



Enhancing Ellagitannin Production in Pecans and Strawberry Fruits Through Pre-harvest Biotic Stresses

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Abstract

Purpose of Review This review intends to examine the role of phytochemicals in plant defense mechanisms against environmental stresses and their potential health benefits. Specifically, it aims to explore how pre-harvest insect damage can enhance the production of phytochemicals in pecan and strawberries fruits. Additionally, the review intends to examine the regulation of plant phenolics and ellagitannin derivatives through signal transduction pathways and how these pathways are influenced by biotic stresses.

Recent Findings The article mentions that signal transduction pathways in plants can be triggered and modulated by stress factors, including the wounding damage caused by chewing insects, leading to changes in plant secondary metabolism. Additionally discusses the speculation that increased biotic stress in plants grown without synthetic chemicals in pesticide-free systems as suggested by organic agriculture practices lead to higher levels of phytochemicals, especially phenolic compounds. Furthermore, it shows up two examples, strawberries and pecans, which exhibit increased phytochemical levels when facing biotic stressors like infections or pest attacks.

Summary This concise review highlights the significance of phytochemicals for human health, indicating their potential roles in preventing and treating chronic cardiovascular and inflammatory diseases, as well as cancer. It emphasizes that organic fruits and vegetables are believed to contain elevated levels of secondary metabolites associated with plant defenses. The review remarks the importance of understanding the mechanisms of biotic stress in plants and the relationship between phytochemicals and their potential health benefits within the context of organic agriculture, ultimately contributing to human well-being.

Keywords Organic agriculture · Phytochemicals · Phenolic compounds

Introduction

Over the last 20 years, the organic food market has experienced substantial growth, around 20%, compared to the 2–4% growth observed in the conventional food product market [1, 2]. European countries and the USA lead the global market in both production and consumption, while other nations, including Australia, China, Argentina, Brazil, and Uruguay, have emerged as significant producers for export markets [3]. For the US Department of Agriculture, organic products must ensure the preservation of natural

resources, respect for biodiversity, and the exclusive use of approved substances [4]. Certification and labeling of organic products positively influence consumer choices and support higher prices in this expanding market [5]. Additionally, studies indicate that organic products may possess superior qualities, such as higher dry matter content, increased levels of healthy fatty acids in dairy products, reduced nitrates, and elevated concentrations of antioxidants, particularly polyphenols and vitamin C, in fruits and vegetables [6, 7]. Several investigations have suggested that higher levels of phytochemicals, particularly phenolic compounds, are associated with increased biotic stress in plants grown under organic conditions [8–17, 15]. Furthermore, various authors have estimated that the heightened levels of phytochemicals, with a specific emphasis on phenolic compounds, can be attributed to the increased biotic stress experienced by plants in organic conditions [18–20]. This inference holds

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significance due to the potential role of phytochemicals in human health, encompassing their involvement in the treatment and prevention of chronic cardiovascular conditions, inflammatory diseases, and cancer [21–24].

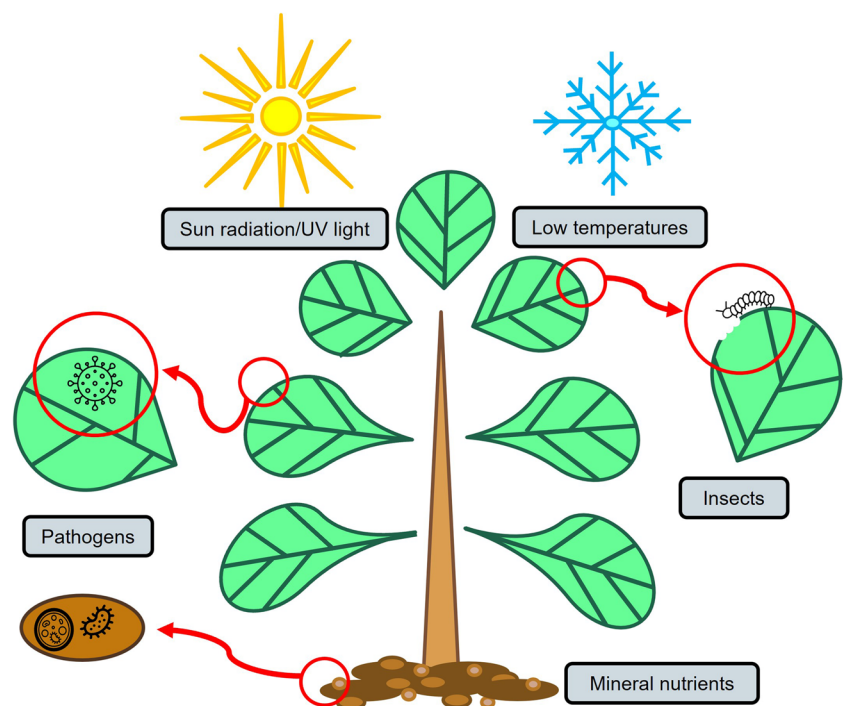
Phytochemicals and Environmental Stresses

Biotic stresses represent a significant challenge to the cultivation of plants and can have profound implications for both agricultural productivity and the nutritional quality of crops. One notable response of plants to biotic stress is the enhancement of phenolic compounds in their fruits. Phenolic compounds are a diverse group of secondary metabolites with well-documented antioxidant and defensive properties. When plants are exposed to biotic stressors such as pathogens or herbivores, they often increase the production of phenolics as part of their defense mechanisms. These compounds can act as chemical barriers against herbivores, deter pathogens, and mitigate oxidative damage caused by stress. Consequently, the enhancement of phenolics in fruits is not only a vital component of plant defense but also holds considerable significance for human nutrition. The consumption of fruits rich in phenolic compounds has been associated with numerous health benefits, including reduced risk of chronic diseases. Thus, understanding the regulation of phenolic production in response to biotic stresses is crucial for both plant resilience and the promotion of human health.

Plant secondary metabolites are under the regulation of signal transduction pathways, which can be triggered

and modulated by various abiotic and biotic stress factors (Fig. 1) [25, 26]. Research on the production of secondary metabolites influenced by biotic stresses has demonstrated the induction of phenolic compounds and phytoalexins as plant defense responses. These studies have been conducted in tissues damaged by piercing-sucking or leaf-chewing insects [27–33]. Stressors like wounding and herbivores have been shown to alter plant secondary metabolism [34–36]. Moreover, systemic induction of secondary metabolites has been observed within the same type of plant organ, such as the leaf-leaf model in tobacco, tomato, and poplar [37–46]. Wounded tissues affect the production of phenylpropanoid secondary metabolites both locally and systemically within the same organ tissue (e.g., leaves) [26, 47–53]. An early study showed that wounded potato and tomato leaves enhanced the production of proteinase inhibitors [54]. After the recognition of the wounding event, plants under insect attack respond with direct and indirect defense mechanisms [55, 56]. These responses involve a complex interplay of signal molecules, including phytohormones like salicylic acid (SA), jasmonic acid (JA), ethylene (ET), abscisic acid (ABA), indolacetic acid (IAA), and gibberellic acid (GA), along with various reactive oxygen species (ROS) [29, 57–60]. ROSs play critical roles in signaling related to plant defenses and other functions [61–64]. Specific elicitors released due to insect damage activate multiple signaling pathways, resulting in a metabolic rearrangement that includes the expression of defense-related genes and the release of volatile organic compounds [65]. JA, methyl jasmonate (MeJA), and its precursor, 12-oxo-phytodienoic

Fig. 1 Plant secondary metabolites are regulated by signal transduction pathways that can be triggered and regulated by abiotic stresses (e.g., minerals in soil, temperatures, radiation) and the main biotic stress factors (e.g., insects and pathogens)



acid (OPDA), are known as inducers of proteinase inhibitors, a key defense mechanism against herbivores [66, 67]. JA and ET serve as positive regulators of plant defense against insects and some pathogens, while SA is associated with resistance against most pathogens [68]. Crosstalk between these pathways allows plants to optimize their responses against herbivores and pathogens, creating a complex defensive system [29, 63, 64, 69–75].

Biotic Stress in Pecans and Strawberries

The significance of plant secondary compounds (phytochemicals) for human health has prompted research into pre- and post-harvest factors that influence the production of bioactive phenylpropanoids [18, 20, 76–80]. For instance, a comparison of two strawberry cultivars under organic and conventional production methods demonstrated that organic cultivation led to greater accumulation of total phenolics, with these differences maintained under different storage conditions [77]. Of particular interest are phenolics like phenylpropanoids and ellagitannins, which have garnered attention due to their biological activities associated with health benefits, including antioxidative, anti-allergic, anti-hypertensive, and anti-tumor effects in both in vitro and in vivo studies [22–24, 81, 82]. Strawberry (*Fragaria × ananassa*) and pecan (*Carya illinoensis*) are recognized for their high content of ellagitannins [83–89].

Strawberries hold a significant position among small fruits produced on a global scale. The Food and Agriculture Administration (FAO) data shows, in 2020, an output of 8,861,381 tons worldwide [90]. In South America, key strawberry producers include Argentina, Brazil, and Chile, with substantial cultivation and yields [91–93]. Uruguay, while having a comparatively smaller production area of 120 hectares, boasts impressive yields at 37 tons per hectare. This production primarily caters to the local market, supplying a range of national cultivars [91, 94]. Strawberries are a valuable source of nutrients such as vitamin C, folate, and essential microelements. Moreover, they are rich in beneficial phytochemicals [95]. The phytochemical profile of strawberries includes anthocyanins, ellagitannins, gallotannins, ellagic acid, and other phenolic compounds, contributing to their antioxidant potential and associated health benefits [95–99].

Strawberries have exhibited a range of biological activities related to phytochemicals, including the inhibition of human colon carcinoma proliferation, anti-inflammatory effects on macrophages, modulation of oxidant-antioxidant balance in blood phagocytes, anti-hyperglycemic potential, mitochondrial protection, neuroprotective potential, and antimicrobial properties against human pathogens [89, 100–104]. Numerous studies have indicated that the levels

of phytochemicals in strawberries are higher when grown using organic methods compared to conventional cultivation practices. A study conducted by D’Evoli et al. [100] showed that the level of vitamin C increased from 45.9 mg/100 g in conventional production to 62.2 mg/100 g of fresh fruit from biodynamic production (a holistic and ecological approach to farming). Biodynamic strawberries had concentrations of pelagornidin-3-glucoside (38.8 mg/100 g) significantly higher than that detected in conventionally grown strawberries (24.9 mg/100 g). Also, the biodynamic fruits contained significantly higher amounts of ellagic acid (53.3 mg/100 g) compared to conventional ones (37.9 mg/100 g). The authors of this study correlated the elevated level of phenolics with improved antiproliferative activity in Caco-2 cell lines, derived from human colon adenocarcinoma [100].

Despite the primary biotic stressors affecting strawberry cultivation being bacteria and fungi, some arthropods, including the aphid *Chaetosiphon fragaefolii* and the spider mite *Tetranychus urticae*, can negatively impact commercial production [105–108]. Ellagic acid, a prominent phenolic compound, was found in substantial concentrations in strawberries, ranging from 39.6 to 52.2 mg/100 g fresh weight in nine analyzed cultivars [109]. Another study comparing organic and conventional production methods revealed higher antioxidant activity (8.5%) and increased levels of kaempferol (25%) and ellagic acid (9%) in organically grown strawberries [110]. Notably, the addition of organic and conventional soil nutrients did not significantly affect strawberry yield and quality parameters related to phenolics, such as antioxidant capacity [111].

Pecan stands as an important horticultural crop within the southern United States, signifying not only economic value but also cultural importance. The crop’s value in 2021 amounted to \$551 million, marking a 27% increase from the preceding season [112]. This nut, indigenous to the USA, particularly flourishes in states such as Texas, Oklahoma, Louisiana, Arkansas, Mississippi, Kansas, Missouri, Tennessee, and Kentucky, although its cultivation extends to various other southern regions as well [113]. What adds to the attraction of pecans is their reputation as a wholesome food choice, acknowledged with the potential to prevent diseases linked to oxidative stress in humans. This beneficial characteristic can be attributed to pecans’ high content of phytochemicals, including ellagitannins, gallotannins, and proanthocyanidins, which are known for their biological activities [114–117].

Among these phytochemicals, ellagitannins, which comprehend compounds like geraniin and pedunculagin, have demonstrated their ability to inhibit the growth of the green peach aphid (*Myzus persicae*). Additionally, the hydrolysable derivative of ellagitannins, known as ellagic acid, has exhibited remarkable effectiveness against the infestation by barley greenbug (*Schizaphis graminum*) [118]. A notable

hypothesis suggests that geraniin acts as a protoxin, releasing ellagic acid as a hydrolysis product, which has proven detrimental to insects feeding on plants [119]. Moreover, research evidences a direct correlation between the level of ellagitannins relative to total tannins produced by a plant and the extent of harm inflicted upon caterpillars, underscoring the importance of these compounds in plant defense mechanisms [120].

Pecan orchards are exposed to several pests, among which the most prominent are the pecan nut casebearer (*Acrobasis nuxvorella*), the black margined aphid (*Monellia caryella*), and the yellow pecan aphid (*Monelliopsis pecanis*) [121, 122]. These pests pose a significant challenge as they damage pecan trees by engaging in piercing-sucking activities, primarily targeting the plant's phloem [123–125]. This feeding behavior not only weakens the plants, causing economic losses, but also exposes them to diseases vectored by these insects [30, 126]. One specific pest, the black pecan aphid (*Melanocallis caryaefoliae*), stands out as a specialist insect with a preference for pecan leaves. Its damage aligns with the final stages of kernel maturity, typically occurring towards the conclusion of the harvest season in the summer [125].

The effects of the black pecan aphid have been analyzed in field conditions, focusing on its impact on oxidative enzymes such as peroxidase, catalase, lipoxygenase, and esterase [32]. Additionally, research has unveiled the presence of over 100 volatile terpenic derivatives in dormant buds of two pecan cultivars, Western Schley and Wichita, grown in Mexico [127]. Furthermore, an investigation aimed at discerning differences in phenolic compounds and ellagic acid levels between conventional and organic pecan orchards found that organically grown “desirable” pecans boasted ellagic acid and catechin levels two to four times higher than those in conventionally grown orchards [128]. Another study reported increases in total terpenes, condensed tannins, hydrolysable tannins, and lignin in tissues damaged by the fruit tree borer insect (*Euplatypus segnis*) and associated fungi, further underscoring the complex interplay between pecan trees, pests, and secondary metabolites [129]. Nevertheless, while oxidative enzyme activity was assessed in pecan leaves subjected to the influence of the black pecan aphid, the levels of phytochemicals remained unreported in this study [32].

Despite the lack of detailed information regarding the specific phytochemicals produced by pecan trees and their effects on insects, it is well-established that hydrolysable tannins possess detrimental effects on pests, which could play a crucial role in plant defense mechanisms [130–132]. Some pecan varieties, particularly those susceptible to infestation by the black pecan aphid, may struggle to produce chemical compounds that deter these insects, as suggested by Wood and Reilly [125]. Notably, in a comparative study

involving three susceptible and three resistant pecan cultivars facing the black pecan aphid, it was observed that susceptible varieties exhibited increased enzymatic activity associated with oxidative stress and reduced lipoxygenase levels, a key enzyme implicated in resistance against insects [32]. Lipoxygenases play a pivotal role in the production of jasmonic acid derivatives, which, in turn, contribute to plant systemic responses and the synthesis of defensive phenolic compounds [65, 133, 134]. It is important to note that these enzymatic activities were primarily measured in the same leaves where aphids were introduced, and any non-systemic effects were not explicitly addressed [32].

Aphids, when feeding on plants, have the capacity to influence the production of phenolic compounds, with variations that are highly dependent on the specific plant–insect interaction. For instance, an experiment involving aphids (*Sitobion avenae*) and plants (maize and barley) revealed decreased levels of phenolics compared to undamaged plants, although this phenomenon was not valid for another aphid species (*Rhopalosiphum padi*) under similar conditions [33]. The extent of pest damage in pecan trees appears to be closely linked to crop management practices, with factors such as irrigation, nitrogen availability, and fruit load playing a significant role. When pecan trees receive adequate irrigation, optimal nitrogen levels, and maintain a low fruit load, they tend to be more susceptible to hosting pests [135]. Moreover, the timing of aphid infestation in pecan trees is critical, as leaves have already undergone biotic stress towards the end of the growing season, resulting in reduced levels of total phenolic compounds and ellagitannin derivatives compared to more resistant pecan varieties such as Pawnee, Shawnee, or Kiowa [136].

The relationship between aphids and pecan trees centers on the intricate chemical interplay between the insect's piercing-sucking apparatus and the plant's phloem. Multiple secondary metabolites come into play in this interaction, shaping its dynamics and outcomes [30, 137]. Specifically, in the case of the interaction between the black pecan aphid and Choctaw cultivar trees, it appears that the aphid may circumvent the local defense mechanisms of the plant while continuing to sap photosynthates, leading to a depletion of sugars that cannot be efficiently translocated to the sink tissues (kernels). This, in turn, affects the production of high C/N compounds, including ellagitannin derivatives [137].

Conclusions and Future Perspectives

Phytochemical accumulation is influenced by genetics [138], but also significantly shaped by agronomic practices and external environmental factors, including biotic stressors. Notably, ellagitannins, gallotannins, and proanthocyanidins play a pivotal role in the tree's defense

mechanisms against biotic stressors, offering not only vital protection for the tree but also potential health benefits for humans through their antioxidant and anti-inflammatory properties. Pecan trees respond to biotic stressors, such as infestations by the black pecan aphid or fungal attacks, by elevating the production of these phytochemicals. This increased synthesis serves as a defensive strategy, effectively deterring pests, and pathogens, thereby ensuring the tree's survival. The intricate relationship between phytochemicals and biotic pre-harvest effects in pecans underscores the complex interplay between plants and their environment, offering insights into both natural defense mechanisms and the potential utilization of these phytochemicals for human well-being.

Similarly, strawberries boast a repertoire of phytochemicals, including anthocyanins, ellagitannins, gallotannins, and ellagic acid, serving as crucial components for the plant's natural defense mechanisms and holding promise as health-enhancing agents for humans. When strawberries confront biotic pre-harvest stressors, such as bacterial and fungal infections or attacks from arthropods like aphids and spider mites, they respond by upregulating phytochemical production. This heightened synthesis acts as a protective shield, effectively deterring pests and pathogens and bolstering the plant's chances of survival. The intricate connection between phytochemicals and biotic pre-harvest effects in strawberries underscores the dynamic ways plants adapt and protect themselves in their natural environment [139••]. Furthermore, these phytochemicals, with their diverse applications in health and nutrition, ranging from antioxidant and anti-inflammatory properties to their role in preventing chronic diseases, positions strawberries as not just a delectable fruit but also a valuable source of bioactive compounds.

The importance of understanding the relationship between biotic stress and the accumulation of phytochemicals, particularly phenolic compounds, in fruits cannot be overstated. As the demand for organic food products continues to grow globally, the knowledge of how biotic stressors influence the production of these health-enhancing compounds holds significant relevance for both agricultural practices and human nutrition. The examples of pecans and strawberries serve as valuable case studies, highlighting the dynamic interplay between plants and their environment. These plants respond to biotic stressors by increasing the production of phytochemicals as part of their defense mechanisms, ultimately enhancing the resilience of the crops. The implications of this enhanced phytochemical content extend beyond plant defense; they encompass the potential for providing health-promoting benefits to consumers. Therefore, delving into the intricate relationship between biotic stress and phytochemical production in fruits is crucial not only for agricultural sustainability but also for advancing human well-being through nutrition and health.

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Declarations

Competing Interests The authors declare no competing interests.

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 - 139.●● Ibáñez F, Bang WY, Lombardini L, Cisneros-Zevallos L. Solving the controversy of healthier organic fruit: leaf wounding triggers distant gene expression response of polyphenol biosynthesis in strawberry fruit (*Fragaria x ananassa*). *Sci Rep.* 2019; 9:19239. <https://doi.org/10.1038/s41598-019-55033-w>. **Researchers investigated the controversy around higher phytochemical levels in organic crops using strawberries as a model. They found that applying pre-harvest leaf wounding stress significantly increased phenolic compounds and sugars in the fruits, potentially explaining the elevated phytochemical levels in organic produce.**

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