the plant to prevent browsing through higher tannin accumulation, especially in younger plants, suggesting a role for ET in defence mechanisms. This defence strategy is used by plants to prevent attacks by herbivores or human consumption. In addition, different levels of tannins in the diet can have both beneficial and toxic effects, such as 2–4% (beneficial), 5–9% (antinutritional) and more than 9% (toxic) (Seresinhe and Pathirana 2003). Their effects are mainly due to the formation of complexes with enzymes and proteins, which ultimately reduces the ammonia level and antimicrobial activity in the rumen, affecting the forage utilization of the grazing animals. Nevertheless, application of polyethylene glycol (PEG) showed effective results in detoxifying dietary tannins due to its higher affinity for CTs. Interestingly, deer saliva contains proline, which binds with tannins and provides a defence mechanism to promote the browsing of the animals, whereas sheep and cattle have proline-free saliva (Seresinhe and Pathirana 2003).

Consequently, ET-induced tannin accumulation can inhibit biotrophic attack by controlling microbial growth and reducing herbivory; however, at the ripening stage, ET promotes fruit ripening processes in a time-dependent manner by converting soluble tannins to insoluble tannins to increase fruit deastringency.

Abscisic Acid (ABA)

ABA also plays a crucial role in the regulation of plant growth, development and signalling under abiotic and biotic stress conditions (Hewage et al. 2020). ABA is also involved in the regulation of seed germination, seed maturation and the onset of fruit ripening (Iqbal et al. 2023a, b). In addition, ABA regulates stomatal closure and plant–stress responses to drought, salt and cold (Lim and Lee 2020; Fatma et al. 2021; Liu et al. 2022).

The effects of ABA on tannins' production have been extensively studied in wine grapes (*Vitis vinifera* L.). First, it was shown that ABA is involved in the regulation of enzymes responsible for tannin biosynthesis, and thus ABA can also influence tannin levels in green grapes during the berry ripening stage (Lacampagne et al. 2010). ABA treatment significantly reduced the enzymatic activities of LAR and ANR by decreasing the expression of their respective genes in grape skin, suggesting the involvement of ABA in tannin biosynthesis without affecting tannin composition. These two enzymes are involved in the biosynthesis of proanthocyanidins (CT), and in the production of (−) epicatechin and (+) catechin, respectively (Lacampagne et al. 2010; Setha 2012). Similarly, the essential role of ABA in seed and berry development of Syrah grape, along with the accumulation of phenolic and tannin compounds, was assessed (Mallea 2010). ABA was sprayed at anthesis and at the veraison stage of plants in the field, and seeds were also soaked in ABA solution for 4 days after 3, 5 and 9 weeks at anthesis, then seeds and berry skins were analysed for phenolic and tannin content (Mallea 2010). Interestingly, ABA treatment in the field increased the number of seeds per berry, while ABA did not alter the trends of tannin and phenolic compounds. The results also showed a higher accumulation of tannin and phenolic compounds in seeds and berry skin at an early stage of berry development, followed by a rapid decline after 4 weeks and a stable level during the ripening stage of the fruit (Mallea 2010). Similarly, the effect of the exogenous application of ABA on *V. vinifera* was analysed for 70 days from veraison. The ABA treatment significantly increased the sugar and tannin content, and the enzymatic activities of the phenylpropanoid pathway. In addition, foliar ABA application initially reduced gene expression of *LAR2* and *Myb4A* involved in flavonol synthesis, but then increased after 40 days of veraison (Villalobos-González et al. 2016). At the same time, tannins are also produced by plants during the early development to provide bitterness and astringency to deter herbivores. ABA application upregulated the expression of *DFR*, *ANS* and *PAL* genes, encoding dihydroflavonol-4-reductase, anthocyanidin synthase and phenylalanine ammonia lyase, respectively. Treatment with ABA also resulted in more pronounced transcript levels of *UFGT* (involved in anthocyanin synthesis) initially, followed by a decrease after 40 days, while the expression level of *LAR2* (involved in tannin synthesis) was initially reduced, followed by an abrupt increase after 40 days (Villalobos-González et al. 2016). These results show that tannin production occurs at the late stage after the application of ABA. It was also found that exogenous treatment with ABA significantly increased total phenolic and antioxidant capacities, flavonol and anthocyanin content, and ellagic acid production (produced by hydrolysis of ellagitannins) in the skin of *Vitis rotundifolia*, but these changes were grape genotype-dependent, with more significant ellagic acid production in the noble type (Sandhu et al. 2011).

In another fruit, persimmon, the involvement of both ABA and ET in the ripening process was tested (Wu et al. 2022). Via modulation of ET levels using CO_2 and 1-MCP it was found that CO_2 treatment enhanced ABA and ET production and reduced tannin levels, while the combined treatment (CO_2 + 1-MCP) inhibited their production in the fruits (Wu et al. 2022). These results suggest that there is a strong correlation between ABA and ET in the regulation of fruit ripening and tannin metabolism in fruits.

Similarly, both ABA and SA significantly increased the levels of secondary metabolites such as tannins, flavonoids, alkaloids and polyphenols in *S. glauca* under water stress as a function of time (Awate and Gaikwad 2014), confirming their role in activating plant defence mechanisms.

These findings suggest a role for ABA not only in tannin production, but also in the case of other secondary metabolites such as flavonoids and phenolic compounds, which could significantly reduce plant–stress acting as potent antioxidants. In addition, these findings suggest a time- and concentration-dependent, as well as a developmental phase-dependent role for ABA in tannin biosynthesis. At the same time, further research is needed to explore the direct effects of ABA on the transcriptional and post-transcriptional regulation of tannin metabolism in various plant organs such as in leaves and fruits.

Conclusions and Future Prospects

It can be concluded that tannins are present at different levels in different parts of plants from roots, stems and leaves to fruits, protecting them against various stresses. They play a role especially under biotic stress including bacterial and fungal pathogens as well as herbivore attack due to their antimicrobial effects, bitter taste caused in different plant parts and inhibition of various enzyme activities. Thus, tannins, as key compounds in plant defence responses, need to be regulated by different phytohormones to enhance plant–stress tolerance and defence, which may be dependent on environmental conditions such as light or cold (Fig. 3). Several studies have reported the protective role of tannins against biotic stresses, but only a few studies have shown their involvement in stress responses mediated by some phytohormones under abiotic stresses. Therefore, more research could be carried out to increase plant tolerance to abiotic stressors due to their potential antioxidant effects.

In the case of biotic stress, SA-regulated local and systemic tannin production was described in infected plants. In addition, although the time-, concentration-, organ- and genotype-dependent role of SA in tannin biosynthesis was investigated, but only regarding the levels of different tannins rather than by analysing their biosynthesis at the genetic or biochemical level. In terms of post-harvest biology, the application of SA and changes in tannin levels were evaluated as a useful method to improve disease resistance during storage. In addition, the effects of environmental stimuli such as light have also been studied in relation to SA, but more research is needed on other abiotic stressors such as cold to obtain more data about the relationship between phytohormones and tannins. While SA mainly increased the content of CTs, JA primarily increased the levels of anthocyanidin and HTs, also at tissue and organ levels based on previous studies. In addition, the effects of exogenous treatments with different types of jasmonates such as JA, MeJA and Z-jasmone were tested and the adverse effects on tannin accumulation were summarised. In contrast to SA, analysis of the changes in the expression of several genes related to tannin biosynthesis, such as *DHQ/SDH* and *UGT*s have been performed and the significant effects of JA on their regulation have been reported. While the role of SA and JA has mainly been analysed under biotic stress, the role of ET and ABA has primarily been investigated during fruit ripening. Based on scientific data, ET plays an important role in reducing tannin content during ripening depending on the

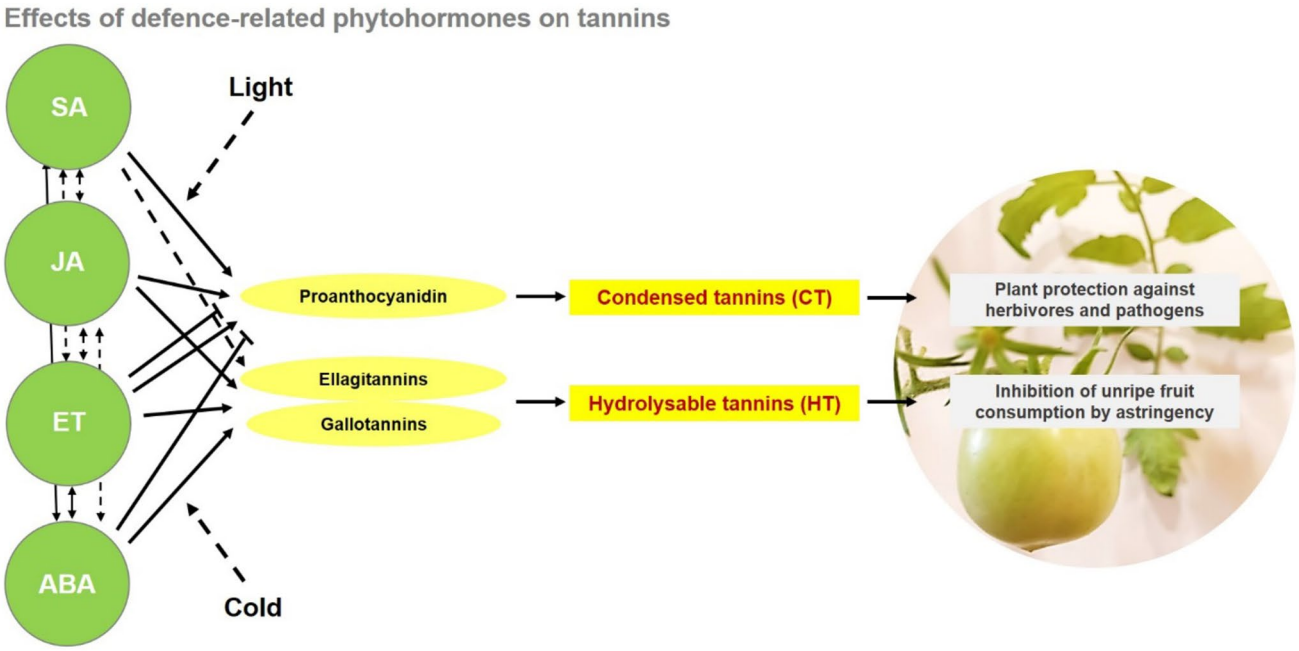

Fig. 3 Effects of defence-related phytohormones on tannins (dashed arrow indicates no or partially known effect)

ripening stage or environmental conditions such as temperature. Under infection, ET can increase procyanidin and CT levels in sprouts. In addition to ET, the role of ABA in tannin biosynthesis is also dependent on the ripening stage. It was found that ABA can down-regulate the activity of LAR, ANR and thus decrease the level of proanthocyanidins (CT) depending on the developmental stage. In the case of ABA, the expression of key genes involved in tannin biosynthesis, such as *UFGT*s, *DFR*, *ANS* and *PAL* was also studied in wine grape fruit.

While the effects of ABA and SA or ABA and ET have been investigated, other hormone interactions such as SA–ET or JA–ET in the induction of tannin production are not clearly understood. In addition, the involvement of tannins in phytohormone-mediated stress responses and their exact time- and organ-dependent molecular mechanisms are still not fully understood, so further research in this area could provide several new insights in this field. Unfortunately, the simultaneous changes in CT and HT levels and their transcriptomic and biochemical regulation have not been investigated systemically. The analysis of the role of phytohormones in tannin metabolism could provide broad application possibilities in plant breeding and creating transgenic plants further enhancing plant defence systems. Furthermore, based on their defensive role in plants, tannins could be used as alternatives of chemicals against pathogenic attack.

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Declarations

Conflict of interest No conflict of interest is declared.

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